PROCEEDINGS
OF THE INTERNATIONAL SYMPOSIUM
INSULAR VERTEBRATE EVOLUTION
THE PALAEONTOLOGICAL APPROACH
SEPTEMBER 16-19 2003 MALLORCA

Josep Antoni Alcover & Pere Bover
Editors

Monografies de la Societat d'Història Natural de les Balears, 12

SOCIETAT D'HISTÒRIA
NATURAL DE LES BALEARS

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INSULAR VERTEBRATE EVOLUTION

Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach" September 16-19 Mallorca

Josep Antoni ALCOVER & Pere BOVER
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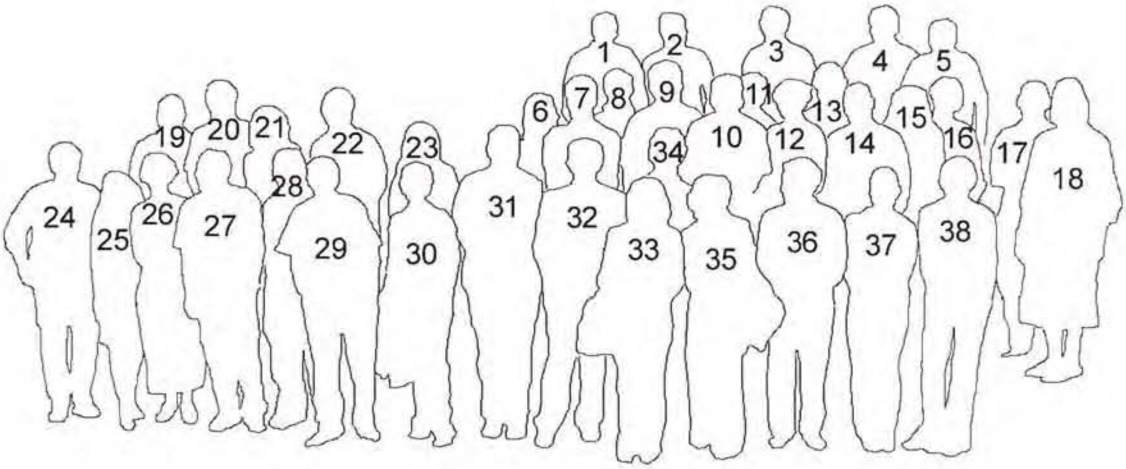

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Tel. 971 69 76 76
e-mail: sairpa@terra.es

Maquetació i fotomecànica:
Colorgràfic
C/ Llampúgol, 33.
07005 Palma de Mallorca
Tel. 971 27 83 55
e-mail: colorgrafic@terra.es

Contents

CONTRIBUTORS LIST

Konstantina **Agiadi**, Department of Historical Geology and Palaeontology, Panepistimioupoli 157 84, Zografou, Athens, Greece. e-mail: kagiadi@geol.uoa.gr

Josep Antoni **Alcover**, Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Cta. de Valldemosa km 7.5, 07071 Palma de Mallorca, Spain. e-mail: vieapba@uib.es

Chiara **Angelone**, Dipartimento di Scienze Geologiche, Università Roma Tre, Largo S. Leonardo Murialdo, 1 – 00146 Roma, Italy. e-mail: angelone@uniroma3.it

Marisa **Arca**, Soprintendenza Archeologica per le Province di Sassari e Nuoro, Via Ballero, 30 – 08100, Nuoro, Italy.

Carlos **Arredondo**, Instituto Superior Pedagógico "Enrique José Varona" , Facultad de Biología, 108 No.29E06, Marianao. C. Habana. Cuba. e-mail: gener@upejv.edu.cu

Salvador **Bailon**, Laboratoire départemental de Préhistoire du Lazaret, Département de Sciences Préhistoriques, 33bis Bd. Frank Pilatte, 06300, Nice, France. e-mail : sbailon@lazaret.unice.fr.

Jean Christophe **Balouet**, 14 rue Gaston Margerie, 94130 Nogent-sur-Marne, France. e-mail: JCBalouet@aol.com

Jaume **Bertranpetit**, Unitat de Biologia Evolutiva,Facultat de Ciències de la Salut i de la Vida, Universitat Pompeu Fabra, Doctor Aiguader 80, 08003 Barcelona, Spain. e-mail : jaume.bertranpetit@upf.edu

Marie Françoise **Bonifay**, Chercheur CNRS honoraire. UMR 6636 du CNRS, Aix en Provence, France.

Rafael **Borroto-Páez**, Instituto de Ecología y Sistemática, Carretera de Varona Km 3.5, Boyeros, A. P. 8029, C. P. 10800. C. Habana, Cuba. e-mail: zoologia.ies@ama.cu; borroto@yahoo.com

Mathieu **Boudin**, Royal Institute for Cultural Heritage, Jubelpark 1, B- 1000 Brussels, Belgium. e-mail: mboudin@yahoo.com

Pere **Bover**, Institut Mediterrani d'Estudis Avançats de les Illes Balears (CSIC-UIB), Cta. de Valldemosa km 7.5, 07071 Palma de Mallorca, Spain. e-mail: vieapba@uib.es

Michael **Bunce**, Henry Wellcome Ancient Biomolecules Centre, Department of Zoology, University of Oxford, OX1 3PS, United Kingdom.

Marjorie Mahe **Condis Fernández**, Instituto de Ecología y Sistemática, Carretera de Varona, Km 3 fi, Capdevilla. AP: 8029. CP. 10800. C. Habana. Cuba. e-mail: maximiliano.condis@infomed.sld.cu

Alan **Cooper**, Henry Wellcome Ancient Biomolecules Centre, Department of Zoology, University of Oxford, OX1 3PS, United Kingdom. e-mail: alan.cooper@zoology.oxford.ac.uk

Joanne H. **Cooper**, Bird Group, Department of Zoology, The Natural History Museum, Akeman Street, Tring, Hertfordshire, HP23 6AP, United Kingdom. e-mail: jhc@nhm.ac.uk

Michael **Dermitzakis**, National and Kapodistrian University of Athens, Panepistimiopolis 157 84 Athens, Greece. e-mail: mdermi@geol.uoa.gr

Anton **Ervynck**, Institute for the Archaeological Heritage of the Flemish Community, Phoenix-building, Koning Albert II-laan 19 box 5, B-1210 Brussels, Belgium. e-mail:
anton.ervynck@lin.vlaanderen.be

Joan Josep **Fornós**, Departament de Ciències de la Terra, Universitat de les Illes Balears, Cta. de Valldemossa km 7,5, 07122 Palma de Mallorca, Balears, Spain. e-mail: joan.fornos@uib.es

Joan **Garcia Porta**, Societat Catalana d'Herpetologia, Passeig Picasso s/n, 08003, Barcelona, Spain.

Sergio **Ginesu**, Istituto Scienze Geologico Mineralogiche, Università degli Studi di Sassari, Corso Angjoi 10, 07100 Sassari, Italy. e-mail: ginesu@uniss.it

Caterina **Giovinazzo**, Dipartimento di Scienze della Terra, Università degli Studi di Roma "La Sapienza", Piazzale Aldo Moro, 5–00185 Roma, Italy. e-mail: caterina.giovinazzo@uniroma1.it

Frederick V. **Grady**, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560, USA.

Paul J. **Hearty**, School of Earth Sciences, James Cook University, Townsville, Queensland 4811, Australia. e-mail: e-mail: paulh@uow.edu.au

Julian Pender **Hume**, Bird Group, Department of Zoology, The Natural History Museum, Akeman St., Tring, Herts HP23 6AP, UK and Palaeobiology Research Group, Department of Earth and Environmental Sciences, Portsmouth University, Portsmouth, PO1 3QL, United Kingdom. e-mail: J.Hume@bun.com

Helen F. **James**, Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560, USA. e-mail: James.Helen@NMNH.SI.EDU

Manuel A. **Iturralde-Vinent**, Museo Nacional de Historia Natural, Obispo 61, Plaza de Armas, La Habana 10100, Cuba. e-mail: iturralde@mnhnc.inf.cu

Osvaldo **Jiménez Vázquez**, Instituto de Ecología y Sistemática, Carretera de Varona, Km 3 fi, Capdevilla. AP: 8029. CP. 10800. C. Habana. Cuba. e-mail: zoologia.ies@ama.cu

William **Kilpatrick**, Department of Biology, University of Vermont, Burlington VT 05405-0086, USA. e-mail: C-William.Kilpatrick@uvm.edu

Meike **Köhler**, Institut de Paleontologia "M. Crusafont". 08028 Sabadell, Spain.

Tassos **Kotsakis**, Dipartimento di Scienze Geologiche, Università Roma Tre, L.go S. L. Murialdo, 1 – 00146 Roma, Italy. e-mail: kotsakis@uniroma3.it

Carles **Lalueza-Fox**, Laboratori d´Antropologia, Facultat de Biologia, Universitat de Barcelona, Avda. Diagonal 645, 08028 Barcelona, Spain. Adresa actual: Unitat de Biologia Evolutiva,,Facultat de Ciències de la Salut i de la Vida, Universitat Pompeu Fabra, Doctor Aiguader 80, 08003 Barcelona, Spain. e-mail: carles.lalueza@upf.edu

Antoine **Louchart**, Université Claude Bernard – Lyon 1, Bât. Geode, 27-43 bd du 11 novembre, 69622 Villeurbanne cedex, France. e-mail: antoine.louchart@worldonline.fr

George **Lyras**, National and Kapodistrian University of Athens, Panepistimiopolis 157 84 Athens, Greece. e-mail: glyras@geol.uoa.gr

R.D.E. **MacPhee**, Division of Vertebrate Zoology, American Museum of Natural History, New York NY 10024, USA. e-mail: macphee@amnh.org

Jan **van der Made**, Consejo Superior de Investigaciones Científicas, Museo Nacional de Ciencias Naturales, c. José Gutiérrez Abascal 2, 28006 Madrid, Spain. e-mail: mcnjv538@mncn.csic.es

Miguel **McMinn**, Santa Florentina 13, 3^{er}, 07007 Palma de Mallorca, Spain. e-mail: miguel.mcminn@skuacb.com

Federica **Marcolini**, Dipartimento di Scienze della Terra, Università di Pisa, Via Santa Maria 53 — 56126 Pisa, Italy. e-mail: fmarcolini@dst.unipi.it

Tomàs **Marquès**, Unitat de Biologia Evolutiva, Facultat de Ciències de la Salut i de la Vida, Universitat Pompeu Fabra, Doctor Aiguader 80, 08003 Barcelona, Spain. e-mail: tomas.marques@upf.edu

Antonella Cinzia **Marra**, Dipartamento di Scienze della Terra, Universitá degli Studi di Messina, Via Sperone 31, 98166 S Agata, Messina, Italy. e-mail: amarra@unime.it

Rita Teresa **Melis**, Dipartimento di Scienze della Terra, Università degli Studi di Cagliari, Via Trentino, Cagliari, Italy. e-mail: rtmelis@unica.it

Jacques **Michaux**, Institut des Sciences de l'Evolution (CC064), UMR 5554, Université Montpellier 2, 34095 Montpellier Cedex 05, France. e-mail: michaux@isem.univ-montp2.fr

Sophie **Montuire**, Centre des Sciences de la Terre, UMR 5561, 6, boulevard Gabriel 21000 Dijon. e-mail: Sophie-Montuire@u-bourgogne.fr

Cécile **Mourer-Chauviré**, UMR 5125 du CNRS "Paléoenvironnements et Paléobiosphère", Université Claude Bernard - Lyon 1, 27-43 boulevard du 11 Novembre, 69622 Villeurbanne Cedex, France. e-mail: Cecile.Mourer@univ-lyon1.fr

Salvador **Moyà-Solà**, Institut de Paleontologia "M. Crusafont". 08028 Sabadell, Spain. e-mail: moyass@diba.es

Maria Rita **Palombo**, Dipartimento di Scienze della Terra, Università degli Studi di Roma "La Sapienza", CNR - Istituto di Geologia Ambientale e Geoingegneria, Piazzale Aldo Moro, 5, 00185 Rome (Italy). e-mail: mariarita.palombo@uniroma1.it

Elisabeth **Pereira**, IUT de Corse, Université de Corse, La Citadelle, 20250 Corte. UMR 6636 du CNRS, Aix en Provence, France. e-mail : pereira@univ-corse.fr

Storrs L. **Olson**, Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560, USA. e-mail: Olson.Storrs@NMNH.SI.EDU

Josep **Quintana**, Institut de Paleontologia "M. Crusafont". 08028 Sabadell (Barcelona, España). Adresa actual: Gustau Mas, 79-1º.07760 Ciutadella de Menorca, Balears, Spain. e-mail: picoguevo@hotmail.com

Damià **Ramis**, Institut Mediterrani d'Estudis Avançats de les Illes Balears (CSIC-UIB), Cta. de Valldemosa km 7.5, 07071 Palma de Mallorca, Spain. e-mail: vieapba@uib.es

Monica **Salotti**, Professeur agrégée, RN 193, 20250 Corte. e-mail: msalotti@wanadoo.fr

Lourdes **Sampietro**, Unitat de Biologia Evolutiva, Facultat de Ciències de la Salut i de la Vida, Universitat Pompeu Fabra, Doctor Aiguader 80, 08003 Barcelona, Spain. e-mail: lourdes.sampietro@cexs.upf.edu

Borja **Sanchíz**, Museo Nacional de Ciencias Naturales, José Gutiérrez Abascal 2, 28006 Madrid, Spain. e-mail: mcnb105@mncn.csic.es

Paul **Scofield**, Canterbury Museum, Rolleston Avenue, Christchurch, New Zealand. e-mail: pscofield@canterburymuseum.com

Bartomeu **Seguí**, Cr. Magallanes, 17, 1er, 07470 Port de Pollença, Mallorca. e-mail: bartomeusegui@terra.es

Stefania **Sias**, Istituto Scienze Geologico Mineralogiche, Università degli Studi di Sassari, Corso Angjoi 10, 07100 Sassari, Italy. e-mail: stesi@uniss.it

Elizabeth **Stathopoulou**, Department of Historical Geology and Palaeontology, Faculty of Geology and Geoenvironment, Athens University, Panepistimiopolis, 15784 Athens, Greece. E-mails: estathop@geol.uoa.gr

George **Theodorou**, Department of Historical Geology and Palaeontology, Faculty of Geology and Geoenvironment, Athens University, Panepistimiopolis, 15784 Athens, Greece. E-mail: gtheodor@geol.uoa.gr

Ferran **Tolosa**, ENT Department, Clínica Planas, Ruiz de Alda 5, 07011 Palma de Mallorca, Balears, Spain. e-mail: ftolosa@arrakis.es

Caterinella **Tuveri**, Soprintendenza Archeologica per le Province di Sassari e Nuoro, Via Ballero, 30 – 08100, Nuoro, Italia

Alexandra **Van der Geer**, Archimedes Foundation for the Advancement of Research in Natural History; Boerhaavelaan 98, 2334 ET Leiden, The Netherlands. e-mail: avandergeer@planet.nl; a.a.e.van.der.geer@umail.leidenuniv.nl

Mark **Van Strydonck**, Royal Institute for Cultural Heritage, Jubelpark 1, B- 1000 Brussels, Belgium. e-mail: mark.vanstrydonck@kikirpa.be

John **de Vos**, Nationaal Natuurhustorisch Museum, P.O. Box 9517, 2300 RA Leiden, The Netherlands. e-mail: vos@naturalis.nnm.nl

David B. **Wingate**, P.O.Box CR 86, Crawl CR BX, Hamilton Parish, Bermuda.

Charles A. **Woods**, Bear Mountain Natural History Center, Island Pond, Vermont, USA and Department of Biology, University of Vermont, Burlington VT 05405-0086, USA.

Trevor H. **Worthy**, Palaeofaunal Surveys, 2A Willow Park Drive, Masterton, New Zealand. E-mail: twmoa@wise.net.nz

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"SA NOSTRA"

PREFACI

És un plaer realitzar la presentació de la publicació del present recull de comunicacions del simposi internacional *Insular Vertebrate Evolution: the Palaeontological Approach* que es va dur a terme a Mallorca el setembre de 2003, organitzat per la Societat d'Història Natural de les Balears i l'Institut Mediterrani d'Estudis Avançats, rebent el suport de diverses entitats autonòmiques i estatals, entre elles, la Conselleria d'Economia, Hisenda i Innovació del Govern de les Illes Balears i la seva precedent Conselleria d'Innovació i Energia.

És important destacar que aquest simposi és el fruit de la col·laboració entre una entitat privada i una entitat pública, que han unit novament els seus esforços per assolir un objectiu comú exitós, talment com ho varen fer l'any 2000 per a la creació de l'exposició "Les Balears abans dels Humans".

La primera d'aquestes entitats, la Societat d'Història Natural de les Balears, que fa poc ha complert el mig segle de vida, és bressol de naturalistes i investigadors professionals i aficionats que han aportat, aporten i aportaran importants treballs d'investigació a la llarga llista de publicacions d'aquest caire a les Balears. La serietat científica de la Societat d'Història Natural està demostrada per les seves diferents publicacions i activitats, i ha obtingut el reconeixement de diverses institucions mitjançant l'atorgament de prestigiosos premis, com per exemple el Premi Ciutat de Palma, el Premi Alzina i el Premi Jaume I. L'interès en la divulgació del coneixement naturalístic per part d'aquesta institució l'ha dut a promoure la creació d'un Museu de la Naturalesa de les Illes Balears.

La segona, l'Institut Mediterrani d'Estudis Avançats (IMEDEA), és un clar exemple de la integració d'esforços per a la consecució d'important resultats en el camp de la investigació científica. L'IMEDEA és un centre mixt entre la Universitat de les Illes Balears i el Consejo Superior de Investigaciones Científicas, ambdues entitats, segell de qualitat en les tasques d'investigació. Al departament de Recursos Naturals de l'IMEDEA s'integren diferents equips d'investigació tan diferents com oceanografia, ecologia terrestre, ictiologia, oceanografia i paleontologia, aquest darrer, màxim promotor de la investigació en el camp de la paleontologia de vertebrats insulars a les Balears.

Les illes Balears són i han estat terra d'importants investigadors científics en el camp de la paleontologia, i més en concret de la paleontologia de vertebrats insulars. No ens podem oblidar de noms com Guillem Colom, Joan Cuerda, Andreu Muntaner, Rafel Adrover, Basilio Angel, Benet Mercadal, Joan Pons, Lluis Gasull, així com tampoc d'altres investigadors més recents que han dut a terme una tasca d'investigació admirable per al coneixement i comprensió de les faunes insulars que habitaren les nostres illes abans de que els humans hi arribessin. No tan sols del coneixement d'autors locals s'ha nodrit la paleontologia balear, sinó que altres figures internacionalment reconegudes han aportat informació rellevant en aquest camp, com Miss Dorothea M.A. Bate, descobridora de *Myotragus balearicus*, Miquel Crusafont, Paul Y. Sondaar.

És per això que una illa balear, Mallorca, hagi estat el lloc triat al Japó per a la realització d'un simposi sobre faunes insulars. Totes les Balears són móns singulars, segons demostra l'estudi paleontològic del seu passat. Les Pitiüses, les úniques illes de la Mediterrània amb unes faunes pleistocèniques sense mamífers. Les Gimnèsies, les úniques illes de la Mediterrània que durant el Quaternari contenien un caprí summament modificat, *Myotragus balearicus*. Destaca Menorca, que en el passat va hostatjar una fauna extraordinària que està començant a ser coneguda gràcies a la feina feta per un menorquí, el Dr Josep Quintana, amb un conill gegant altament modificat que es presenta a aquestes planes. Les Balears són illes amb fòssils insulars espectaculars. Encara hi sobreviuen alguna d'aquestes espècies, autèntics llegats de la nostra paleo-història i del nostre passat sense presència humana i un autèntic patrimoni natural i cultural que hem de preservar.

El nombre i la diversitat de participants en el simposi fa palesa la importància i l'interès global sobre aquesta temàtica. Apart d'importants investigadors nacionals, hi han assistit investigadors de renom d'altres països europeus com Itàlia, Grècia, França, Regne Unit, Holanda, Bèlgica, Suïssa, Portugal, i de països fora d'Europa com Estats Units, Nova Zelanda, Japó i Cuba. Ben segur que l'intercanvi de coneixements i idees, objecte primordial de les reunions científiques d'aquesta categoria, ha estat de gran utilitat per a tots els participants i resultaran de vital importància en la consecució d'objectius futurs a tots els nivells.

En aquest sentit s'ha de dir que la qualitat de la investigació científica radica en la col·laboració entre diferents investigadors o disciplines, i sense cap dubte, aquest és un dels objectius que s'han complert en aquest simposi.

Una mostra inequívoca d'aquesta qualitat investigadora i divulgadora és el considerable nombre d'articles que se presenten en aquest volum. Tots ells d'una qualitat científica demostrada per un control rigorós mitjançant sistemes d'arbitratge científic i la serietat que s'espera d'una publicació d'aquesta índole.

Esperem que la realització de simposis d'aquesta importància, així com la publicació de volums d'aquesta categoria suposin un estímul per a la investigació científica en el camp de la paleontologia insular, així com també serveixi de vehicle per a donar a conèixer aquesta disciplina al gran públic.

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Lluís A. Ramis de Ayreflor
Conseller d'Economia, Hisenda i Innovació

INTRODUCCIÓ

El Simposi Internacional "Insular Vertebrate Evolution: the Palaeontological Approach" va tenir lloc a Palma de Mallorca entre els dies 16 i 19 de setembre de 2003 i fou organitzat conjuntament per l'Institut Mediterrani d'Estudis Avançats (CSIC – UIB) i la Societat d'Història Natural de les Balears. La idea i el compromís per fer aquest Simposi va néixer el 7 de novembre de 1998 a la ciutat japonesa de Kagoshima, en el transcurs de la sessió de cloenda del Simposi Internacional "The Ryukyu Islands: The arena of adaptive radiation and extinction of island fauna, organitzat per la Universitat de Kagoshima sota la coordinació del Dr Hiroyuki Otsuka, i un dels promotors de la realització d'aquest Simposi a Mallorca fou el Dr Paul Y. Sondaar.

Tot i que aquest Simposi s'havia previst inicialment que es realitzaria dintre de l'any 2002, la seva realització fou endarrerida un any per distanciar-ho un poc més d'un altre Congrés Internacional que es va realitzar a Deià, Mallorca, el setembre de 2001, sobre "World Islands in Prehistory". Tot i que els dos Simposis tractaven una temàtica diferent, hi existia una possibilitat real de solapament, com es pot veure comparant les respectives llistes de participants.

El dia 16 de setembre, a la mesa inaugural del Simposi varen ser presents el Sr Lluis Moragues (President de la Societat d'Història Natural de les Balears), el Dr Damià Jaume (en representació del Dr Joaquim Tintoré, director de l'Institut Mediterrani d'Estudis Avançats), el Dr Francesc Muñoz (vice-rector de la Universitat de les Illes Balears, en representació del Rector, Dr Avel·lí Blasco), el Dr Ross MacPhee (de l'American Museum of Natural History, New York, membre del Comité Científic d'aquest Simposi i participant al Simposi de Kagoshima) i el Dr Josep Antoni Alcover (President del Comité Organitzador i membre de l'Institut Mediterrani d'Estudis Avançats i de la Societat d'Història Natural de les Balears).

Les sessions del Simposi "Insular Vertebrate Evolution: the Palaeontological Approach" es varen celebrar al centre de cultura de Sa Nostra, al centre de Palma de Mallorca, en sessions de matí i horabaixa, durant els dies 16, 17 i 19 de setembre. En el transcurs d'aquestes sessions es varen presentar un seguit de comunicacions de temes molt diversos que tenien com a fil comú l'evolució en condicions d'insularitat des de la perspectiva dels paleontòlegs de vertebrats. Es varen celebrar 9 sessions de presentacions orals amb 43 comunicacions, a més d'una sessió de posters i la presentació d'una filmació sobre la cova Genovesa (Manacor). El dia 19 es va celebrar també un petit taller sobre problemes i interpretacions a les excavacions paleontològiques de vertebrats insulars.

El dia 18 de setembre es va fer una excursió de camp per visitar diferents jaciments mallorquins. Es va visitar la cova des Moro (Manacor), important jaciment paleontològic del Pleistocè superior i Holocè de Mallorca, i el talaiot de Sa Canova (Artà), un dels talaiots més espectaculars de l'illa, i tot el grup va a dinar a la possessió de ses Cabanasses, hostatjats pel Sr Damià Jaume Bosch, un dinar excel·lent en un marc inoblidable.

Dintre del Simposi es va presentar una filmació sobre la cova Genovesa, on es troba un interessant dipòsit paleontològic sota l'aigua, a una quinzena de metres de fondària. Estam molt agraïts al Dr Damià Jaume Llabrés per la presentació que en va fer.

Ja acabat el Simposi, però amb una àmplia participació dels assistents al mateix, el dia 20 de setembre es va fer una nova excursió per visitar un altre jaciment important de Mallorca, la cova Estreta, prop del Rafal d'Ariant. L'excursió fou un poc dificultosa pel terreny abrupte que cal superar per arribar al jaciment, però tothom hi va arribar.

Aquest Simposi s'ha pogut fer en bona part gràcies a l'interès institucional de les dues entitats organitzadores en fer-ho, gràcies a l'impuls d'una sèrie de persones, i gràcies a l'ajuda rebuda per part de diferents institucions. Per a la Societat d'Història Natural de les Balears la realització d'aquest Simposi va representar no tan sols un acte que es troba en la línia de potenciació de la creació d'un Museu de la Naturalesa de les Illes Balears a Palma, sinó un exemple de la seva vocació i inserció internacionals i va ser un preàmbul del seu 50è aniversari (celebrat el 2004). Per a l'Institut Mediterrani d'Estudis Avançats (centre mixt del Consejo Superior de Investigaciones Científicas i de la Universitat de les Illes Balears) va representar una passa més en les seves activitats destinades a la potenciació d'una recerca de qualitat, especialment inserida a la Comunitat Autònoma de les Illes Balears, i d'abast internacional.

Les persones gràcies a les quals s'ha pogut fer aquest Simposi són moltes, i com a coordinadors d'aquest volum volem esmentar d'una manera especial na Laura Celià i na Margalida Roig, així com als restants membres del Comitè Organitzador. Na Francisca Comas va encoratjar molt a JAA amb la realització d'aquest simposi. En Miquel Trias va elaborar el logotipus del Simposi, així com tota la part de disseny del mateix. També ha elaborat la portada d'aquest volum. Tota la maquetació i bona part del disseny de les Actes del Simposi es deu a na Natàlia Llorente, de Colorgràfic. Les sessions es varen realitzar al Saló d'Actes del Centre Cultural de Sa Nostra. Xisca Niell, directora del Centre Cultural de Sa Nostra, i tot el personal del centre ens varen facilitar totes les activitats que s'hi varen fer.

Hem rebut suport econòmic de diferents entitats. Han recolzat aquest Simposi el Ministerio de Ciencia y Tecnologia, la Universitat de les Illes Balears, Sa Nostra, el Govern de les Illes Balears a través principalment de la Conselleria d'Economia, Hisenda i Innovació (igual que la Conselleria precedent d'Innovació i Energia), de la Conselleria de Medi Ambient, i de la Conselleria d'Educació i Cultura, així com de les dues entitats organitzadores. Tot i no haver participat directament amb aquest Simposi, estam també agraïts als Consell de Mallorca, de Menorca i d'Eivissa i Formentera, que al llarg dels darrers anys han autoritzat i finançat parcialment diferents excavacions paleontològiques de les quals provenen molts dels materials que es varen presentar a aquest Simposi.

En aquest volum es publiquen 35 treballs sobre vertebrats insulars. A *grosso modo* es pot dir que una tercera part dels treballs es refereixen a paleontologia de vertebrats de les Balears, una altra tercera part correspon a treballs de paleontologia de vertebrats d'altres illes mediterrànies, mentre que la tercera part restant tracta de faunes insulars d'altres illes i para-illes del món (Bermuda, Hawaii, Nova Zelanda, Antilles, etc.) i altres temes relacionats. La majoria dels treballs publicats tracten sobre faunes fòssils de mamífers, mentre que uns pocs tracten sobre ocells fòssils i només dos tracten sobre amfibis i rèptils fòssils.

Els treballs presentats han estat avaluats mitjançant un sistema d'avaluació externa. Els avaluadors han estat bàsicament reclutats entre els mateixos participants al Simposi, però també altres col·legues externs han col·laborat. Estam agraïts al Dr Jordi Agustí, al Dr Joan Mestres, al Dr Dick Mol, al Dr Antonio Sánchez i al Dr Carlos Lorenzo Merino pels comentaris que ens han enviat sobre diferents treballs. Volem agrair els autors per la seva paciència durant el procés de publicació dels treballs, que ha estat més llarg del que voliam.

Hem volgut dedicar el Simposi, i en conseqüència aquest volum, a tres col·legues molt preuats que ens varen deixar el 2003, abans de la realització del Simposi. Joan Cuerda Barceló (1912 – 2003), President d'Honor de la Societat d'Història Natural de les Balears, ha estat un dels personatges claus en l'estudi del Quaternari de les Balears, inclosos els vertebrats que hi visqueren, i fou una persona que va obrir les portes de ca seva a tots els investigadors interessats en el Quaternari de les Balears, va crear escola a Mallorca i va ser un dels grans impulsors de la Societat d'Història Natural de les Balears i dels seu projecte museístic. Joan Pons Moyà (1955-2003) fou el més entusiasta dels estudiosos de la fauna de vertebrats del Quaternari de les Balears, des de la seva més tendra infància, i a ell es deu la descripció d'un bon nombre de taxons de vertebrats fòssils d'aquestes illes. Sense ell, el coneixement dels mamífers fòssils del Pliocè i Quaternari de les Balears no estaria al nivell en que es troba actualment. Paul Sondaar (1934 – 2003) ha estat un dels grans especialistes internacionals en l'estudi de faunes vertebrades insulars. La seva carrera científica ha estat centrada en les grans illes mediterrànies i en les illes de la Wallacea. El seu entusiasme contagiador ha estat l'origen de moltes vocacions de paleontòlegs. Dintre del Simposi, el dia 20 se'ls va dedicar una sessió in memoriam, emotiva i senzilla, que va comptar amb l'assistència de les seves respectives famílies. Els Drs Josep Antoni Alcover, Salvador Moyà-Solà i Jelle Reumer varen presentar un curta i sentida rememorança d'aquests tres investigadors que ens varen deixar. Aquests parlaments acabaren amb una curta frase que sentim com ben vigent: Paul Sondaar, Joan Pons, Joan Cuerda, mestres i amics, gràcies per donar-nos llum en l'estudi del passat amb la vostra honestedat, coneixement i passió!

Pere Bover i Josep Antoni Alcover

01

TUSK PALEOHISTOLOGY AS A TOOL IN THE DISCRIMINATION OF FOSSIL TUSKS FROM GREECE

Konstantina AGIADI & George THEODOROU

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Resum

En aquest estudi intentam discriminar entre les defenses de *Mammuthus meridionalis, Elephas antiquus* i les dels elefants nans de l'illa de Tilos, en base a les característiques histològiques de la dentina. El tret mesoscòpic examinat és el Patró d'Schreger, en relació a l'angle, la longitud d'ona i l'aparença qualitativa, i els trets microscòpics són la mida dels túbuls de dentina i la seva densitat. Les mostres de defenses de mamut es diferencien clarament de les d'elefants. A més, trobam una petita variança en l'aparença qualitativa del Patró d'Schreger entre les mostres d'*Elephas antiquus* i les defenses dels elefants nans. Finalment, la mida dels túbuls de dentina de les defenses dels elefants endèmics és, clarament, la major.

Paraules clau: defenses, Paleohistologia, dentina, elefants nans, *Elephas antiquus, Mammuthus meridionalis.*

Summary

In the current study, we have attempted to distinguish between the tusks of *Mammuthus meridionalis, Elephas antiquus* and the dwarf elephants from the island of Tilos, based on the tusk dentine's histological characteristics. The mesoscopic feature examined is the Schreger Pattern, in respect to its angle, wavelength and qualitative appearance, and the microscopic features are the dentinal tubule's size and density. The mammoth samples strongly discriminate against the elephant tusks. In addition, we were able to find a small variance in the Schreger Pattern's qualitative appearance, between the samples of *Elephas antiquus* and the tusks of the dwarfs. Finally, the size of the dentinal tubules is clearly greatest in the tusks of the endemic elephants.

Key words: tusks, Palaeohistology, dentine, dwarf elephants, *Elephas antiquus, Mammuthus meridionalis.*

INTRODUCTION

The aim of this study is to compare the dwarf elephant tusks, found on the island of Tilos, to those of *Elephas antiquus* and *Mammuthus meridionalis*, in respect to the dentine's histological characteristics. In the past, Proboscidean tusk dentine has been used to distinguish tusks and tusk fragments of different taxa (Espinoza & Mann, 1993; Fisher *et al.*, 1998; Palombo & Villa, 2001; Palombo, 2003). For the most part though, these examinations included only the Schreger angle. On previous papers (Agiadi, 2001; Theodorou & Agiadi, 2001; Agiadi, 2003), we have examined other histological features, namely the dentinal tubule density and diameter. At the same time, Trapani & Fisher (2003) used the Schreger Pattern's angle, wavelength, and qualitative appearance, to distinguish between tusks of mammoths (*M. primigenius* and *M. columbi* undifferentiated), mastodons (*Mammut americanum*) and extant elephants (*Elephas maximus* and *Loxodonta africana*). In the current study, we examine for the first time all the above features in conjunction, in order to discriminate between tusks of *Elephas antiquus* and *Mammuthus meridionalis*, the two Proboscidean taxa, which dominated the Greek Peninsula during the Quaternary. Furthermore, we compare the obtained results to the corresponding ones for the dwarf elephant tusks from the Tilos Island. Specifically, the characteristics examined herein (Fig.1) are: the Schreger angle (*sa*), the Schreger Pattern's phenomenon wavelength (*w*), the Schreger Pattern's qualitative appearance(*q*), the dentinal tubule density (*dtd*) and the dentinal tubule diameter (*tdi*).

The material used for the present study (Table 1) consists of: 1) two tusks from the Lower Pleistocene locality of Vlachioti (Lakonia, Peloponnisos, Greece), which have been attributed to *Mammuthus (Archidiskodon) meridionalis*, by identification of other skeletal and dental material (Symeonidis & Theodorou, 1986), 2) one tusk found near the village Nissoi (Ileia, Peloponnisos, Greece) by Associate Prof. Theodorou during a field trip to the area on July 1994. According to Assoc. Prof. Theodorou, this specimen exhibits the typical features of *Elephas antiquus* and is consequently attributed to this species (data under publication), 3) five tusks from the area of Megalopolis (Arcadia, Pelopo-

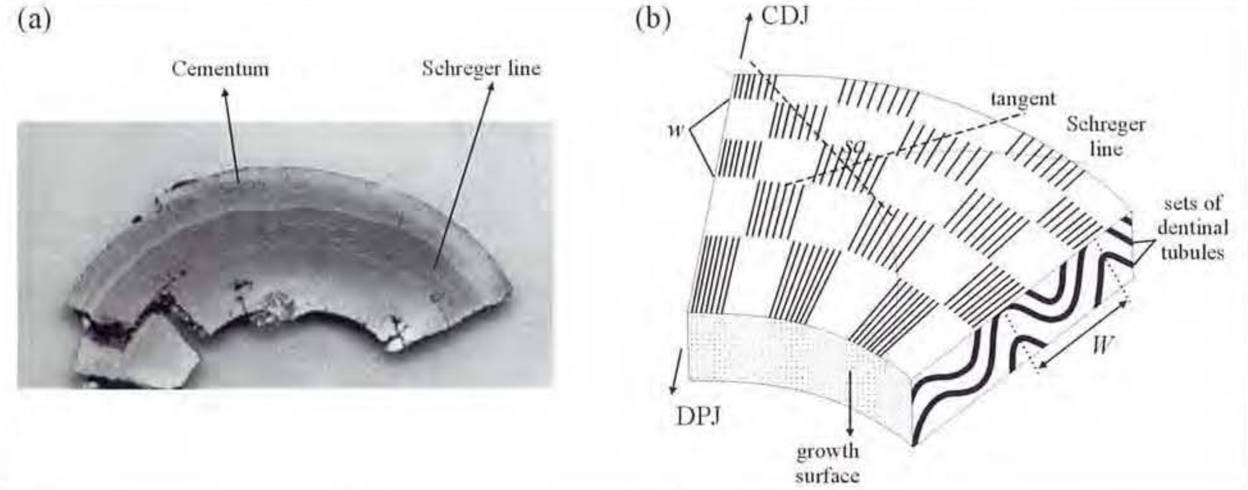

Fig. 1.

(a) Polished transverse section of a tusk belonging to a dwarf elephant from Tilos (T.00/144). On the outermost part we can see the thin layer of cementum, covering the dentine. The first layer of dentine, adjacent to the cementum-dentine junction (CDJ), is called mantle dentine. In the extant elephant species, this layer has a thickness of 40-80μm, and is characterized by irregularly spaced, extensively branched dentinal tubules, which are strongly curved toward the tip of the tusk (Raubenheimer et *al.*, 1998). Underneath the mantle dentine there is the main part of the tusk's dentine, which exhibits the Schreger Pattern.

(b) Schematic block diagram of the tusk's dentine, presenting the Schreger Pattern features. The growth surface coincides with the circumferential view of the dentine. The Schreger Pattern is visible on the transversal view, whilst on the radial view we can see part of the sinusoidal organization of the sets of dentinal tubules. As we can observe on this diagram, the true dentinal tubule wavelength (*W*) remains constant, while the angle between the sinusoidal direction of the tubules and the transversal view changes as we move from the dentine-pulp junction (DPJ) towards the CDJ. As a result, the phenomenon Schreger Pattern wavelength (*w*) increases towards the DPJ. The phase difference between the sinusoidal movement of adjacent bundles of odontoblasts, when it is projected on the transversal plane of the tusk, results in the intersecting Schreger lines. On the transverse section, we can measure the Schreger angle (*sa*), by drawing the tangents to the Schreger lines.

Fig. 1.

(a) Secció transversal polida d'una defensa pertanyent a un elefant nan de Tilos (T.00/144). A la part més exterior podem veure una capa prima de ciment, la qual cobreix la dentina. La primera capa de dentina, adjacent a la unió ciment-dentina (CDJ) s'anomena dentina mantell. A les espècies d'elefants vivents aquesta capa té un gruix de 40-80μm, i es caracteritza per túbuls de dentina extensament ramificats, espaiats irregularment, que estan fortament corbats cap a l'extrem de la defensa (Raubenheimer et al.*, 1998). Per sota de la dentina mantell es troba la part principal de la dentina de la defensa, la qual exhibeix el Patró d'Schreger.*

*(b) Diagrama de blocs esquemàtic de la dentina de les defenses, presentant els trets del Patró d'Schreger. La superfície de creixement coincideix amb la norma circumferencial de la dentina. El Patró d'Schreger és visible en norma lateral, mentre que en norma radial podem veure part de l'organització sinusoidal dels conjunts de túbuls de dentina. Com podem observar, a aquest diagrama, la veritable longitud d'ona dels túbuls de dentina (*W*) roman constant, mentre que l'angle entre la direcció sinusoidal dels túbuls i la norma transversal canvia a mesura que ens movem des de la unió polpa-dentina (DPJ) cap a la CDJ. Com a resultat, el fenomen de la longitud d'ona del Patró d'Schreger (*w*) s'incrementa cap al final del DPJ. La diferencia de fase entre el moviment sinusoidal dels bonys adjacents d'odontoblastes resulta en la intersecció de línies d'Schreger. A la secció transversa podem mesurar l'angle d'Schreger (*sa*) dibuixant les tangents a les línies d'Schreger.*

nnisos, Greece) identified by Melentis (1961) as belonging to *Elephas (Palaeoloxodon) antiquus*, 4) two tusk pieces also from Megalopolis (Melentis, 1961), which belong to *Mammuthus meridionalis*, and 5) fourteen tusks and tusk pieces found in the Charkadio Cave (Tilos, Dodekanese islands, Greece). It has been noted by previous studies (Theodorou, 1983), that no proof of any interaction between the dwarf elephants from Tilos islands and the dwarfs from Malta has been provided to date. Consequently, the two endemic evolutionary phenomena have progress separately. However the fossil elephant material found on the island of Tilos is still provisionally attributed to *Palaeoloxodon antiquus falconeri* (Theodorou, 1983).

Concerning methodology, the structure of the tusks' dentine was observed by combination of mesoscopic and microscopic investigation. The features were observed in detail using an optical petrographic and a scanning electron microscope (S.E.M.), under various magnifications. For this purpose, transverse sections were cut and thin sections were prepared whenever necessary. Our observations mainly concerned the perpen-

	Mammuthus meridionalis	*Elephas antiquus*	Dwarf elephants
sa	83 – 128 degrees	131 – 158 degrees	108 – 158 degrees
w	0.55 – 0.95 mm	0.56 – 0.92 mm	0.47 – 0.87 mm
q	Uniform throughout dentine's thickness, "X", occasionally "C"	"V" and some "X"	"V/C" on the outer zone, "X" on the inner zone
dtd	25500-43000 dt/mm^2	18300-40365 dt/mm^2	11524-45500 dt/mm^2
tdi	1.0-2.0 μm	0.5-1.0 μm	2.1-2.9 μm

Table 2. Identifying and discriminating characteristics of the tusk dentine of *Mammuthus meridionalis*, *Elephas antiquus*, and the dwarf elephants from the island of Tilos. The Schreger Pattern's features (angle, wavelength and qualitative appearance) are observed macroscopically, as well as under the optical microscope, while the dentinal tubules can only be seen under high magnification, with the use of a scanning electron microscope.

Taula 2. *Trets diferencials característics de la dentina de les defenses de* Mammuthus meridionalis, Elephas antiquus, *i dels elefants nans de l'illa de Tilos. Les característiques dels Patrons d'Schreger (angle, longitud d'ona i semblança qualitativa) s'observen macroscòpicament, igual que amb un microscopi òptic, mentre que els túbuls de dentina només es poden veure a grans augments, amb l'ús del microscopi electrònic d'escandallatge.*

dicular plane to the tusks' axes, since this is the direction were the Schreger Pattern appears. Only stub samples examined under the S.E.M. were orientated parallel to the tusks' long axes and outer surfaces (circumferential plane), so that we could measure the dentinal tubule's density and diameter. Occasionally, we also examined stubs on the radial direction, in order to see the longitudinal sections of the dentinal tubules.

In order to evaluate the Schreger Pattern's characteristics, on our samples, pieces of the tusks were encased in polyester resin. The blocks were cut perpendicularly to the tusks' axes and were then polished throughly with emery dust of two sizes. Afterwards the polished surfaces were scanned and the *sa* was measured at high magnification, using image processing software. In particular, the program CorelDraw vs.10 was used for this purpose. The scanned pictures were processed to enhance the Schreger lines. Then, under magnification, the tangents were drawn on each side of the angle. The *sa* was measured on the printouts. For the purpose of measuring the *w* and to characterize the *q*, thin sections were cut, using the same encased fragments. We must note, at this point, that the classification of the Schreger Pattern's qualitative appearance follows here the categories proposed by Trapani & Fisher (2003). In particular, these authors separated three main categories, "V", "C", and "X". When we observe a transverse section of the tusk, i.e. perpendicular to the growth surfaces, the "V" pattern occurs when there are continuous lines, oblique to the incremental features, with one direction (dextral or sinistral), being locally dominant. The "C" pattern consists of rectangular light and dark areas resembling a checkerboard. The diagonally neighbouring dark or light areas may share only a corner, or may be more broadly confluent. Finally, the "X" pattern is described as having criss-crossing continuous lines, oblique to the incremental features and occuring in both dextral and sinistral direction [Trapani & Fisher, 2003].

ABBREVIATIONS

sa	Schreger angles
w	Schreger Pattern's phenomenon wavelength
q	Schreger Pattern's qualitative appearance
dtd	dentinal tubule density
tdi	dentinal tubule diameter
S.E.M.	Scanning Electron Microscope
S.P.	Schreger Pattern
CDJ	cementum-dentin

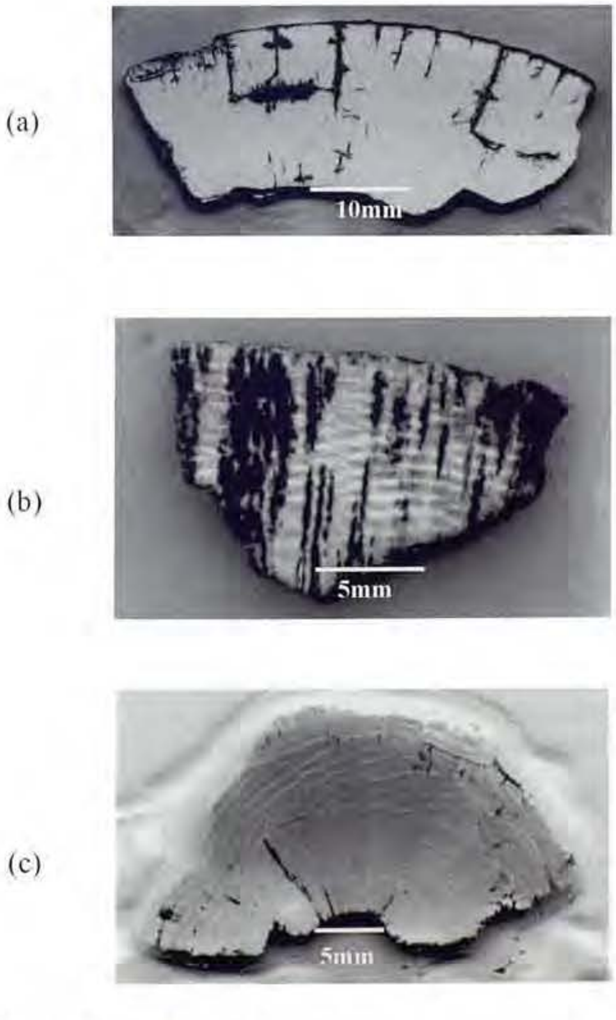

Fig. 2. According to Trapani & Fisher (2003), there are three categories of qualitative appearance that can be used to classify the Schreger Pattern. The "V" pattern consists of "continuous lines, oblique to the incremental lines, with one direction locally dominating". "Rectangular light and dark areas resembling a checkerboard, with the diagonally neighboring dark or light areas sharing only corners", result in the "C" type of Schreger Pattern. If however the Pattern is made of "criss-crossing continuous lines, oblique to the growth increments, occurring in both dextral and sinistral directions", then we place this to the "X" category. We can also distinguish the intermediate categories "X/C", "V/C", and "X/V".

(a) Transverse section on a tusk piece of *Mammuthus meridionalis* from Vlachioti (Lakonia). We can see that the dominant feature is "X/C".

(b) Transverse section on a tusk piece of *Elephas antiquus* from Nissoi (Ileia), where we can observe mostly "V", and rarely "X" patterns.

(c) Transverse section on a tusk piece from a dwarf elephant (Tilos, Dodekanese). On the outer zone of the Pattern, we can clearly observe the "C" type, which changes to "V" towards the pulp cavity. The "X" type can be seen only on the inner zone.

Fig. 2. *D'acord amb Trapani & Fisher (2003) hi ha tres categories de semblança qualitativa que poden ser emprades per a classificar el Patró d'Schreger. El patró en "V" consisteix en "línies contínues, obliqües a les línies d'increment, amb una direcció localment dominant". El tipus "C" del Patró d'Schreger consisteix en "àrees rectangulars clares i fosques que s'assemblen a una taula d'escacs, amb les àrees clares i fosques properes diagonalment compartint només els cantons". No obstant, si el Patró està fet per "línies contínues entrecreuades, obliqües als increments de creixement, que es donen tant en direcció dreta com esquerra" ens trobam a la categoria "X". També podem distingir les categories intermèdies "X/C", "V/C", i "X/V".*

(a) Secció transversa d'una peça de defensa de Mammuthus meridionalis *de Vlachioti (Lakonia). Podem veure que el tret dominant és "X/C".*

(b) Secció transversa d'una peça de defensa d'Elephas antiquus *de Nissoi (Ileia), on podem observar principalment patrons "V" i rarament "X".*

(c) Secció transversa d'una peça de defensa d'un elefant nan (Tilos, Dodecanès). A la zona externa del Patró podem observar clarament el tipus "C", amb canvis cap a "V" cap a la cavitat polpar. El tipus "X" només es pot veure a la zona interna.

TUSK PALEOHISTOLOGY

Proboscidean tusks are enlarged incisors formed by orthodentine, which is covered on the outer surface by a thin layer of cellular cementum. Enamel, in the species examined here, is found only as a very thin layer, covering the tip of the tusks. Due to the special functions and the consequent enlargement of tusks, the dentine has formed certain features, unique to Proboscidean tusks, which combine to produce the Schreger Pattern (S.P.). This Pattern was first observed, by Bernard Schreger (1800), on sections perpendicular to the tusk's axis. It consists of two sets of light and dark lines, radiating from the outer dentine surface, towards the axis of the tusk, in a spiral fashion. One set of Schreger lines radiates clockwise and the other counter-clockwise, thus intersecting to form the Schreger angles.

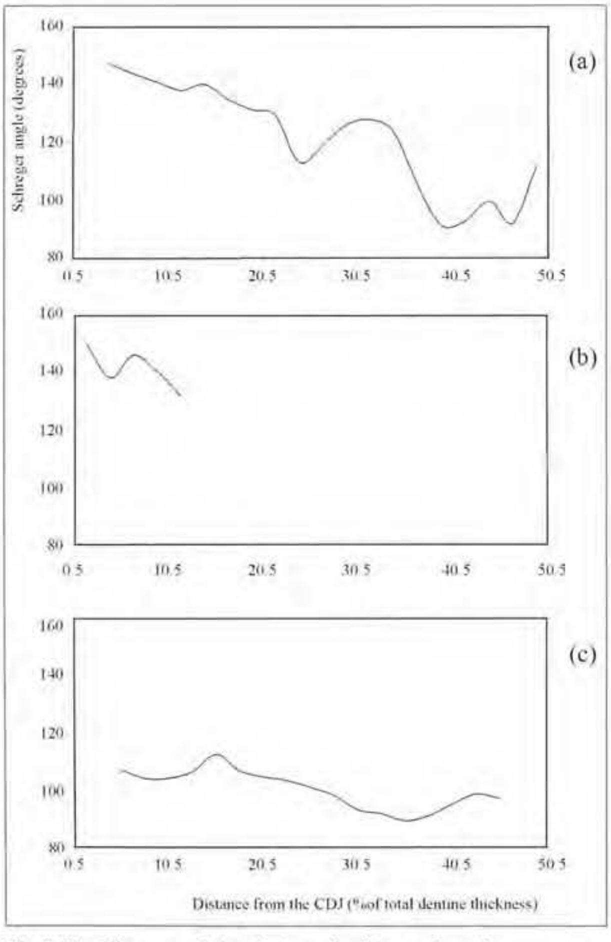

Fig. 3. The Schreger angle in relation to the distance from the cementum-dentine junction (CDJ). The distance is expressed as a percentage of the total dentine thickness at the position of each measurement.
(a) Diagram for the dwarf elephant tusks.
(b) Diagram for *Elephas antiquus* from Megalopolis.
(c) Diagram for *Mammuthus meridionalis* from Vlachioti.

***Fig. 3.** L'angle d'Schreger en relació a la distància des de la unió ciment-dentina (CDJ). La distància s'expressa com a percentatge del gruix total de dentina a la posició de cada mesura presa.*
(a) Diagrama per a les defenses d'elefants nans.
(b) Diagrama per a Elephas antiquus *de Megalopolis.*
(c) Diagrama per a Mammuthus meridionalis *de Vlachioti.*

The Schreger Pattern (Fig. 1a) is the macroscopic manifestation of the microscopic architecture of tusk dentine. During odontogenesis, as the odontoblasts move towards the proximocentral part of the tusk's pulp cavity, they leave behind them the dentinal tubules, which are the traces of the odontoblasts' sinusoidal movement (Raubenheimer *et al.*, 1998). As a result, when observing a transverse section of the tusk, we can essentially observe the undulation of the dentinal tubules, projected as the dark and light lines of the Schreger Pattern (Figs. 1 & 2). Dark lines correspond to the concave part of the undulation, while the light lines represent the convex part. The fact that, on a transverse section, we do not observe alternating light and dark concentric rings, but rather the dextral and sinistral Schreger lines, leads to the conclusion that the periodic movement of the odontoblasts, towards the proximocentral part of the pulp cavity, does not occur simultaneously for the entire band of odontoblastic cells. On the contrary, the cells are organized in bundles that move simultaneously, producing sets of dentinal tubules, which are in phase with each other, but have a phase difference of π, in relation to the neighbouring sets.

In respect to all the above, the parameters characterizing the Schreger Pattern are the size and density of the dentinal tubules, the wavelength of their undulation, and the size of the dentinal tubule sets. These parameters are defined by the shape of the original pulp cavity, the size and density of the odontoblasts and the rate of dentine deposition, which in turn produce the final shape and size of the tusk. On the circumferential view of the tusk, we can directly measure the size and density of the dentinal tubules. Also, on a transverse section of the tusk, we measure the Schreger Pattern phenomenon wavelength, as the distance between two adjacent dark or light lines. As for the size of the dentinal tubule sets, this is expressed instead by the Schreger angles, which we also measure on transverse sections.

OBSERVATIONS

Mammuthus meridionalis

The Schreger Pattern on *M. meridionalis*, as observed on the transversal plane, appears continuously throughout the thickness of the tusk's dentine. The *sa* decreases from the outermost surface of the dentine towards the pulp cavity. Measurements of the *sa*, on the outer approximate 45% of the dentine's thickness, give values between 83° - 128°, with the maximum value appearing at 15%. Fig. 3c shows the relationship between the *sa* values and the distance from the outer dentine surface. There are four areas of deviation, from the general decrease of the *sa*, namely at: 13.6-19.1% (maximum value of *sa* at 16.4%), 21.8-23.6% (max at 22.7%), 26.4-28.2% (max at 27.5%), and 40%-48.2% (max at 43.6%). Regarding the *w*, measurements were made at the same area as the *sa* and produced values between 0.55-0.95 mm. Qualitatively the Schreger Pattern exhibits mostly "X" patterns and occasionally "C" patterns, as those were described by Trapani

& Fisher (2003) (Fig. 2a). We are not able to distinguish any "V" patterns, although our examination does not include the inner part of the tusk's thickness, where the above authors mention the appearance of the "V" pattern on the tusks of *M. primigenius* and *M. columbi.*

On the microscopic level, we observe the organization of the dentinal tubules (Fig. 4a & b), and measure their *tdi* and *dtd*, near the cementum-dentine junction (CDJ), but below the mantle dentine. Due to the sinusoidal movement of the odontoblasts, the dentinal tubule sections, on a circumferential view of the tusk's dentine, are ellipses with their large diameters parallel to the direction of the tusk's axis. Thus the large diameter of an elliptical section is a phenomenon diameter of the tubule. Additionally, the lateral component of the odontoblasts' movement is relatively small, and it varies amongst adjacent tubules in a sinuous fashion. Consequently, calculating the mean tubule small diameter, for an area of about $11*10^{-3}$ mm^2, should eliminate the fluctuation due to the lateral movement. As a result we accept this mean value as the true dentinal tubule diameter (*tdi*). For the samples of *Mammuthus meridionalis* the measurement of the dentinal tubule small diameter produces values between 1.0-2.0μm. On the same circumferential microscopic views, we also measured the *dtd*, which ranges from 25500 to 43000 dt/mm^2. Both the *tdi* and *dtd* was measured on a total of 20 samples.

Elephas antiquus

The tusks of *E. antiquus* from both localities exhibited the same microstructural features. The *sa* decreases from the outer part of the dentine towards the pulp cavity. Measurements of the *sa* were taken only within the outer 15% of the dentine's thickness (Fig. 3b), because our tusk samples did not allow for the separation of a larger piece. The *sa* ranges between 131° - 158°, reaching a maximum at 5.8% of the dentine's thickness, which also constitutes an irregularity in the general decrease of the *sa* toward the central tusk axis. It is important to note, at this point, that the *sa* was measured in our samples only in relation to the distance from the cementum-dentine junction, because we have previously established that there is no particular pattern of a *sa* variation along the proximodistal direction, i.e. the Schreger Pattern does not change with the age of the tusk, but rather depends on the shape of the pulp cavity (Theodorou & Agiadi, 2001). This allows us to use tusk fragments even though their position along the tusk was not always known. Qualitatively, the Schreger Pattern exhibits mostly "V" and some "X" patterns. In addition, the *w* ranges between 0.56-0.92 mm, increasing towards the pulp cavity.

Regarding the dentinal tubules' size and distribution (Figs. 4c & 5a), we measure the *dtd* on stubs taken from both the areas near the cementum-dentine and the pulp-dentine junction. There does not appear to be any significant differentiation of this characteristic, among the two areas. In particular, the *dtd* measures between 18300-40365 dt/mm^2. Furthermore we measure the mean dentinal tubule small diameter, which is the true dentinal tubule diameter (*tdi*), at the same areas, to range between 0.5-1.0μm. The total number of samples examined for *tdi* and *dtd* was 18.

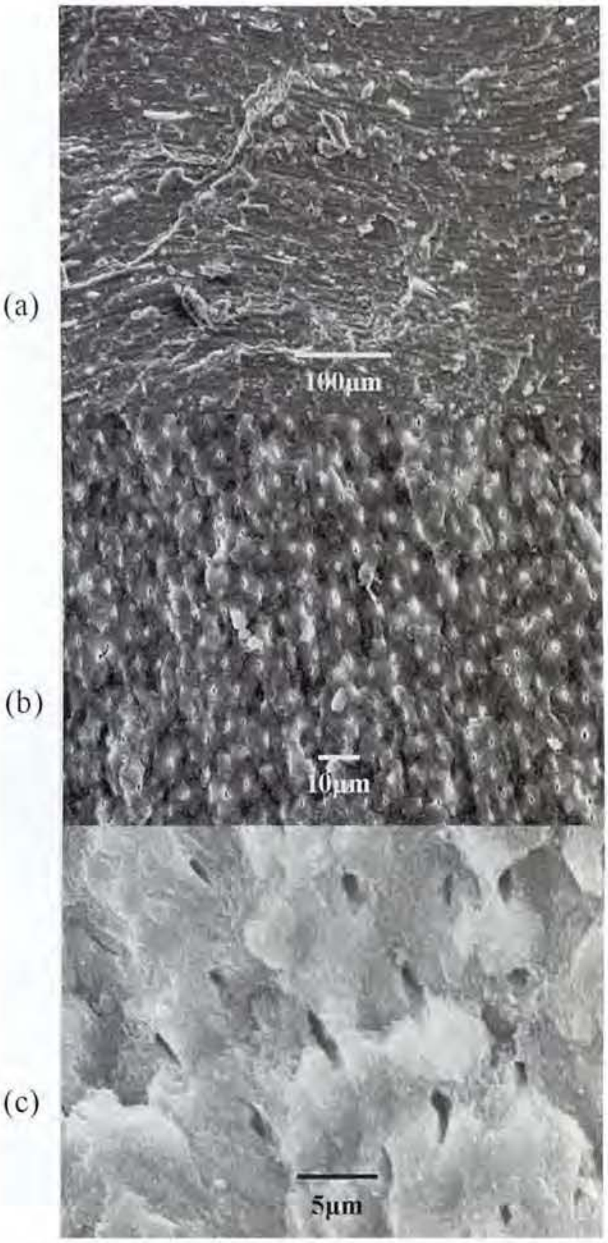

Fig. 4. S.E.M. images of tusk dentine, showing the distribution of the dentinal tubules.

(a) Tusk specimen of *Mammuthus meridionalis* from Vlachioti (Lakonia), where a stub has been taken at a distance of about 7.0 mm from the CDJ. We can see the transverse sections of the dentinal tubules.

(b) On the same specimen, we have a radial view of the dentine, where we can see the longitudinal sections of the undulating dentinal tubules.

(c) Tusk specimen of *Elephas antiquus* (1960/183), stub taken from the outer dentine layers, at about 9.5 mm from the CDJ. We observe oblique sections of the dentinal tubules, at a view almost parallel to a growth surface.

Fig. 4. *Imatges SEM de la dentina de les defenses, mostrant la distribució dels túbuls de dentina.*

(a) Mostra de defensa de Mammuthus meridionalis *de Vlachioti (Lakonia), on s'ha agafat una peça a una distància de 7,0 mm del CDJ. Podem veure les seccions transverses dels túbuls de dentina.*

(b) Al mateix exemplar, tenim una vista radial de la dentina, on es poden veure les seccions longitudinals dels túbuls de dentina ondulants.

*(c) Mostra de defensa d'*Elephas antiquus *(1960/183), peça agafat a les capes de dentina exterior, a devers 9,5 mm del CDJ. Observam seccions obliqües dels túbuls de dentina, en norma quasi paral·lela a la superfície de creixement.*

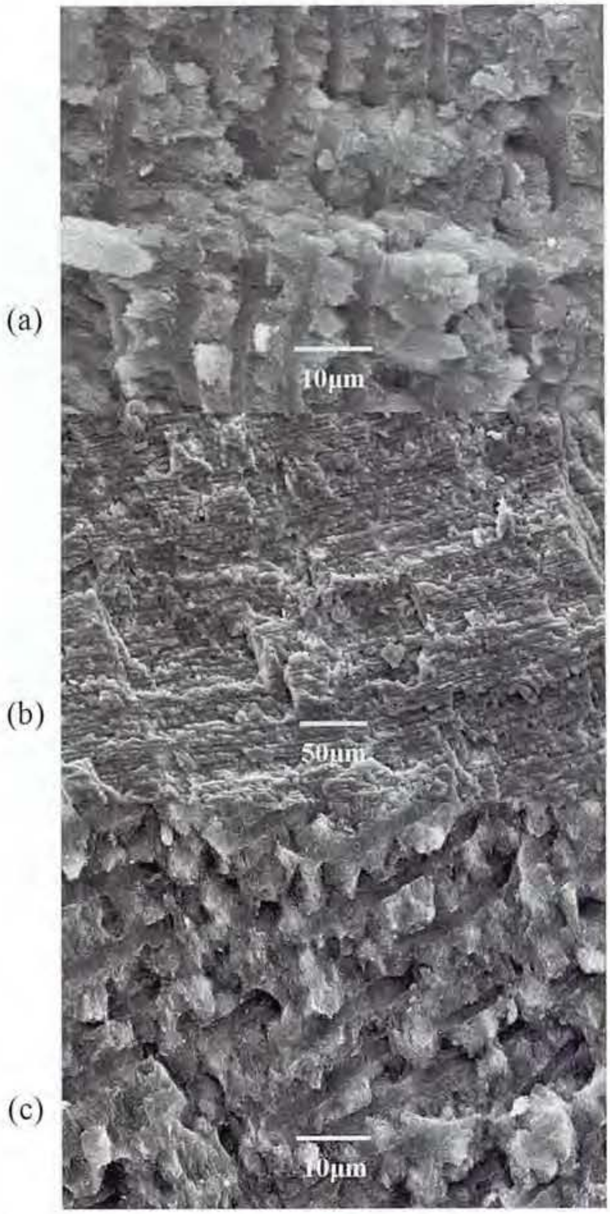

Fig. 5. S.E.M. images of tusk dentine, showing the distribution of the dentinal tubules.
(a) Tusk specimen of *Elephas antiquus* from Nissoi (Ileia), where we can see nearly longitudinal sections of the dentinal tubules.
(b) Radial view of a dwarf tusk (unnumbered sample), where we can see the longitudinal sections of the undulating dentinal tubules. The width of the undulation is greater than that on the specimens of *M. meridionalis.*
(c) Oblique sections of the dentinal tubules, at an almost radial view of the same sample.

Fig. 5. *Imatges SEM de la dentina de les defenses, mostrant la distribució dels túbuls de dentina.*
*(a) Mostra de defensa d'*Elephas antiquus *de Nissoi (Ileia), on podem veure seccions quasi longitudinals dels túbuls de dentina.*
(b) Vista radial d'una defensa d'elefant nan (mostra no numerada), on podem veure les seccions longitudinals dels túbuls de dentina ondulants. L'amplada de l'ondulació és major que als espècimens de M. meridionalis.
(c) Seccions obliqües dels túbuls de dentina, en una vista quasi radial de la mateixa mostra.

Dwarf elephants from Tilos island

On the transverse sections of the Tilos elephant tusks, we can clearly distinguish two zones of dentine, with obvious differences in the Schreger Pattern's qualitative and quantitative characteristics. The qualitative appearance exhibits a combination of "V" and "C" patterns on the outer zone, with "C" patterns dominating as we move towards the CDJ. The "X" type of Schreger Pattern is confined to the inner zone, where we some times also observe the "V" type. We concentrate on the Schreger angle variance regarding the outer zone, so that our results would be comparable to our measurements on the samples of the other species. To this end, we examined approximately the outermost 50% of the dentine's thickness. Our *sa* values for this show a range from 108° to 158°. By plotting the *sa* against the distance from the CDJ, on the specimen T.00/144, we confirm its decrease toward the tusk's axis. However there is an anomaly, between 26-36% of the dentine's thickness, with a maximum being achieved at about 31% (Fig. 3a). Finally, on the same areas, we also measured the *w*, which varies between 0.47-0.87 mm, increasing towards the pulp cavity.

Microscopically, the *dtd* on our samples has a range from 11524 to 45500dt/mm^2, and the *tdi* varies between 2.1-2.9μm (Fig. 5b & c). We examined 13 stub samples from the tusks, each time noting their position on the specimen. There is no differentiation of the size and density values, along the periphery of the tusks, or across the radial, although the greatest density values (*dtd* > 35000dt/mm^2) can indeed be measured on the outermost part of the dentine. However this can be explained by the existence of the mantle dentine, which is characterized by an extreme branching of the tubules.

DISCUSSION

In the present study, we have reached valuable results, which further our understanding of the Schreger Pattern. The Schreger angle is related to the phenomenon wavelength and the width of the dentinal tubule sets, in a given position in the tusk (Fig. 1b). The *sa* increases towards the CDJ and so does the sets' width, but the wavelength decreases. Although we have not examined the relationship between the Pattern's wavelength and the distance from the CDJ, we expect it to be similar to that observed between the angle and the CDJ distance. Such a pattern would be able to differentiate between taxa in the similar manner. However, simply comparing the range of the wavelength, in a given part of the tusks' thickness, does not provide any discrimination. Regarding the Schreger Pattern's qualitative appearance, this depends on how abrupt the boundaries of the tubule sets are. When they are very abrupt, we observe the "C" pattern. When the boundaries on direction are abrupt, and on the other smooth, they produce the "V" pattern. And finally, smooth boundaries, i.e. progressive transmission of the proximocentral movement of the odontoblasts, produce the "X" type of pattern.

Locality	Taxon	L (cm)	d1 (cm)	d2 (cm)	Specimen
Vlachioti	*M.meridionalis*	100.0	12.00*	9.50*	unnumbered (sin.)
Vlachioti	*M.meridionalis*	44.5	11.80*	10.30*	unnumbered (dext.)
Nissoi	*E. antiquus*	265.0	18.64	17.46	NS. 1994/1
Megalopolis	*E. antiquus*	145.5	15.30	14.5	1960/94 (dext., M.)
Megalopolis	*E. antiquus*	186.0	8.60	8.00	1960/96 (sin., F.)
Megalopolis	*E. antiquus*	77.5	6.70	6.60	1960/183 (sin. F.)
Megalopolis	*E. antiquus*	51.0	6.20	6.00	1960/187 (dext., M.)
Megalopolis	*E. antiquus*	289.5	16.40	15.00	1960/188 (sin.M.)
Megalopolis	*M. meridionalis*	87.0	9.30	7.50	1960/182 (F.)
Megalopolis	*M. meridionalis*	145.0	11.90	10.10	1960/95 (dext., F.)
Charkadio cave	dwarf elephants	47.0	9.50	7.50	T.00/53
Charkadio cave	dwarf elephants	20.55	4.05	3.65	T.00/144
Charkadio cave	dwarf elephants	42.0	3.84	3.74	T.70/1999 (sin., F.)
Charkadio cave	dwarf elephants	28.5	2.85	2.75	T.1/98 (sin., d)
Charkadio cave	dwarf elephants	25.5	2.40	2.17	T.00/41 (d)
Charkadio cave	dwarf elephants	40.5	3.51	3.20	T.85/91 (sin., F.)
Charkadio cave	dwarf elephants	39.0	4.15	3.61	T.89/91
Charkadio cave	dwarf elephants	49.0	4.14	3.78	T.10481 (sin., F.)
Charkadio cave	dwarf elephants	44.5	3.98	3.47	T.143b/82 (M.)
Charkadio cave	dwarf elephants	42.5	4.22	3.80	T.143a/82
Charkadio cave	dwarf elephants	50.5	4.38	4.01	T.293/98 (dext., F.)
Charkadio cave	dwarf elephants	-	-	-	unnumbered
Charkadio cave	dwarf elephants	-	-	-	T.354/99 (d)
Charkadio cave	dwarf elephants	68.0	7.14	6.69	T.88/91 (dext., F.)

Table 1. Tusk material examined in this study, including macroscopic measurements. L: tusk or tusk piece's length following the proximodistal direction in a straight line, d1: maximum diameter at approximately the middle of the tusk's length, d2: minimum diameter at the same position. The measurements followed by * have been taken at the proximal end of the tusk. All of the specimens are deposited in the Museum of Palaeontology and Geology of the University of Athens.

Taula 1. *Material de defenses examinat a aquest estudi, incloent les mesures macroscòpiques. L: llargària de la defensa o part de la defensa disponible seguint la direcció proximo-distal en línia recta. d1: diàmetre màxim agafat aproximadament a la meitat de la llargària de la defensa, d2: diàmetre mínim a la mateixa situació. Les mesures seguides per un asterisc han estat preses a la part proximal de la defensa. Tots els espècimens estan dipositats al Museu de Paleontologia i Geologia de la Universitat d'Atenes.*

Very important also are the microstructural observations, which once more present the uniqueness of the tusk dentine tissue. Concerning the microstructural features of dentine, the dentinal tubule density does not present any discriminating power, in the samples examined herein. Besides, the tissue is the same in all three taxa, and would be expected to have the same needs in intratubular material (odontoblastic material, neural fibers, etc.). In addition, there appears to be no variance in density amongst different areas of the dentine's thickness, a fact also expected for the same reasons. The dentinal tubule's branching process, in this case, compensates for the increased periphery of the tusk, as we move toward the outer part. However the dentinal tubule size differs between our samples. In particular, the tusks of the dwarf elephants from Tilos island have much larger tubules, than the samples of *Elephas antiquus* and *Mammuthus meridionalis*. The reasons for this differentiation are not yet clear to us. Although the fossilization processes could have affected this feature, a low degree of calcification, in the first place, may account for the larger tubule diameter found in the tusks of the dwarfs. In such a case, we should think that the smaller and lighter tusks of the dwarf elephants have less need for solidity and resistance to stress than do the ones of larger animals.

Comparing the results for the tusks from the three taxa (Table 2), distinction of mammoths from elephants is clear, by means of the Schreger angle and qualitative appearance, as well as the dentinal tubule diameter. Discriminating however, between the mainland *Elephas antiquus* from the endemic elephants of Tilos island, is more difficult. We measured an important difference in the dentinal tubules' diameter, which is much larger than the dwarf elephant tusks. Additionally, we were able to find a slight variance in the Schreger Pattern, in reference to its qualitative appearance. In particular, the dwarf elephant tusks exhibit the "V" and "C" patterns on the outer dentine zone ("C" being dominant towards the CDJ), and the inner zone has mostly "X" patterns, while the *E. antiquus* tusks have "V" and "X" motives on the outer part of the Schreger Pattern. We cannot provide a definite explanation for this difference. It may be caused by an alteration in the odontogenetic process. However, changes in the entire appearance of the Schreger Pattern, due to mechanical or chemical alterations, without the simultaneous deformation of the entire tusk, have been mentioned before as a result of the fossilization processes (Agiadi, 2003).

To present, archaeologists have always accepted Asia and Africa as the only source of ivory for the ancient Greeks (Hayward, 1990). However, considering the wealth of Proboscidean tusk findings in many continental and island localities of Greece, fossil ivory should be considered as an alternative source. In particular, tusks of the Pleistocene and Holocene endemic and continental species (i.e. *E. antiquus*, *M. meridionalis* and the dwarf elephants from the Aegean islands) could provide usable ivory. In fact, fossilization would have progressed on these tusks for only a small period of time. Consequently, any alteration of the chemical and structural properties of this ivory may not be severe, by the time the tusks would have to be cut, curved and processed in order to be used.. Therefore, the distinction of ivory from different elephant species becomes greatly important in the assessment of such artefacts' true archaeological value. Perhaps some of the archaeological specimens, which are at present thought to be the product of Mediterranean sea trade may, after thorough examination with the above methodology, turn out to have domestic origin. To this end, we propose the review of the ivory specimens found on Greek archaeological cites, examining all the mesoscopic and microscopic features explained in this study, and the comparison of these specimens with paleontologically identified tusks of known origin.

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02

FOSSIL RAILS (GRUIFORMES: RALLIDAE) FROM THE BALEARIC ISLANDS

Josep Antoni ALCOVER, Miguel MCMINN & Bartomeu SEGUÍ

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Resum

Es presenta el registre fòssil de rasclons de les Illes Balears. Aquest registre és peculiar per a cada una de les tres illes principals. A Mallorca consisteix en un ràl·lid petit indeterminat trobat a la Pedrera de s'Ònix (Manacor) i restes de *Porzana porzana* trobades al jaciment del Pleistocè superior – Holocè de la Cova de Moleta. A Menorca, les escasses restes disponibles provenen de dos dipòsits pleistocènics del nord de Ciutadella (Punta Esquitxador 12, Punta Esquitxador 17). A aquests dipòsits pleistocènics s'han identificat *Rallus* cf. *quaticus*, *Gallinula chloropus* i Rallidae indet. *Rallus* cf. *aquaticus* és l'espècie més abundant i els fòssils obtinguts són lleugerament més grossos que els ossos corresponents d'exemplars actuals de *Rallus aquaticus*. El ràl·lid indeterminat és un rascló de mida similar a la de *Porzana pusilla*, però que presenta alguns trets morfològics que l'apropen a *Rallus*. Només s'han exhumat tres ossos fragmentats d'aquest ràl·lid i la seva diagnosi taxonòmica resta sense resoldre. Es coneixen tres ràl·lids a partir de materials pel jaciment del Pleistocè superior d'Es Pouàs (Sant Antoni de Portmany, Eivissa, Illes Pitiüses). Un és *Crex crex*, una espècie present a altres dipòsits de la Mediterrània. El segon és una espècie nova, encara no descrita, que representa un parent insular del *Rallus aquaticus* del continent europeu. Es tracta del primer rascló insular endèmic de la regió mediterrània. Comparat amb el rascló europeu vivent, aquesta nova espècie era més petita i arrodonida, tenia les cames més curtes i robustes i les ales més curtes, amb una capacitat de vol presumptament reduïda. Les Pitiüses eren les úniques illes de la Mediterrània que durant el Pleistocè superior estaven mancades de mamífers terrestres i, sense cap dubte, aquesta absència ha d'estar relacionada amb l'evolució del rascló endèmic. La cronologia de l'extinció de *Rallus* n.sp. se solapa amplament amb la cronologia on se situa l'arribada dels humans, suggerint que existeix una relació entre aquests dos esdeveniments. El tercer ràl·lid fòssil d'Eivissa és *Porzana porzana*.

Paraules clau: *Rallus*, *Porzana*, Eivissa, Mallorca, Menorca, Late Pleistocene, Pliocene.

Abstract

The fossil record for rails from the Balearic Islands is presented in this paper. This record is highly distinctive for the three main islands. It consists in an indeterminate small rail from Pedrera de s'Ònix (Pliocene-Pleistocene boundary) and *Porzana porzana* in the Upper Pleistocene - Holocene deposit of Cova de Moleta on Mallorca. On Menorca the scarce available materials come from two Pleistocene deposits in Northern Ciutadella (Punta Esquitxador 12, Punta Esquitxador 17). *Rallus* cf. *aquaticus*, *Gallinula chloropus* and Rallidae indet. have been identified in these Pleistocene deposits. *Rallus* cf. *aquaticus* is the more abundant species and its obtained fossil material is slightly more robust than the current populations of *Rallus aquaticus*. The undetermined rallid is a rail similar in size to *Porzana pusilla*, but displaying some features close to *Rallus*. Only three fragmented bones of this rail have been exhumed, and their diagnosis remains unsolved. From the upper Pleistocene deposit of Es Pouàs (Sant Antoni de Portmany, Eivissa, Pityusic Islands), three rails are known. One of them is *Crex crex*, a species also present in other Mediterranean deposits. The second one is a new undescribed species of rail that represents an insular relative of the European rail *Rallus aquaticus*. It represents the first insular endemic rail from the Mediterranean region. Compared with the extant European rail, this new species was smaller and stouter, had shorter and more robust hind limbs and shorter wings, with presumed reduced flight ability. The Pityusics were the only Mediterranean islands with a vertebrate upper Pleistocene fauna without terrestrial mammals, and this absence is no doubt related with this Eivissan rail evolution. The chronology of the *Rallus* n.sp. extinction overlaps widely with the timing of the human arrival, suggesting a close relation between these two events. The third one is *Porzana porzana*, only present in low numbers.

Key words: *Rallus*, *Porzana*, Eivissa, Menorca, Mallorca, Late Pleistocene, Pliocene.

INTRODUCTION

On the Mediterranean Islands there is a small number of extant endemic bird species, mainly recruited within the Passeriformes (e.g., *Sylvia sarda*, *Sylvia balearica*, *Sylvia melanothorax*, *Oenanthe cypriaca*, *Sitta whiteheadi*) and Procellariiformes (*Puffinus yelkouan* / *mauretanicus*). The study of the fossils reveals that in the recent past the number of endemic species was considerably larger on the Mediterranean islands. Endemic recently disappeared species consist mainly in wing predators belonging to Accipitriformes (*Aquila*; Weesie, 1988; Louchart, 2002) and to Strigiformes (*Tyto*, *Athene*, *Bubo*; e.g., Weesie, 1982; Mourer-Chauviré & Weesie, 1986; Louchart, this volume).

In the last twenty years, the palaornithological exploration of the islands allowed to discover a clear evolutive pattern consisting in the presence of endemic rails in many islands of the world. Recent research allowed to discover a lot of insular endemic species of rails, and some of them have been described. Recent estimates suggest that several thousands of endemic species of rails could have inhabited the Pacific isolated islands. Insular living rails (Aves: Rallidae) are currently known from a small number of islands in the world (e.g., Galápagos, Guam, Okinawa, Inaccessible, New Zealand, Lord Howe). They are mainly recruited within *Gallirallus,* although other genera (e.g., *Porphyrio, Porzana, Amaurornis, Gallinula*) contain small numbers of insular species, and there are even several insular endemic genera (e.g., *Atlantisia, Nesoclopeus*). The increased palaeontological work of the last two decades has revealed that a huge number of insular endemic rails disappeared after the arrival of first human settlers into the islands (e.g., Steadman, 1991, 1995, 1997).

The biogeographic pattern discovered by palaeornithologists shows that rails are prone to evolve on islands originating endemic species or populations, and that the current diversity of insular rails merely reflects the survivals of a much larger past diversity. Several genera that currently do not include insular endemic species included some in the past (e.g., Olson, 1990; Steadman, 1995).

Up to the present, no endemic fossil rails have been described from the Mediterranean islands. Usually fossil insular endemic rails have been discovered on islands lacking of terrestrial mammals, and all the large Mediterranean islands, with a single exception, contains them. The goal of the present paper consists in to update the knowledge that we have on fossil rails of the Balearic Islands, as well as in to explore the insular evolution in the Mediterranean rails. The current record is relatively poor, and it will be presented here by islands.

FOSSIL RECORD

On Mallorca, the fossil remains of rails are coming from two deposits. On Pedrera de s'Ònix (Manacor), a single tarsometatarsus reveals the presence of a small sized rail, probably a *Porzana* (Mourer-Chauviré, in Alcover et al., 1981). This material was associated to a rich bird fauna, with *Tyto balearica* as the most probable bioaccumulator agent. The estimate age of the fossil assemblage is the uppermost part of the Pliocene or the Plio-Pleistocene boundary, with an estimate palaeomagnetic age close to 1.8 My.

Fig. 1. Map of the Western Mediterranean showing the location of Es Pouàs (Eivissa, Pityusic Islands).

Fig. 1. Mapa de la Mediterrània occidental que mostra la localització d'Es Pouàs (Eivissa, Illes Pitiüses).

There is only another deposit on Mallorca that yielded rail bones: the Moleta cave (Sóller; Seguí *et al.*, 1997). This cave has been excavated at the sixties (see Waldren, 1982), and, unfortunately, it has many stratigraphic problems (see Ramis & Alcover, 2000; Alcover *et al.*, 2001),

	Rallus n.sp.						*Rallus aquaticus*				
	Mean	min	max	n	sd		mean	min	max	n	sd
Humerus Length	35.26	32.44	37.94	18	1.58		38.87	34.97	42.10	35	1.73
Ulna Length	26.97	24.84	28.62	14	1.23		31.40	27.96	33.93	34	1.44
Carpometacarpus Length	18.53	15.89	20.85	13	1.66		21.49	19.37	23.31	33	1.00
Femur Length	37.23	34.23	40.77	13	2.02		41.38	37.56	44.76	36	2.00
Tibiotarsus Length	54.56	49.69	60.30	11	2.96		64.50	57.56	68.49	34	3.08
Tarsometatarsus Length	34.31	29.79	37.22	22	2.15		41.23	37.04	45.32	35	2.29

Table 1. Lengths (in mm) of selected skeletal elements of *Rallus* n.sp. from the Upper Pleistocene and Holocene of Eivissa and *Rallus aquaticus* (several localities). Mean, range (max and min), sample size (n) and standard deviation (sd) are indicated.

Taula 1. *Llargàries (en mm) d'elements esquelètics seleccionats de* Rallus *n.sp. del Pleistocè superior i Holocè d'Eivissa i de* Rallus aquaticus *(diferents localitats). S'indiquen la mitjana, l'espectre de mides (màxima i mínima), la mida de la mostra i la desviació típica.*

that involve some imprecision in the chronological position of the obtained fossils. Roughly, the cova de Moleta fossil materials are from Upper Pleistocene and Holocene. Six bones have been identified as belonging to *Porzana porzana*.

Two unpublished deposits from Menorca delivered a few rail fossil remains (Seguí, 1998). Both deposits are situated at the northern part of Ciutadella, at Punta Esquitxador. Two taxa have been specifically identified: *Rallus* cf. *aquaticus* and *Gallinula chloropus*. There are, additionally, several bones that are presented here as Rallidae unidentified genus and species. The bones of this unidentified taxon are of the size of *Porzana pusilla*, but they display some shared features with *Rallus aquaticus*. The identity of these bones currently remains unsolved.

Only one Eivissan deposit has delivered rail remains: Es Pouàs, an extraordinary fossiliferous deposit of the island, the larger of the Pityusic Islands (541 sq km), situated 90 km far from the Eastern Iberian Peninsula and about 80 km from Mallorca (see Fig. 1). The Pityusic archipelago consists in two main islands (Eivissa and Formentera) surrounded by about 60 small islets (Kuhbier 1984). Its biogeographic history reveals that they were, during the Upper Pleistocene and the Holocene (until the human arrival), the only territories in the whole Mediterranean area without terrestrial mammals (e.g., Florit *et al.* 1989; Alcover, *et al.*, 1994, 1999; Palmer *et al.*, 1999). This faunistic anomaly has been analysed by Seguí and Alcover (1999) who consider that the ecological parallels of the prehuman bird fauna from Eivissa may be found in some of the Pacific islands, like the Hawaiian Islands.

From Es Pouàs three species of Rallidae have been identified: the corncrake *Crex crex*, a still undescribed rail of genus *Rallus*, and *Porzana porzana*.

Crex crex is the most abundant rail species in the Pityusic fossil record. Some fossil specimens are slighly more robust that the studied bones of extant populations of the species. This slightly larger size fits well with a general size pattern documented in a great number of bird species. Nevertheless, it must be remarked than the scarcity of comparison material delimitates greatly a precise comparison. One of the fossil specimens (MNIB 30775) corresponds to an immature specimen, and consequently the breeding of the species on the island some time in the past shoud be deduced.

The very long and slender bill of the Eivissan species clearly places the smaller Eivissan rallid in the genus *Rallus* (Olson, 1973). This genus contains no insular living species, although two Pleistocene species have been recently described from Bermuda (Olson & Wingate, 2000, 2001) and a new undescribed species has been recorded from Miyakoshima, southern Ryukyu islands (Matsuoka, 2000, table 1), although the later could belong to *Gallirallus*. This is the only western Palaearctic Rallidae genus displaying this characteristic type of bill.

In addition to the shorter bill, this species has larger orbits. The fonticuli interorbitalis are larger than in *Rallus aquaticus*. There are no impressions for salt glands on the interorbital bridge, suggesting a life style independent of saline habitats.

The smaller fossil Eivissan rail differs from *Rallus aquaticus* and represents a new species of bird. It will be referred here as *Rallus* n.sp. Slightly smaller than *Rallus aquaticus*, the only species of the genus currently living in the Western Palaearctic and its presumably ancestor, *Rallus* n.sp. displays different proportions in the legs and body shape. Its wings are relatively smaller, suggesting some reduction in the development of the flight apparatus, although without achieving a flightless condition. Distal hindlimb elements are shorter and slightly more robust (see a comparison of bones of *Rallus* n.sp. from Eivissa and *Rallus aquaticus* in Fig. 2). Its body has a build which is shorter and relatively wider than in *Rallus aquaticus*. In relation to the size of the skull, the bill is slightly shorter than in *Rallus aquaticus*.

The available sternum of *Rallus* n.sp. is in a fragmentary state, but on the basis of the placement of the insertion of the trabecula lateralis in the corpus sterni, it is slightly shorter and wider than in *Rallus aquaticus*. Its carina is reduced, since the carina edge goes up following a smaller angle with the basis of the sternum, a good indicator for a lower carina. The carina reduction seems not achieve the degree recorded in the Bermudan species *Rallus ibycus* and *Rallus recessus*, the only other described insular species of the genus in the Northern Hemisphere (Olson & Wingate, 2000, 2001). Nevertheless, it seems to be indicative for a smaller size of the musculus supracoracoideus and musculus pectoralis, two muscles involved in the fight. All the wing bones are reduced, specially the carpometacarpus.

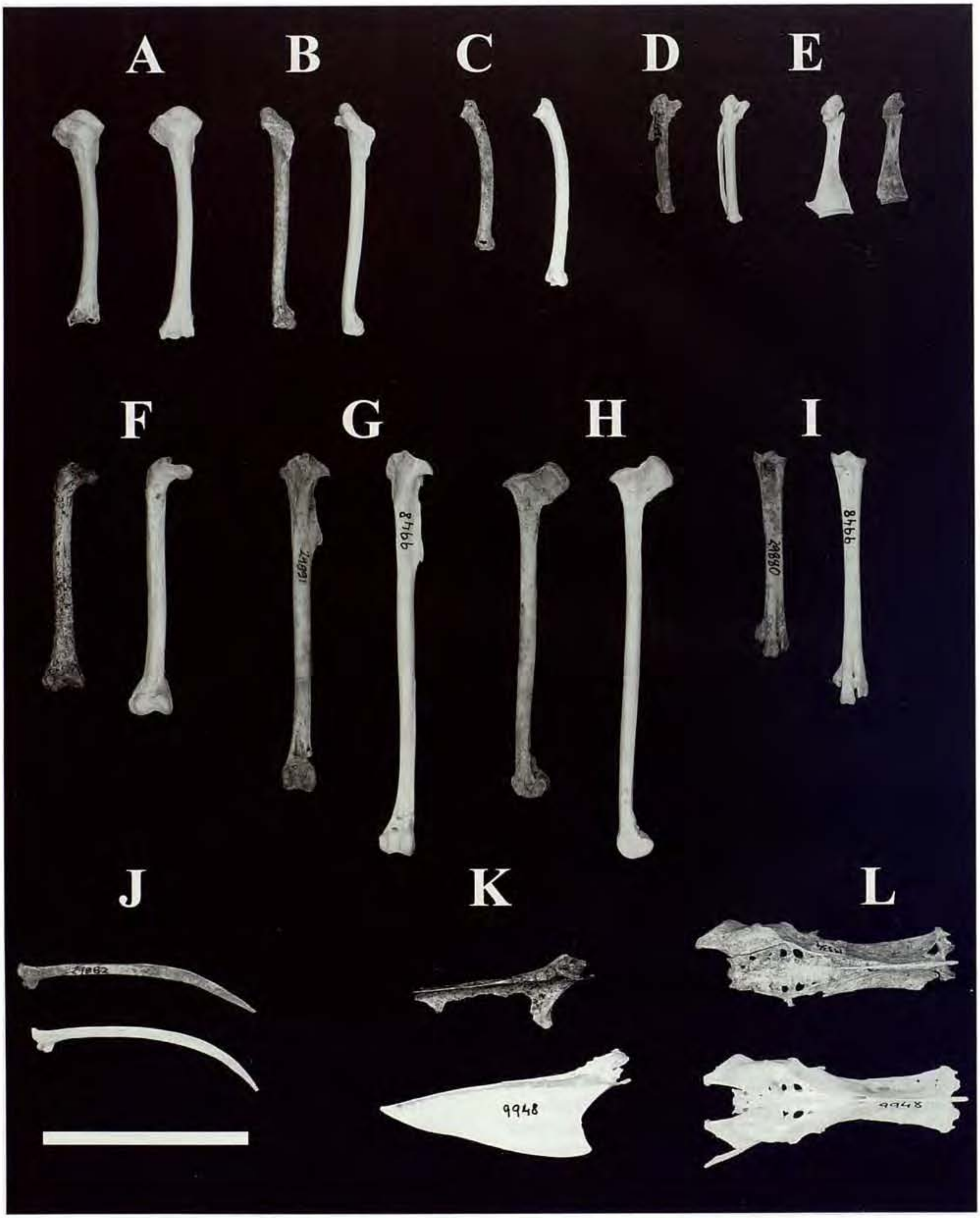


Fig. 2. Long bones of *Rallus* n.sp. in comparison with bones of *Rallus aquaticus* (MNIB 9948). A: Right humerus (MNIB 28624) in caudal view; B: Right humerus (MNIB 28624) in lateral view; C: Ulna MNIB 29870; D: Left carpometacarpus (MNIB 32496) in ventral view; E: Left coracoid (MNIB 29680) in caudal view; F: Left femur (MNIB 19818) in caudal view; G: Left tibiotarsus MNIB 29891) in cranial view; H: Left tibiotarsus (MNIB 29891) in lateral view; I: Left tarsometatarsus (holotype, MNIB 29880) in cranial view; J: Scapula (MNIB 29882) in ventromedial view; K: Sternum (MNIB 29881) in lateral view; L: Pelvis (MNIB 19334) in dorsal view. Scale 2 cm.

Fig. 2. Ossos llargs de Rallus *n.sp. en comparació amb ossos de* Rallus aquaticus *(MNIB 9948). A: Húmer dret (MNIB 28624) en norma caudal; B: Humer dret (MNIB 28624) en norma lateral; C: Ulna MNIB 29870; D: Carpometacarp esquerre (MNIB 32496) en norma ventral; E: Coracoid esquerre (MNIB 29680) en norma caudal; F: Fèmur esquerre (MNIB 19818) en norma caudal; G: Tibiotars esquerre (MNIB 29891) en norma cranial; H: Tibiotars esquerre (MNIB 29891) en norma lateral; I: Tarsometatars esquerre (MNIB 29880) en norma cranial; J: Escàpula (MNIB 29882) en norma ventromedial; K: Esternó (MNIB 29881) en norma lateral; L: Pelvis (MNIB 19334) en norma dorsal. Escala, 2 cm.*

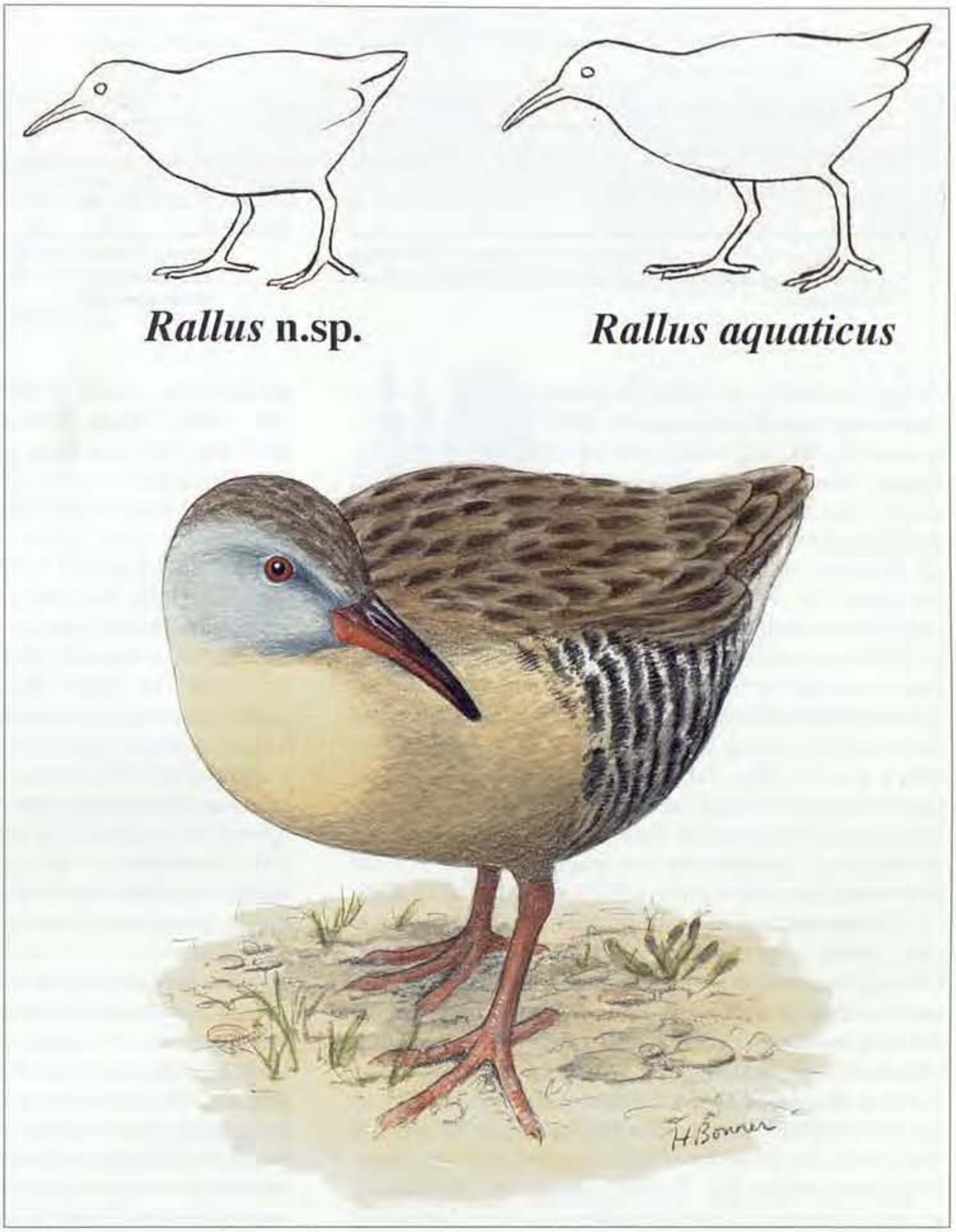


Fig. 3. An artistic reconstruction of *Rallus* n.sp. Author: Aina Bonner (Boston/Palma de Mallorca).

Fig. 3. Reconstrucció artística de Rallus *n.sp. Dibuix Aina Bonner (Palma de Mallorca/Boston).*

The two available pelvis are relatively robust, slightly wider and longer than in *Rallus aquaticus*. The hindlimb elements, specially the distal ones, are shorter and more robust.

Measurements of the long bones of *Rallus* n.sp. are presented in Table 1. A statistical comparison (ANCOVA) between the long bones of *Rallus* n.sp. and *R. aquaticus* using the General Linear Model (GLM) of the SYSTAT v.10 package has been performed. The total length and the shaft width have been used to characterise each long bone. Previously to the covariance analysis, the regression lines between the two measurements have been examined within each species and they were found significantly correlated. Independently of size, for any analysed length value, *Rallus* n.sp. shows proportionally higher values of shaft width than *Rallus aquaticus*. A non-isometrical reduction of the bones of *Rallus* n.sp. in comparison to those of *R. aquaticus* is clearly detected. This is due to a larger degree of shortening than of narrowing of the long bones. The shortening is larger at the distal bones, and more reduced at the proximal ones. As a mean, the humerus length reduction is about 9%, the ulna shortening is about 14% and the carpometacarpus shortening achieves about 17%. In the hindlimb, the femora length reduction is about 10%, the tibiotarsus shortening is about 15% while the tarsometatarsus shortening achieves about 17%. All the length measurements present significant differences ($p < 0.05$) between both species. The tarsometatarsus represents the only long bone displaying an actually wider shaft in *Rallus* n.sp. in comparison to *R. aquaticus*. The stouter configuration of the tarsometatarsus together with its highest displayed shortening gives to this bone the most peculiar shape. An artistic reconstruction of the animal is presented in Fig. 3. Although body proportions are accurately presented, the coloration is a subjective approach based on extant relatives.

The new rail species spread over the Late Pleistoce-

	Mean	xmin	xmax	n	sd
Humerus length	41.61	35.42	45.41	14	2.849
Carpometacarpus length	26.31	26.05	26.51	6	0.174
Femur Length	45.85			1	
Tarsometatarsus length	37.43	35.94	38.75	8	0.859

Table 2. Lengths (in mm) of selected skeletal elements of *Crex crex* from the Upper Pleistocene and Holocene of Eivissa . Mean, range (max and min), sample size (n) and standard deviation (sd) are indicated.

Taula 2. *Llargàries (en mm) d'elements esquelètics seleccionats de* Crex crex *del Pleistocè superior i Holocè d'Eivissa. S'indiquen la mitjana, l'espectre de mides (màxima i mínima), la mida de la mostra i la desviació típica.*

ne and the Holocene. A distal fragment of a tibiotarsus of *Rallus* n.sp. was directly dated by AMS C14 (MNIB 19979, square D4, UtC 6222: 6130 ± 80 BP, 5300-4840 calBC 2σ; Fig. 4). The lowermost level (square A3, level 7) from where *Rallus* n.sp. bones has been obtained, furnished the dating UtC-6674: 23030±150 BP; 21400-20750 cal BC 2σ. The level immediately above this (level 6), furnished the dating UtC-6673: 16170±90 BP; 18000-16700 cal BC 2σ. All these datings were performed on bone collagen, and all the analytical steps went correctly. Given than the levels were defined as constituted by successive sublevels, and than no indication to what sublevel belongs the dated samples, these datings only allow us to document with a $p > 95\%$ that the species was living in Eivissa at least between 5300 and 16700 calBC. Although this is the isotopically documented known age range, there are stratigraphical evidence of later materials, and no doubt exists about its earlier presence.

The assessment of relationships of the new species is clear. *Rallus* n.sp. is a close relative to *Rallus aquaticus*, the only species of the genus currently present in the western Palaearctic region. Both species share not only the long and slender bill, but also a large number of other characteristics. Actually, they differ only in the characters that can be related to a reduction of the flight ability, to the size of hindlimb bones and to the proportions of the legs. Given the presence of *Rallus aquaticus* in the European fossil record (e.g., Tyrberg, 1998), and the existing shared characters, it is reasonable to assume that *Rallus n.sp.* is an insular derivative from *Rallus aquaticus*. No comparison has been made with the sub-Saharan species *Rallus caerulescens* and the Malagasian species *Rallus madagascarensis*, the only other two species of *Rallus* from the Old World, but according to the available external measurements both are larger than *R. aquaticus* (Taylor, 1996). No direct relationships with these two species are expected.

The studied sample of *Rallus aquaticus* reasonably includes the variation range of the species. No differences between the recent insular sample of Mallorca and the mainland specimens have been detected. Although a study of the variation of this species along all its distribution range is not available, no great differences are expected between the different populations of this species. The four recognized subspecies of *R. aquaticus* are separated on plumage (Taylor, 1996), and no size differences between them have been ever quoted.

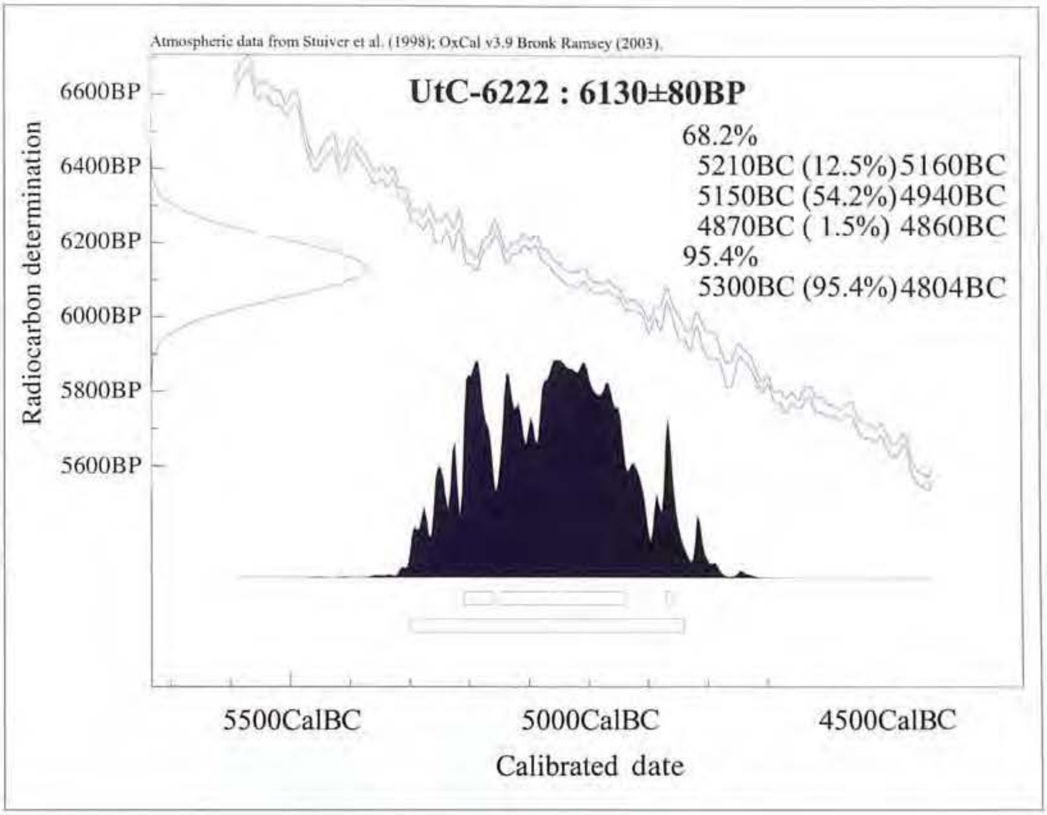
No data exists about the timing of the divergence between *Rallus* n.sp. and its assumed ancestor, *R. aquaticus*. The palaeontological record from Eivissa is discontinuous (e.g., Agustí & Moyà Solà, 1990; Alcover *et al.*, 1981, 1994). Some Pliocene/Lower Pleistocene (sensu latu) deposits have been recorded (e.g., Cova de ca na Reia, Pedrera de can Besora, Cala Salada). They delivered an insular fauna containing rodents (Alcover & Agustí 1985; Alcover *et al.*, 2000a, 2000b), a giant tortoise (Bour 1985; Gàsser & Ferrer, 1997; Filella *et al.*, 1999), a lizard (Kotsakis 1981), bats and birds (Alcover 1989), as well as a land molluscan fauna including between 17 and 21 taxa (Gasull & Alcover, 1982; Paul, 1982 1984; Paul & Altaba, 1992). The Upper Pleistocene and Holocene fauna lacks of terrestrial mammals, tortoises and contains only 6 land molluscs. Nevertheless, this fauna contains huge quantities of birds (Florit *et al.*, 1989). Between the later fauna and the former one it is a fossiliferous hiatus that spread over hundreds of thousands years (Alcover *et al.*, 1994). Probably the divergence of an insular species of *Rallus* started in an indeterminate time within this hiatus. A postglacial divergence cannot definitively be excluded.

The general body shape of *Rallus* n.sp. differs from that of *Rallus aquaticus* in the same way, but in an smaller degree, that *R. recessus* differs from *Rallus elegans*. Its body was slightly wider than that of *R. aquaticus*. The shape of the tarsometatarsus suggests a proportionally heavy body. In life, *Rallus* n.sp. should have had a plumper body, in spite of the sternum carina reduction. Its hindlimbs were shorter and more robust, and its wings were relatively shorter. Such combination of characters suggests a more terrestrial life-style for *Rallus* n.sp., including a reduced flight ability, although there is no evidence for complete flightlessness.

The species bred in Eivissa, as can be deduced from the presence of several juvenile bones in the fossiliferous record (e.g., humeri MNIB 19183, 19487, 23303, 28626, 29703, sinsacrum MNIB 29677, tibiotarsi MNIB 29468, 29859). Although *Rallus aquaticus*, its presumably ancestor, is partially migratory, a migratory condition for *Rallus* n.sp. can be ruled out on the basis of its assumed reduced flight ability, and we believe that *Rallus* n.sp. lived exclusively in the Pityusic Islands. Consequently, its distribution range must to have been small, and it probably consisted in some patches of suitable habitats in the Pityusics. Although its ecology is widely unknown, its reduced potential distribution area and the size of the obtained sample (161 identified bones within an estimation of >120.000 bird bones obtained in Es Pouàs) suggest that the Pityusics actually supported a small population size for *Rallus* n.sp.

Fig. 4. Corba de calibratge de la datació UtC-6222, que documenta la presència més recent coneguda de *Rallus* n.sp. a Eivissa.

Fig. 4. Calibration curve for the UtC-6222, which records the most recent available evidence for Rallus *n.sp. on Eivissa.*



Rallus n.sp. represents the first endemic species from the Pityusic islands that became extinct in recent times. The more recent evidence for its presence post-dates, with a p > 95 %, 5300 cal BC. The evidence of human presence on the island pre-dates 1880 cal BC, with a p > 95%. The close timing of the human arrival into the Pityusics (Alcover *et al.*, 2001) as well as the proneness of the insular rail species to became extinct after the human arrival suggests strongly that its disappearance can be related to the first human arrival. Its reduced flight ability and its presumed small population size probably strongly influenced on its extinction proccess.

Finally, the third species of rail present in the Pityusic fossil record is *Porzana porzana*. The fossil record consists exclusively in seven bones: tree humeri, three carpometacarpi and one tarsometatarsus. Their morphology and size is similar to that of the extant specimens.

CONCLUSION

The fossil record of rails from the Balearic Islands is scarce. The fossil rail fauna is related with the extant one, and have a clear Mediterranean character. The finding of a new species of rail recently extinct in Eivissa, derived from *Rallus aquaticus*, emerges as a new singularity of the single Mediterranean insular fauna without terrestrial mammals. The extinction of *Rallus* n.sp. is the sole recent documented Holocene bird extinction at the Balearics.

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03

EVOLUTIONARY TRENDS IN DENTAL MORPHOLOGY OF THE GENUS *PROLAGUS* (OCHOTONIDAE, LAGOMORPHA) IN THE MEDITERRANEAN ISLANDS

Chiara ANGELONE

ANGELONE, C. 2005. Evolutionary trends in dental morphology of the genus *Prolagus* (Ochotonidae, Lagomorpha) in the Mediterranean islands. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 17-26.

Resum

Igual que altres taxa de vertebrats, el gènere *Prolagus* va sofrir modificacions morfo-funcionals importants als ambients insulars mediterranis. El més evident és un increment al·lomètric de la mida general, seguit per altres canvis notables a nivell dentari: increment de la hipsodòncia i del nivell de complexitat de plegament de l'esmalt, i modificacions de les proporcions de diversos trets dentaris. Aquests canvis peculiars es podrien explicar com a adaptacions paral·leles a ambients oberts secs, amb una vegetació molt dura i amb pressions de depredació baixes. Esdevenen a totes les espècies endèmiques de *Prolagus* diferenciades a ambients insulars mediterranis, fins i tot encara que no tinguin un ancestre directe comú. Algunes formes europees continentals poden mostrar algunes de les característiques esmentades (per exemple, només gegantisme o només presència d'esmalt dentari molt plegat) degut a adaptacions locals alimentàries o ambientals. Només la presència conjunta dels trets dalt esmentats identifica les espècies de *Prolagus* insulars.

Paraules clau: *Prolagus*, insularitat, endemisme, adaptacions ambientals/alimentàries, illes mediterrànies.

Abstract

As other vertebrate *taxa*, genus *Prolagus* undergoes major morpho-dimensional modifications in Mediterranean insular environments. The most evident is an allometric general size increase, followed by other remarkable changes at the dental level: increase of hypsodonty and of enamel folding complexity, modification of relative proportions of some dental features. Such peculiar changes could be explained by a parallel adaptation to dry, open environments with harder vegetation and by a minor predatory pressure. They occur in all the *Prolagus* endemic species differentiated in insular Mediterranean environments, even if they do not share a common direct ancestor. Some continental European forms, actually, can show some of the listed features (e.g.: giantism only, or highly folded dental enamel only) due to particular dietary/environmental local adaptations. Only the coincident occurrence of the above mentioned characters identifies an insular endemic *Prolagus* species.

Key Words: *Prolagus*, insularity, endemism, environmental/dietary adaptations, Mediterranean islands.

INTRODUCTION

Lagomorphs, and especially the genus *Prolagus* among them, are quite well represented in Mediterranean insular faunal assemblages. Nevertheless, they were object of very few specific works (Major, 1882; Tobien, 1935; López Martínez & Thaler, 1975) and except for López Martínez (1978) no modelization and/or explanation for the morpho-dimensional changes they undergo in insular domains does exist so far.

Lagomorph fossil findings are usually included in micromammalian lists, even if their size, habits and escaping strategies differ quite markedly from that of the bulk of micromammals, but they can not be considered as macromammals either. So, verifying which pattern of morpho-dimensional modifications (the macromammalian one, the micromammalian one, or a patchwork of the two) will a lagomorph follow as a response to the permanence in an insular environment is the main aim of this paper.

The genus *Prolagus* is one of the three representatives of the family Ochotonidae found in insular environments of the Mediterranean area up to now. The others are *Gymnesicolagus gelaberti* Mein & Adrover (Santa Margalida, Mallorca, Middle Miocene; Mein & Adrover, 1982) and *Paludotona etruria* Dawson (Baccinello V1 - and two related forms both named *Paludotona* aff. *P. etruria* in levels V0 and V2 -, Western central Italy, MN11-basal MN13; Dawson, 1959; Kotsakis *et al.*, 1997). The following endemic insular *Prolagus* species have been differentiated in Mediterranean insular domains (Fig. 1): *Prolagus apricenicus* Mazza and *P. imperialis* Mazza from the Gargano Peninsula (South-Eastern Italy, MN13/14;

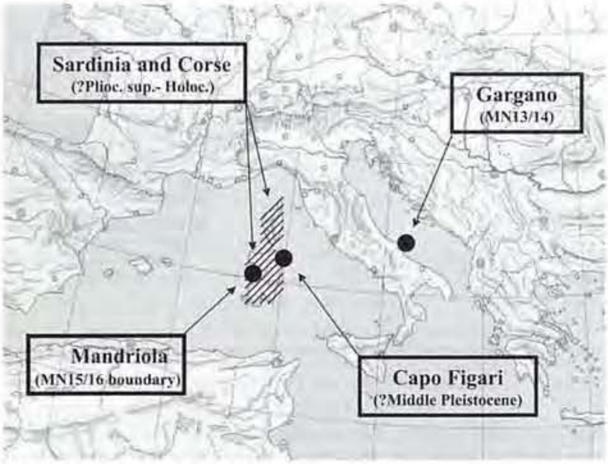


Fig. 1. Geographical localization of endemic insular *Prolagus*-bearing fossiliferous sites in the Mediterranean area.

***Fig. 1.** Localització geogràfica de les localitats que han lliurat* Prolagus *endèmics insulars a l'àrea mediterrània.*

Mazza, 1986a, 1986b, 1987), a probable new species, *Prolagus* aff. *P. depereti* from Mandriola (Western Sardinia, MN15/MN16 boundary; Angelone & Kotsakis, 2000), *P. figaro* Lopez Martinez from Capo Figari (Eastern Sardinia, ?Early/Middle Pleistocene; López Martínez & Thaler, 1975) and *P. sardus* (Wagner) found in several fossiliferous sites in Sardinia and Corsica (Pleistocene-Recent). These species show marked morphological and dimensional modifications due to the permanence in insular environments.

Such morpho-dimensional modifications clearly lack in *Prolagus* species found in present-day insular environments that in the past were connected to mainland, as testified by the presence of continental, well-balanced, fossil faunal assemblages with non-endemic faunal elements: *Prolagus* sp. from Thymiana (Chios, Greece, MN8; Tobien, 1968), *Prolagus* sp. from N Katheni (Evia, Greece, ?MN10; Katsikatsos *et al.*, 1981), *P.* cf. *P. michauxi* Lopez Martinez from Aghios Ioannis (Karpathos, Greece, MN14; Daams & Weerd, 1980), *Prolagus* cf. *P. calpensis* Major from Medes Islands (Spain, Pleistocene; López Martínez, 1989), *P. "corsicanus"* Giebel from Ratonneau Island (France, Pleistocene; Piveteau, 1961). For this reason those species will not be taken into consideration here.

Moreover, as only the morpho-dimensional aspects of insular endemic *Prolagus* species (that, as will be demonstrated, are shared by <u>all</u> the considered species) are discussed here, open systematic discussion, as the presence in the Mandriola fossiliferous site of two distinct and may be heterochronical *Prolagus* species, or the existence of intermediate morphotypes between *P. sardus* and *P. figaro* in the Monte Tuttavista (Orosei, Eastern Sardinia, Italy; ?Late Pliocene-Late Pleistocene) fissure fillings that cast a doubt on the actual separation between the two species, shall be avoided here.

MATERIALS AND METHODS

Fossil remains of *Prolagus*, as it occurs for micromammals in general, mainly consist in dental and secondarily in maxillary and mandibular elements; cranial and postcranial remains are quite rare and/or ill-pre-

Species	D_1 (anteroconid)	D_2 (posterior complex)	D (D_1+D_2)
Prolagus oeningensis	1.15	5.56	6.71
Prolagus major	1.17	5.28	6.45
Ptychoprolagus forsthartensis	1.22	5.84	7.06
Prolagus tobieni	1.35	3.92	5.27
Prolagus michauxi	1.11	4.50	5.61
Prolagus depereti	1.30	5.86	7.16
Prolagus cf. *P. calpensis* (Moreda)	1.16	4.82	5.98
Prolagus cf. *P. calpensis* (I. Medas)	1.52	5.57	7.09
Prolagus aff. *P. depereti*	1.52	-	-
Prolagus sardus	1.42	4.93	6.35
Prolagus cf. *P. sardus* (Orosei)	1.37	5.22	6.59
Prolagus figaro	1.51	6.20	7.71
Prolagus apricenicus	1.77	6.55	8.32
Prolagus imperialis	2.23	7.61	9.84

Table 1. Density indexes ($Dn=L/4\pi F$, where L is enamel length, F the area inclosed by the enamel including enamel thickness+dentine; Schmidt-Kittler, 1986) calculated on different elements of various *Prolagus* species P_3 occlusal surface. D_1: anteroconid; D_2: extant part of P_3 enamel portion; D: D_1 + D_2.

***Taula 1.** Índex de densitat ($Dn=L/4\pi F$; on L és la llargària de l'esmalt, F l'àrea inclosa per l'esmalt, icomptand el gruix de l'esmalt + la dentina; Schmidt-Kittler, 1986) calculats sobre diferents elements de la superficie oclusiva del P_3 de diverses espècies de* Prolagus. *D_1: anterocònid; D_2: part existent de la porció d'esmalt del P_3 ; D: D_1 + D_2.*

served. In order to make the results of this paper applicable in the majority of the cases, comparisons between continental and insular endemic *Prolagus* species have been made on the basis of dental findings.

P_3 is still now considered to be the most significant dental element for systematics at the species level for the genus *Prolagus*. For this reason most of the morpho-dimensional analyses carried out to individuate advanced characters shared by insular endemic *Prolagus* species have been made on P_3 (see López Martínez, 1989, for nomenclature).

It has been possible to recover fossil material of each of the insular endemic above mentioned *Prolagus* species that has been compared morphologically and dimensionally with European continental species and populations.

RESULTS

Dental modifications observed in insular endemic *Prolagus* species of the Mediterranean area are the following:

Size increase

The first, most evident feature that characterizes endemic insular *Prolagus* species, if compared with European continental ones, is size increase (Fig. 2). Size increase of mandibles, cranium and postcranium is surely allometric, but it deserves a more complete and complex discussion and is for the moment excluded: actually, the extreme scarcity of available postcranial elements in almost all European fossil sites bearing *Prolagus* makes osteological comparisons problematic.

Dental size increase, in comparison with coeval European continental species, is rather considerable in *P. apricenicus* and *P. imperialis* from the Gargano fossil archipelago, not so striking in Corso-Sardinian species. Actually, in Messinian times, a very sharp shift occurs in size and dental morphology of continental Europe *Prolagus*: primitive, small *Prolagus* species disappear to be replaced almost everywhere by *P. michauxi*. This species is quite big-sized, and in its dental morphology attains many features till then shown by Gargano insular endemic *Prolagus* species only, as a triangular, lingually-shifted anteroconid on P_3 and the presence of a mesial hyperlophe on P^2. As a matter of fact, a kind of mesial hyperlophe on P^2 has been observed (in species more

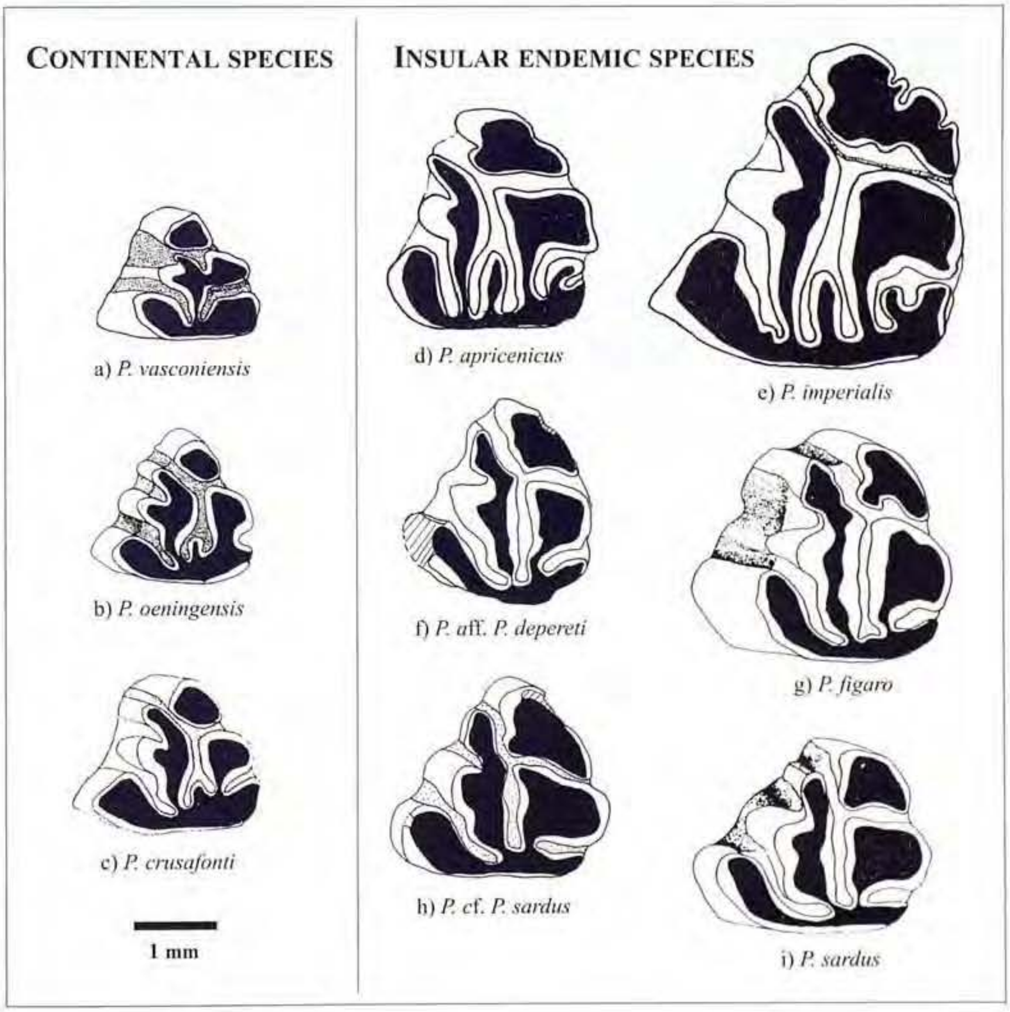
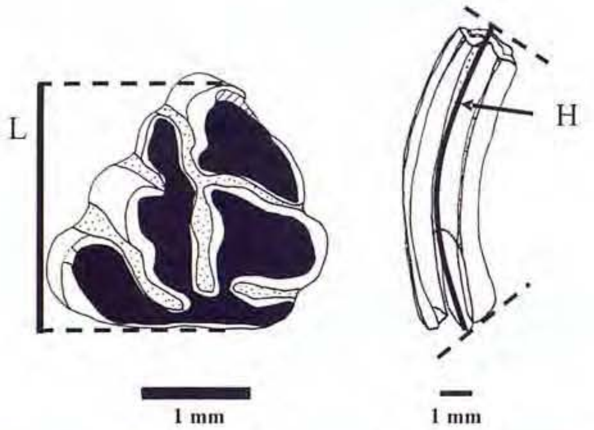


Fig. 2. Comparison of P_3 size between some continental non-endemic species and insular endemic species of genus *Prolagus*. Drawings from López Martínez & Thaler (1975), Mazza (1987), López Martínez (1989) and from unpublished data of the author.

***Fig. 2.** Comparació de la mida del P_3 entre algunes espècies no endèmiques continentals i espècies endèmiques insulars del gènere* Prolagus. *Dibuixos a partir de López Martínez & Thaler (1975), Mazza (1987), López Martínez (1989) i de dades no publicades de l'autora.*

ancient than *P. michauxi*) only in two specimens of a very large population of advanced *P. crusafonti* (López Martínez, 1989); it could be also observed in *Ptychoprolagus forsthartensis* Tobien (that in spite of the generic differentiation, due to its very peculiar appearance, can be legitimately considered as a *Prolagus* species), whose extremely limited distribution in time and space (Forsthart, Southern Germany, Middle Miocene; Tobien, 1975) and whose singular occlusal surface features, attest to a continental endemic condition and to an adaptation to particular environmental conditions (Fig. 4).



Species	L (mm)	H (mm)	I=H/L
Prolagus schnaitheimensis	1.80	6.35	3.53
Prolagus tobieni	1.46	6.30	4.31
Prolagus vasconiensis	1.47	6.72	4.57
Prolagus ibericus	1.38	6.38	4.62
Prolagus oeningensis	1.51	7.09	4.69
Prolagus cf. *P. michauxi*	1.85	8.38	4.53
Prolagus aff. *P. depereti*	2.42	-	-
Prolagus apricenicus	2.36	11.17	4.73
Prolagus imperialis	2.99	14.43	4.83
Prolagus figaro	2.05	9.30	4.53
Prolagus cf. *P. sardus*	2.07	13.10	6.33

Fig. 3. Definition of hypsodonty ratio I = H/L. H is absolute hypsodonty measured in lateral-labial sight from the anteroconid to the lowest part of the tooth (more or less along the protoflexid or protoconid); if the available dental elements are broken in their central lower part, H can be estimated as shown. L is the lenght of the tooth measured on its occlusal part. I ratio, here illustrated for P_3, can be calculated in the same way on other teeth.
In the table: Comparison of P_3 occlusal lenght (L) and absolute hypsodonty values (H) of some selected european continental and endemic insular *Prolagus* specimens. Hypsodonty degree (I) is the result of the H/L ratio.

Fig. 3. *Definició de l'index d'hipsodòncia I = H/L. H és la hipsodòncia absoluta, mesurada en norma lateral – labial, des de l'anterocònid a la part més baixa de la dent (més o menys, al llarg del protoflèxid o protocònid); si els elements dentaris disponibles es troben trencats a la seva part central, es pot estimar H així com es mostra. L és la llargària de la dent mesurada a la seva part oclusiva. L'índex I, que aquí s'il·lustra per al* P_3*, es pot calcular d'una manera similar per a les altres dents.*
A la taula: *comparació de la llargària oclusiva del* P_3 *(L) i els valors d'hipsodòncia absoluta (H) d'alguns espècimens seleccionats de* Prolagus *continentals i endèmics insulars.*

In P_3, the dental element in which specific differences can be more easily recognized, the percentage of lenght (L) increase measured on occlusal surface can reach values higher than 100% (*P. praevasconiensis* Ringeade / *P. imperialis* Mazza). Width is a character that can vary in a remarkable way through ontogeny, so is less fiable for size increase estimations.

The percentage of size increase between continental ancestor and insular endemic descendant is very variable. A size increase of about 50-60% and 100% can be observed in P_3 between *P. oeningensis* and its endemic descendants *P. apricenicus* and *P. imperialis* respectively (Fig. 2); if we consider *P. figaro* as a descendant of *P. depereti*, the size increase of the former is of about 12% only. The same percentage of size increase (about 11%) has been calculated between *P. sardus* and its supposed continental ancestor *P. calpensis*. If size increase percentage calculation is made using *P. michauxi* as continental point of re-ference (actually both *P. depereti* and *P. calpensis* descend from *P. michauxi*), its value grows slightly.

Hypsodonty increase

Increase of absolute hypsodonty of insular endemic *Prolagus* is a natural consequence of the increase of overall size. The hypsodonty degree (I), here meaning the H/L ratio (Fig. 3), has been introduced to verify if hypsodonty increase is just a direct consequence of P_3 overall increase or if there is another component. In insular endemic *Prolagus* species the ratio I is higher (tab. 1), but is very variable and no clear hypsodonty increasing pattern can be deduced: to bigger occlusal surface size do not correspond biggest I ratios (Garganic *Prolagus*, the biggest insular endemic species, have the lowest I ratio).

This character should be further investigated and modelized, such as P_3 radius of curvature: in general, primitive *Prolagus*, such as *P. vasconiensis*, *P. schnaitheimensis*, *P. tobieni*, in most cases appear to be quite straight in lateral lingual or labial view (but they can appear bent on a lateral antero/posterior view), while even slightly more advanced forms (as *P. oeningensis*) or insular endemic *Prolagus* species appear to be curved in lateral lingual view.

Modification of dental occlusal surface

Major modifications of insular endemic *Prolagus* species dentition occur on P_3. Extant lower dental elements have a very conservative morphology. Upper molars do not show remarkable change either, if compared to those of continental non-endemic species. P^2 and P^3, that are in occlusion with P_3, appear to be bulky and massive, with a higher L/W ratio; moreover in P^2 can be observed some more complex modifications (Fig. 4), as the undulations in the lagicone and in the postcone and as the presence of a very developed mesial hyperlophe (also in the most ancient known insular endemic species, *P. apricenicus* an isolated precone is not a common feature). The connection precone-mesial hypercone (mesial hyperlophe) appears in continental Europe

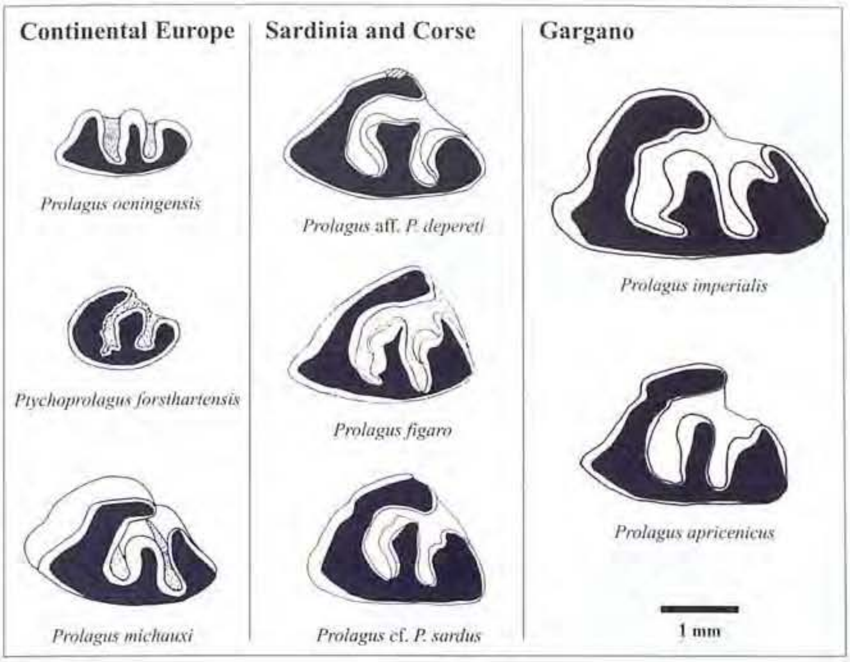


Fig. 4. Comparison of P^3 occlusal surface morphology. In insular endemic species the mesial hyperlophe is present and enamel on lagicone and postcone may be folded. In primitive *Prolagus* species of continental Europe, as *P. oeningensis*, *P. crusafonti*, etc., such features are not present: they appear in latest Neogene with *P. michauxi* and its descendants (*P. calpensis*, *P. depereti*, etc.). Drawings from López Martínez & Thaler (1975), Ziegler & Fahlbusch (1986), Mazza (1987), López Martínez (1989) and from unpublished data of the author.

Fig. 4. Comparació de la morfologia de la superfície oclusiva del P^3. A les espècies endèmiques insulars l'hiperlof mesial és present, i l'esmalt del lagiconus i postconus pot estar plegat. A les espècies primitives de Prolagus *d'Europa continental, tals com* P. oeningensis, P. crusafonti, *etc., no es troben aquests trets: apareixen al Neògen més tardà amb* P. michauxi *i els seus descendents (*P. calpensis, P. depereti, *etc.). Dibuixos a partir de López Martínez & Thaler (1975), Ziegler & Fahlbusch (1986), Mazza (1987), López Martínez (1989) i de dades no publicades de l'autora.*

with *P. michauxi* (late MN12-MN16). Corso-Sardinian *Prolagus* species, as advanced continental ones derived from *P. michauxi*, still retain this feature of their ancestor, while in the Gargano this character appears independently and is due to a convergence phenomenon.

P_3 modifications (Fig. 5) are more complex and deserve a more ample discussion. As already noticed by López Martínez (1978), P_3 anteroconids of insular endemic species appear to have a peculiar indented contour; moreover they become larger than in pre-Pliocene continental species, triangular, elongated and shifted towards the lingual side. Enamel folding complexity increases all over P_3 occlusal surface, even in different degrees in each species. The metaconids of insular endemic *Prolagus* species become larger and quadrangular in shape. The posterior portion of P_3 (entoconid + basal part of hypoconid), on the contrary, becomes much thinner. In general, overall shape of P_3 changes, assuming a quadrangular instead of an approximately triangular shape, due to the enlargement of the anterior side.

A tentative to quantitatively esteem and compare P_3 enamel folding degree has been made (tab. 1) by calculating two density indexes (Schmidt-Kittler, 1986): D1, considering the anteroconid only, and D2, considering the extant part of the tooth. Such density indexes do not express any information about shape similarity, but only about how much the perimeter of the selected dental element increases with respect to its area. As in this case the perimeter represents enamel lenght and development, its increase with respect to enclosed area (here representing dentine+enamel thickness), expressed by D index, indicates how much grin-ding surface increases. Thus, D index values and variations may have a dietary/environmental meaning and may possibly give hints about environmental and climatic changes.

In general, in *Prolagus* species D1 slightly increases with time in continental species and is higher in insular endemic ones. In *P. tobieni* D1 values are rather high, out of the average of continental *Prolagus* species, due to its flattened anteroconid, but D2 value is quite low; anyway, their sum D (D1+D2) falls between the values shown by continental species. *P. tobieni* has a very primitive post-anteroconid structure, still showing a centrolophid instead of a centroflexid, as more advanced species do: maybe a differential enamel lenght increase localized in the anteroconid supplied to the need of a higher grinding surface, attained in continental species from *P. oeningensis* on with the developing of a centroflexid, the growth of the protoconulid and the appearance of structures as the crochet.

D2 (post-anteroconid density index) does not show an equal increase with time in continental European *Prolagus* species and it is evidently higher in *P. figaro*, *P. apricenicus*, *P. imperialis*, but not in *P. sardus* (unfortunately no data of *P.* aff. *P. depereti* are available).

It is worth to remark also a differential size increase of P_3 in comparison with the rest of the mandibular row. Mazza & Zafonte (1987) evidenced that in Garganic *Prolagus* species the highest muscle resultant during mastication is applied on P_3 that becomes the most important dental element for chewing. A difference in the dietary adaptation could have enhanced the stress on P_3: that could explain why it became more massive, increased its enamel folding complexity and underwent a further size increase in addition to an overall enlargement of the whole tooth row (Fig. 6).

Increased complexity of enamel folding noticed in insular endemic species is not a consequence of size increase, neither is in any way related to it. *Prolagus major* (late Early Miocene - early Middle Miocene), Calatayud-Teruel Basin, Spain; López Martínez, 1989), a giant European continental species, is comparable in size to insular species (Fig. 7), but shows no trace of enamel folding.

On the other hand, some continental European species show an increase of enamel folding complexity, but not a considerable size increase, such as the above

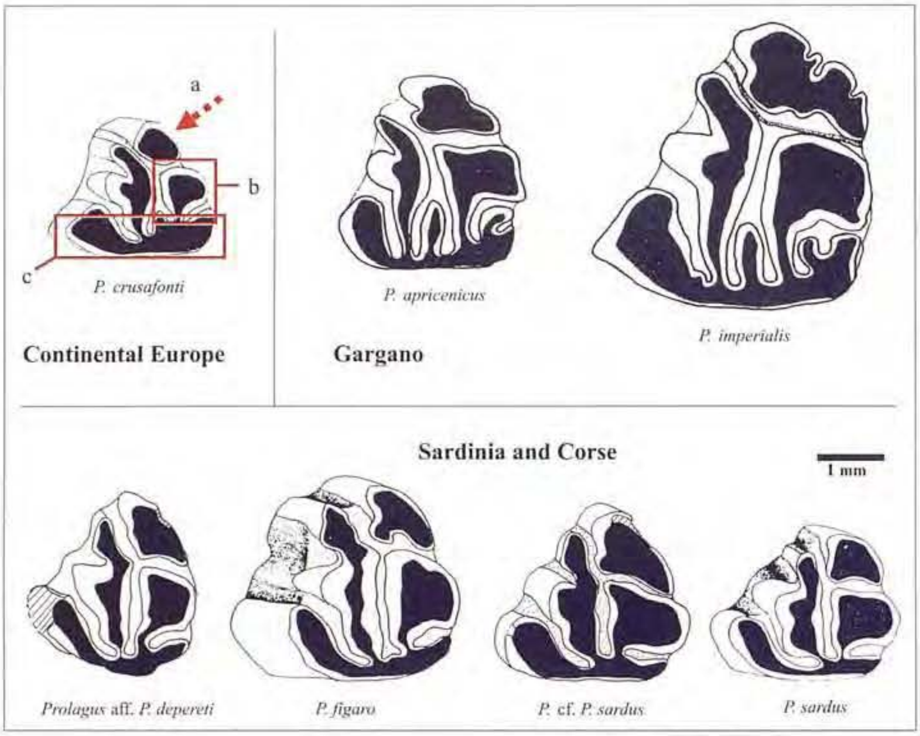


Fig. 5. Comparison of continental and insular endemic *Prolagus* P_3 occlusal surface morphology: a) anteroconid modifications (absent in continental species); b) metaconid shape and size (quadrangular and bigger in insular endemic species); c) size of the posterior part of the tooth (thinner in insular endemic species). Drawings from López Martínez & Thaler (1975), Mazza (1987), López Martínez (1989) and from unpublished data of the author).

Fig. 5. *Comparació de les espècies continentals i endèmiques insulars de* Prolagus. *Morfologia de la superfície oclusiva del* P_3*: a) modificacions de l'anterocònid (absents a les espècies continentals); b) forma i mida del metacònid (quadrangular i més gros a les espècies endèmiques insulars); c) mida de la part posterior de la dent (més robusta a les espècies endèmiques insulars). Dibuixos a partir de López Martinez & Thaler (1975), Mazza (1987), López Martínez (1989) i de dades no publicades de l'autora.*

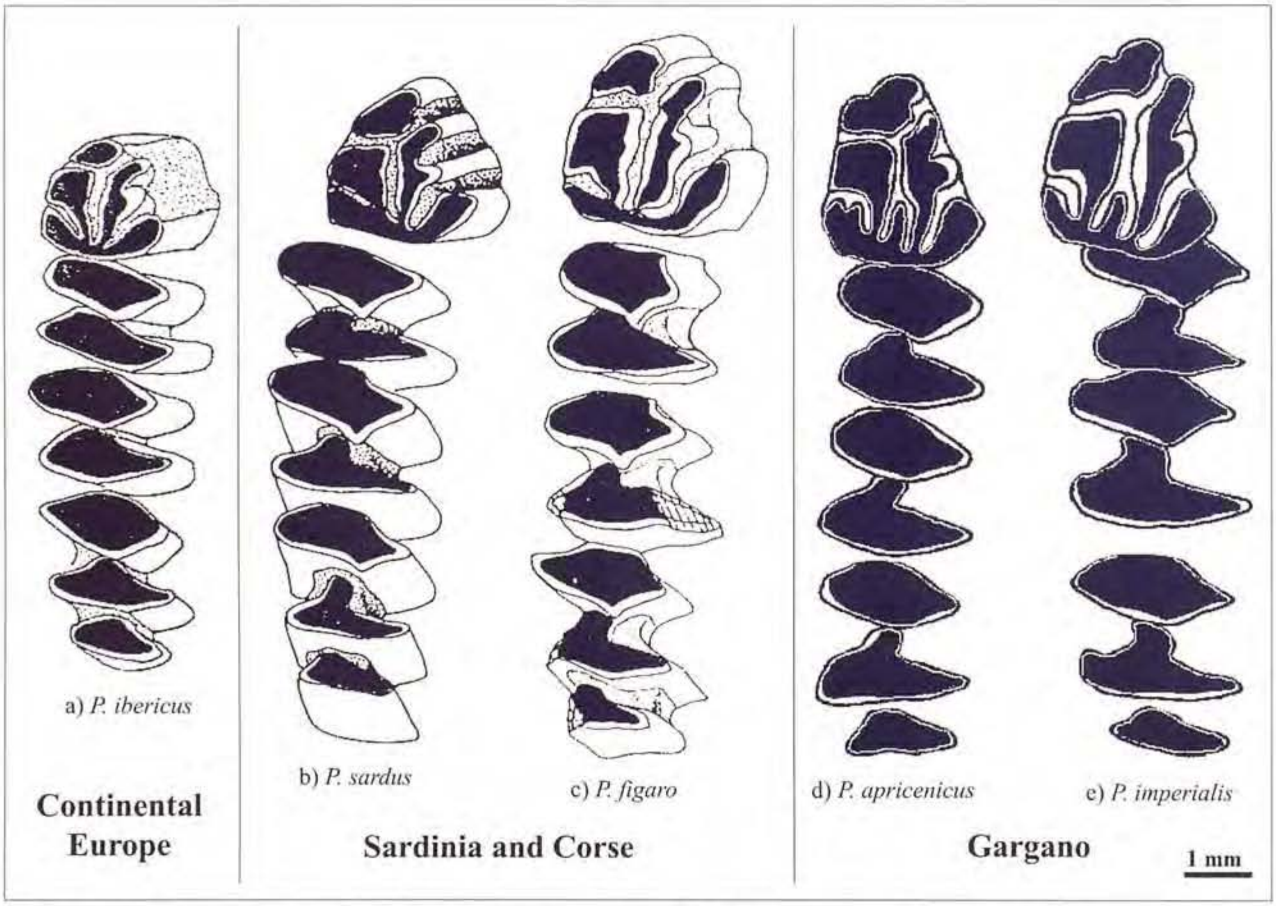


Fig. 6. Comparison of lower tooth rows of a non-endemic continental European species (a) and some endemic insular species. In insular endemic species the whole lower tooth row undergoes a slight overall size increase, while P_3 goes through a differencial, higher size increase, probable consequence of a change in mandibular mechanics. Drawings from López Martínez & Thaler (1975) and Mazza (1987).

Fig. 6. *Comparació de les sèries dentàries inferiors d'espècies europees continentals no endèmiques (a) i algunes espècies endèmiques insulars. A les espècies endèmiques insulars tota la sèrie dentària inferior està afectada per un lleuger increment de la mida promig, mentre que el* P_3 *suporta un major increment diferencial de mida, conseqüència probable d'un canvi als mecanismes mandibulars. Dibuixos a partir de López Martinez & Thaler (1975) i Mazza (1987).*

mentioned *Ptychoprolagus forsthartensis* and, in a lesser way, *Prolagus* cf. *P. calpensis* (Pliocene, Medes Islands, Spain; López Martínez, 1989). These species have a very limited geographical distribution, and this feature is probably due to particular environmental/dietary adaptations.

Therefore, only the contemporaneous occurrence of all the above listed characters individuates an insular endemic species.

Differentiation of *Prolagus* insular endemic species

In spite of all the common characters, it is possible to individuate some differences between the P_3 of endemic insular species, making possible the differentiation of two groups corresponding to Gargano species and to Corso-Sardinian ones (Fig. 8):

1 - in Gargano species, the anteroconid shows much more complex and marked indentations, and it is placed in a more "detached" position, giving to the tooth a more elongated, rectangular shape, while Corso-Sardinian forms have a more "compact", square appearance and a less elaborate anteroconid shape;

2 - in Corso-Sardinian species, the angle protoconid/protoconulid is wider (140-150 degrees against the 110-120 degrees of Gargano species),

3 - in Gargano species, enamel folding is more complex and occurs also in other points of the occlusal surface.

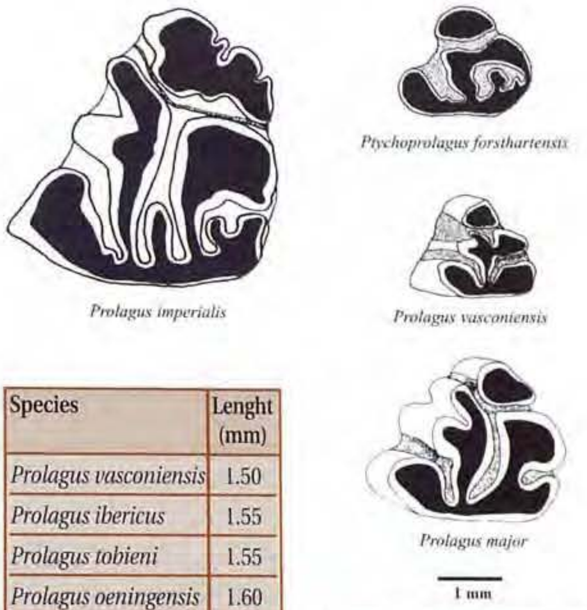
DISCUSSION

Micromammalian pattern of evolution on islands

Micromammalian pattern of evolution on islands has been modelized (Azzaroli, 1982; Mein, 1983; Agustí, 1986) with the individuation of two main phases: a first stage, in which species undergo quite instantaneous modifications taking place immediately after the colonization of the island, followed by a slow anagenetic phase. The first phase is so sharp that it is very unlikely that it can be documented by fossils (an exception is *Rhagapodemus azzarolii*, Mandriola, Western Sardinia, MN15/16 boundary; Angelone & Kotsakis, 2001).

Prolagus pattern of evolution on islands

Members of genus *Prolagus* that populated insular environments followed in general micromammalian pattern of modifications in similar conditions. Actually, even in the bradytelic genus *Prolagus*, size increase, direct consequence of the scarcity of terrestrial predators, is attained in a quite instantaneous way: the oldest findings of Gargano *Prolagus* species already show a very big size and consequently a higher absolute hypsodonty; *Prolagus* aff. *P. depereti* is morphologically less developed, but as big as its descendant *P. figaro*; most primitive *P. sardus* populations already attain big sizes also. Contrary to Western Mediterranean insular endemic glirids (Agustí, 1986), in insular endemic *Prolagus* species occlusal surface modifications appear even in the first phase of rapid evolution. As for hypsodonty



Species	Lenght (mm)
Prolagus vasconiensis	1.50
Prolagus ibericus	1.55
Prolagus tobieni	1.55
Prolagus oeningensis	1.60
Prolagus crusafonti	1.60
Ptychoprolagus forsthartensis	**1.70**
Prolagus vasc. fortis	1.81
Prolagus michauxi	1.85
Prolagus calpensis	1.97
Prolagus depereti	1.97
Prolagus major	**2.40**

Ptychoprolagus forsthartensis	1.70
Prolagus sardus	2.10
Prolagus aff. *P. depereti*	2.34*
Prolagus figaro	2.35
Prolagus major	**2.40**
Prolagus apricenicus	2.50
Prolagus imperialis	2.80

Fig. 7. P_3 size increase, hypsodonty increase and enamel folding should occur simultaneously (even if in a less or more marked way) to individuate an insular endemic *Prolagus* species. *P. major* (see text for details), a giant European continental species, is comparable in size to insular species, but shows no trace of enamel folding. On the other hand, in *Ptychoprolagus forsthartensis*, a high degree of enamel folding, but not an increase of the size (not so different from the primitive continental species *P. vasconiensis*) can be observed. Both size increase and enamel folding are evident on the occlusal surface of *P. imperialis*. Drawings from Ziegler & Fahlbusch (1986), Mazza (1987) and López Martínez (1989).

In the tables is reported P_3 average length in continental, non-endemic species (on the left) and insular endemic species (on the right). Length values of *Ptychoprolagus forsthartensis* and *P. major* are highlighted and reported in the right table too to better compare them with those of insular endemic species.

*Due to the scarcity of *Prolagus* aff. *P. depereti* dental elements, the reported length value is that of the figured specimen; the approximation is by defect as a consequence of its bad state of preservation.

Fig. 7. L'increment de la mida del P_3, l'increment de la hipsodòncia i del plegament de l'esmalt esdevenen simultàniament (tot i que en una forma més o menys marcada) a les espècies endèmiques insulars de Prolagus. P. major *(veure el text per detalls), una espècie europea continental gegant) és de mida comparable a les espècies insulars, però no mostra cap traça de plegament de l'esmalt. Per una altra banda, a* Ptychoprolagus forsthartensis, *hi ha un elevat grau de plegament de l'esmalt, però no es pot observar cap increment de la mida (no és gaire diferent de l'espècie continental primitiva* P. vasconiensis*). Tant l'increment de la mida com del grau de plegament de l'esmalt són evidents a la superfície oclusiva de* P. imperialis. *Dibuixos a partir de Ziegler & Fahlbusch (1986), Mazza (1987) and López Martínez (1989).*

A les taules es presenta la llargària promig del P_3 a espècies continentals no endèmiques (a l'esquerra) i espècies endèmiques insulars (a la dreta). Els valors de llargària de Ptychoprolagus forsthartensis *i* P. major *estan marcats i es registren a la taula dreta, per a que es puguin comparar millor amb els de les espècies insulars.*

**Degut a l'escassesa de materials dentaris de* Prolagus *aff.* P. depereti, *el valor de llargària presentat és el de l'espècimen il·lustrat; l'aproximació és per defecte, degut al mal estat de conservació.*

degree, it should decrease with the increasing complexity of occlusal surface, but data for "primitive" insular endemic species are not available.

A period of slow anagenesis following the first phase has been observed in Sardinia, where a cline of morphotypes in *P. sardus* populations have been individuated (Angelone *et al*, in prep.). A similar situation occurs in the Gargano archipelago: populations evolve increasing size and complexity even in a more clear and evident way than in *P. sardus*, but it is not clear if the appearance of *P. imperialis* is due to anagenesis or to archipelago effect (De Giuli *et al.*, 1986).

Evolutionary parallelism in dental morphology and size

In addition to size increase, the teeth of insular endemic micromammals show at least one of the following modifications:

1- molarization of premolars;

2- augmentation of the area of premolars (compared to extant elements of the tooth row);

3- appearance of additional crests or cusps;

4- increase of the enamel folding complexity;

5- absolute hypsodonty increase.

All of them represent different strategies directed to improve the efficiency of mastication, and they are a consequence of dietary and/or climatic adaptations (e.g.: herbivorous diet in glirids according to Mein, 1983; dry environments according to Agustí, 1986). Moreover, it is very likely that such modifications imply a change in the masticatory movements and consequently in the mandible mechanics.

Insular endemic *Prolagus* share three of the above listed feature (2, 4 and 5) with other micromammals that lived in Mediterranean insular environments. Such characters occur simultaneously, but not with the same evidence: for example, to a hypsodonty degree (I) increase usually does not correspond to an enamel folding complexity growth. It seems that to attain the purpose of improving mastication efficiency, one strategy prevails on the other rather than being combined: *P. imperialis*, for example, in which enamel folding complexity reaches its maximum degree, has a rather low hypsodonty degree (I) (tab. 1); in Sardinia and Corsica, the contrary happens for *P.* cf. *P. sardus* of Orosei fissure fillings, while *P. figaro*, showing a more complex enamel pattern, has a lower I value.

Environmental setting

Probably a change in dietary habits due to environmental/climatic changes and coping with harder vegetables can explain the above listed dental modifications. But that would imply that a same dry, open environmental setting was common to Western Mediterranean islands from Late Messinian on.

However, it should be emphasized that even in continental Europe, from Late Miocene on, a sudden change occurs in *Prolagus* size and morphology. As evidenced above (section: Results - Size increase) the appearance of *P. michauxi* represents a turning point in continental evolution of *Prolagus*, as this species starts acquiring some of the morpho-dimensional features till then exclusive of insular endemic species (even if never all together and in a lesser degree). The only plausible reason that justifies such an enormous morpho-dimensional shift is a climatic/environmental change: if so, on the analogy of insular endemic *Prolagus*, we should suppose an increase of aridity and of open spaces in continental Europe also starting from Late Miocene on. Further, advanced and exclusive modifications observed in *Prolagus* insular endemic species are due to the concurrent influence of climatic changes and insularity conditions.

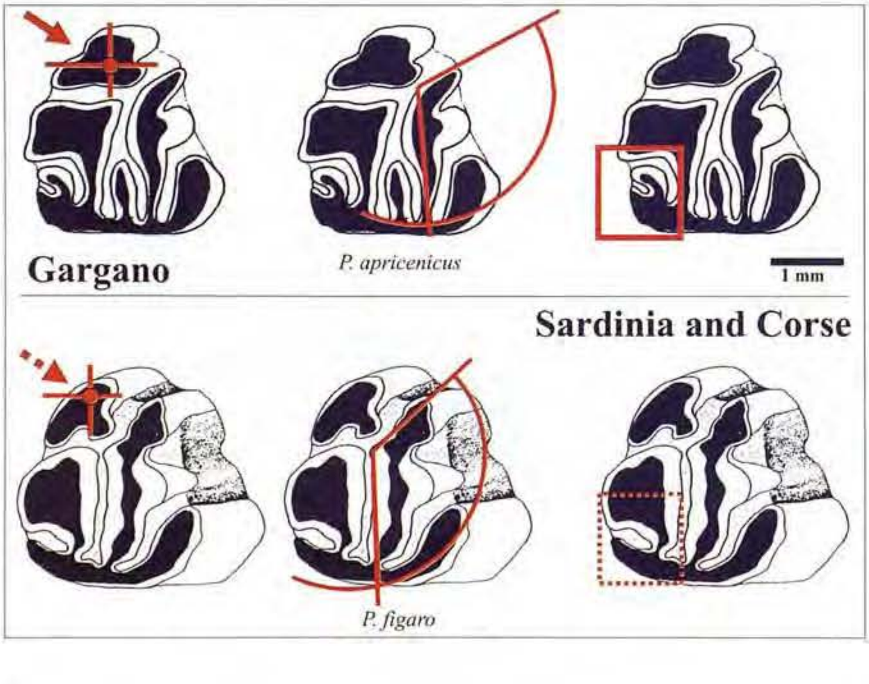


Fig. 8. Main differences between insular endemic *Prolagus* species of the Mediterranean area. Two groups have been distinguished: Gargano species (here represented by *P. apricenicus*) and Corso-Sardinian species (represented by *P. figaro*). Besides being bigger in size, Garganic species have a rectangular than a rather square shape (due to the anteroconid position), a lesser protoconid/protoconulid angle and a more complex and developed enamel folding. Drawings from López Martínez & Thaler (1975) and Mazza (1987).

Fig. 8. *Diferències principals entre les espècies endèmiques insulars de* Prolagus *de l'àrea mediterrània. S'han distingit dos grups: les espècies de Gargano (aquí representades per* P. apricenicus*) i les espècies corsosardes (representades per* P. figaro*). Además de ser més grans, les espècies gargàniques tenen una forma més rectangular que quadrada (degut a la posició de l'anterocònid), un menor angle protocònid/protoconúlid i un desenvolupament més complex del plegament de l'esmalt. Dibuixos a partir de López Martínez & Thaler (1975) i Mazza (1987).*

Another explanation that could partly justify such changes could be a new dietary and/or ecological adaptation as a consequence of size increase, but it frankly is not very likely and it can not be demonstrated.

The peculiar characteristics attained by *P. michauxi* could in part explain why the difference between continental and insular species becomes less marked in Plio-Pleistocene times than in Mio-Pliocene times. Another reason could be the area of the Corso-Sardinian block, much bigger than the islands of the Garganic Mio-Pliocene archipelago, a factor that, influencing populations' size, could have prevented the developing of more marked morpho-dimensional modifications (Heaney, 1978).

CONCLUSIONS

Insular endemic *Prolagus* species have been found in Western Mediterranean area only. *Prolagus* species living in insular environments follow the micromammalian pattern of evolution on islands and undergo similar morpho-dimensional changes. It is by the simultaneous, more or less marked occurrence of such well defined morpho-dimensional modifications that they can be easily recognized. Those convergent features are shared by species that do not have a common direct ancestor: Gargano *Prolagus* species derive from *P. oeningensis*, a

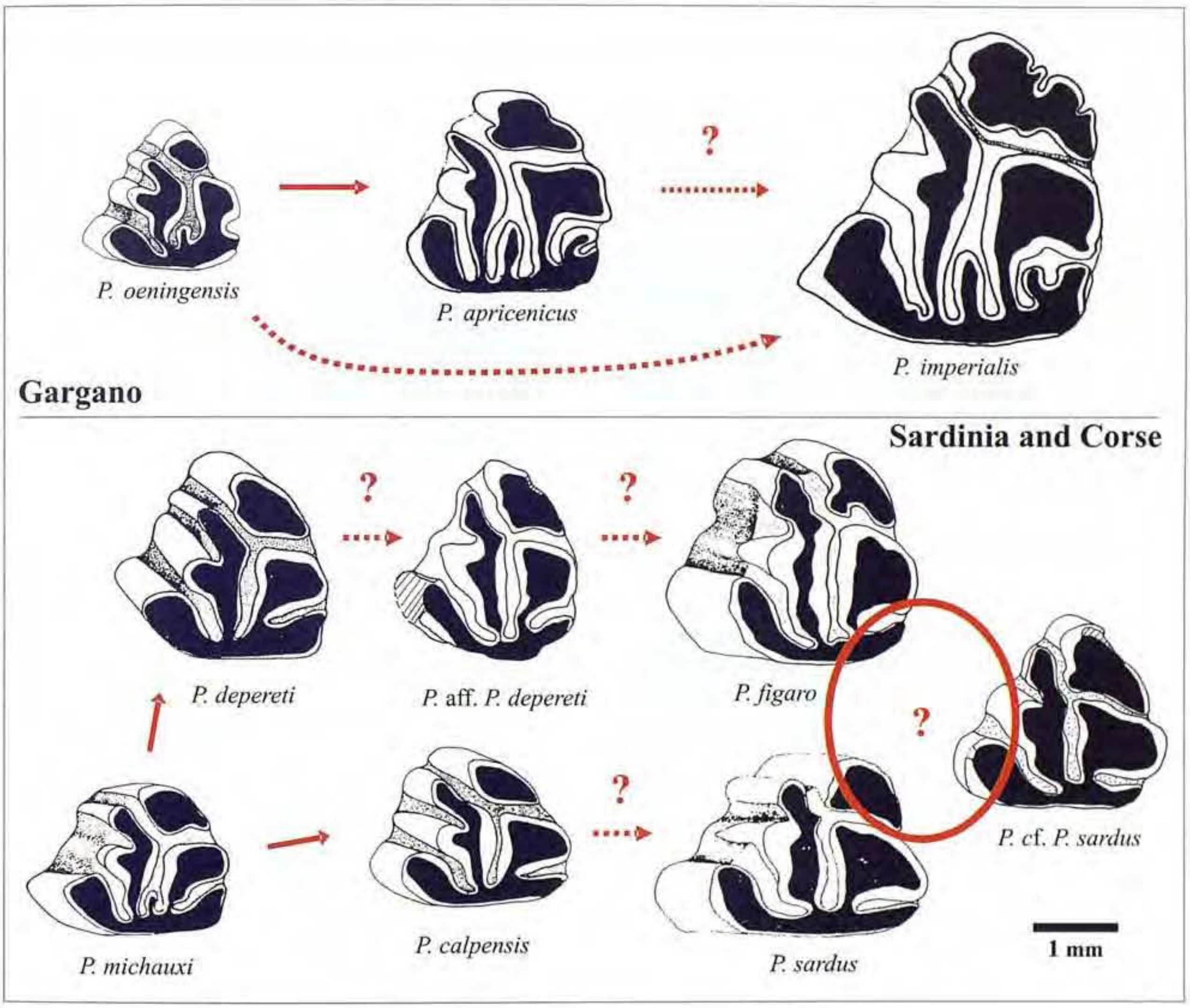


Fig. 9 – Phylogeny of insular endemic *Prolagus* species. *P. apricenicus* and *P. imperialis* descend from *P. oeningensis*, but it is not clear if they are part of an anagenetic lineage, or if they arose independently. Morphology and dimensions of *P. sardus* are very close to those of *P. calpensis*, while *P. figaro* closely resembles *P. depereti*. *Prolagus* aff. *P. depereti* shows intermediate morphologic features between the latter two species. Anyway, recent discoveries in the Monte Tuttavista area (Orosei, Eastern Sardinia, Italy; ?Late Pliocene-Upper Pleistocene) evidenced the existence of intermediate morphotypes between *P. figaro* and *P. sardus* (provisionally determined as *Prolagus* cf. *P. sardus*), opening again the discussion about the systematic of Corso-Sardinian *Prolagus* species. Drawings from López Martínez & Thaler (1975), Mazza (1987), López Martínez (1989) and from unpublished data of the author.

Fig. 9. *Filogènia de les espècies endèmiques insulars de* Prolagus. P. apricenicus *i* P. imperialis *deriven de* P. oeningensis, *però no està clar si formen part d'una línia anagenètica o si sorgeixen independentment. La morfologia i les dimensions de* P. sardus *són molt properes a les de* P. calpensis, *mentre que* P. figaro *s'assembla a* P. depereti. Prolagus *aff.* depereti *mostra unes característiques morfològiques intermèdies entre les de les dues darreres espècies. De totes formes, els descobriments recents a l'àrea del Monte Tuttavista (Orosei, Sardenya oriental, Itàlia; Pliocè superior? – Pleistocè superior) documenten l'existència de morfotipus intermedis (provisionalment determinats com a* P. *cf.* P. sardus*) entre* P. figaro *i* P. sardus, *obrint de nou la discussió sobre la sistemàtica de les espècies de* Prolagus *corso-sardes. Dibuixos a partir de López Martínez & Thaler (1975), Mazza (1987), López Martínez (1989) i de dades no publicades de l'autora.*

quite primitive European species, while the Corso-Sardinian species probably descend from one or two advanced species derived from the continental widespread *P. michauxi* (*P. calpensis* and/or *P. depereti*; López Martínez & Thaler, 1975; López-Martínez, 1978) (Fig. 9).

Increase of absolute and of relative size, of absolute hypsodonty and hypsodonty degree, of enamel folding complexity, reorganization of shape and relative position of occlusal surface elements on P_3 are the main elements that identify an insular endemic *Prolagus* species, to which should be added minor but significant modifications on the maxillary teeth in occlusion with P_3 (especially P^2). Such dental modifications probably involved significant changes in mandibular mechanics.

Almost all those characters can be related to mastication improving and therefore to a change of the diet. The most likely explanation for this phenomenon is a change of the environmental setting due to climatic changes.

The fact that all the above mentioned characters are related to chewing efficiency can also explain why they can not be observed in the same dental element with the same development degree: the result is a mosaic in which a mastication improving strategy prevails on the others that linger in a less developed stage. In Gargano species, for example, the tendency to enhance enamel folding complexity seem to prevail over a hypsodonty degree increase, the opposite seem to happen in Corso-Sardinian species. This distinction between Corso-Sardinian and Gargano species must be added to other differences in P_3 occlusal surface distinguishing the species of the two paleobioprovinces.

ACKNOWLEDGEMENTS

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In the last months, new fossil findings in the Monte Tuttavista karst fissure complex (Orosei, Eastern Sardinia, Italy) and the revision of Italian mainland *Prolagus* remains cast new light on the phylogeny of Corso-Sardinian species [Angelone, 2005: Systematic revision of genus *Prolagus* (Ochotonidae, Lagomorpha, Mammalia) in Italy and in Western Mediterranean Island: new systematic tools, biochronology and palaeogeography. Ph.D. Thesis, Università Roma Tre, 118 pp.]. Nevertheless, the morpho-dimensional and evolutionary observations made in this paper remain valid.

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04

Primer registro fósil de las familias Gekkonidae (Lacertilia) y Colubridae (Serpentes) en el Plioceno de Punta Nati (Menorca, Islas Baleares)

Salvador Bailon, Josep Quintana & Joan Garcia Porta

Bailon, S., Quintana, J. & Garcia Porta, J. 2005. Primer registro fósil de las familias Gekkonidae (Lacertilia) y Colubridae (Serpentes) en el Plioceno de Punta Nati (Menorca, Islas Baleares). *In* Alcover, J.A. & Bover, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 27-32.

Resum

Es descriuen restes atribuïdes a les famílies Gekkonidae (Lacertilia) i Colubridae (Serpentes) del Pliocè de Punta Nati 2 i Punta Nati 13 (Menorca, Illes Balears). Als dos casos es tracta de les úniques citacions fòssils d'aquestes espècies anteriors a l'arribada dels humans. L'estat fragmentari de les restes adscrites a la família Gekkonidae no permet una atribució taxonòmica més precisa. La morfologia de les restes atribuïdes a la família Colubridae permet l'atribució a un representant del gènere *Coluber*, estretament emparentat amb les espècies del Miocè europeu *C. dolnicensis* i *C. puchetti*.

Paraules clau: *Coluber*, Colubridae, Gekkonidae, Illes Balears, Menorca, Pliocè.

Resumen

En el presente trabajo se describen restos atribuidos a las familias Gekkonidae (Lacertilia) y Colubridae (Serpentes) del Plioceno de Punta Nati 3 y Punta Nati 12 (Menorca, Islas Baleares). En ambos casos, se trata de las únicas menciones fósiles de estas familias anteriores a la colonización de las islas por el hombre. El estado fragmentario de los restos atribuidos a la familia Gekkonidae no permite una atribución taxonómica precisa. La morfología de los restos atribuidos a la familia Colubridae permite la atribución de estos a un representante del género *Coluber*, estrechamente relacionado con las especies del Mioceno europeo *C. dolnicensis* y *C. puchetii*.

Palabras clave: *Coluber*, Colubridae, Gekkonidae, Islas Baleares, Menorca, Plioceno.

Abstract

In this work, we describe remains of the Gekkonidae and Colubridae families from the Pliocene of Punta Nati 3 and Punta Nati 12 (Minorca, Balearic Islands). This is the first fossils record of these families before man settlement in Balearic Islands. The important fragmentation of the Gekkonidae remains doest not allows us more precise taxonomical determination. The remains of the Colubridae family show a clear morphology of the genus *Coluber*, in closed relationship with the European Miocene species *C. dolnicensis* and *C. puchetii*.

Key words: Coluber, Colubridae, Gekkonidae, Balearic Islands, Minorca, Pliocene.

Introducción

El material estudiado proviene de dos yacimientos del Noroeste de la isla de Menorca (Islas Baleares): Punta Nati 3, situado entre el faro de Punta Nati y el canal de Cala's Pous (Quintana, 1998 y Seguí *et al.*, 2001) y Punta Nati 12 ubicado en Cala's Pous (Quintana, en preparación). Ambos yacimientos forman parte de un antiguo complejo cárstico formado sobre las dolomías del Jurásico y los sedimentos marinos del Mioceno (Quintana, 1998; Seguí *et al.*, 2001).

Punta Nati 3 es un yacimiento de escasas dimensiones y pobre en restos faunísticos. La lista preliminar de vertebrados de Punta Nati 3 incluye restos de *Muscardinus cyclopeus*, un lepórido de gran tamaño, un quiróptero, aves (entre las cuales se encuentra *Tyto balearica*), *Cheirogaster gymnesica*, *Blanus* sp. (observación inédita), *Podarcis* aff. *P. lilfordi* y *Vipera* sp. (Agustí *et al.*, 1982; Seguí, 1998; Quintana, 1998 y en preparación; Bailon *et al.*, 2002; Bailon, 2004). Punta Nati 12 se caracteriza por la presencia de bandas centimétricas formadas casi exclusivamente por huesos de vertebrados de pequeño tamaño. Dominan por su abundancia los restos de un anfibio anuro representante de la familia Discoglossidae. En menor proporción también se encuentran restos del lagomorfo anteriormente citado en Punta Nati 3, aves, *Blanus* sp., *Podarcis* aff. *P. lilfordi* y *Vipera natiensis* (Quintana, 1998 y en preparación; Bailon *et al.*, 2002; Bailon, 2004; García Porta *et al.*, en prensa). Entre estas bandas, y englobados por los limos rojos que forman el yacimiento, han aparecido algunos restos de mayor tamaño pertenecientes al lagomorfo mencionado anteriormente. La elevada densidad ósea encontrada en estas bandas, parece ser el resultado de una acumulación de egagrópilas, probablemente de *T. balearica.*

Resulta difícil de establecer una datación de estos yacimientos ya que se trata de depósitos cársticos de pequeña extensión carentes de continuidad lateral y los criterios geológicos pudiendo permitir una correlación precisa entre ellos faltan. No obstante, cuenta tenida de las especies representadas en estos yacimientos, así como de la edad de los sedimentos que los contienen, una edad comprendida entre el Mioceno superior y el Pleistoceno, es decir, muy probablemente Plioceno en sentido amplio, puede ser admitida (Quintana, 1998; García Porta *et al.*, en prensa).

El trabajo aquí presentado representa un avance de un estudio más completo en curso de realización sobre la herpetofauna del conjunto de yacimientos descubiertos en Punta Nati.

ESTUDIO SISTEMÁTICO

Lacertilia Owen, 1842
Familia Gekkonidae Gray, 1825
Gekkonidae indeterminado (Fig. 1).

Material : cuatro fragmentos de dentarios y una vértebra sacra (Punta Nati 3) y una vértebra dorsal fragmentada (Punta Nati 12).

Descripción

Los dentarios solo se encuentran representados por fragmentos. A pesar de ello, la morfología general de cada uno de ellos muestra de forma inequívoca su pertenencia a la familia Gekkonidae, presentando una forma esbelta y delgada hacia la extremidad anterior. En norma medial, el dentario se fusiona hasta la sínfisis mandibular constituyendo una cavidad tubular en la que se aloja el cartílago de Meckel. La plataforma dental es horizontal y en norma dorsal presenta un canal longitudinal a la base de los dientes. Los dientes son numerosos, de implantación pleurodonta, isodontos, cilíndricos, relativamente finos y monocúspides.

Las vértebras son anficelas, con un límite ventral del centro vertebral cóncavo en norma lateral y, en norma dorsal, un arco neural escotado entre las prezigapófisis. La vértebra dorsal posee un centro vertebral relativamente corto, sinapófisis ovaladas e inclinadas en sentido anteroposterior y una corta y delgada carena hemal sobre la porción central del centro vertebral. De uno y otro lado de esta carena hemal se abren dos forámenes subcentrales bien desarrollados. La vértebra sacra se caracteriza por la presencia de un centro vertebral corto y de procesos transversos (parcialmente fragmentados) anchos y aplastados dorsoventralmente.

Comentarios

Los dentarios y las vértebras de Punta Nati muestran una morfología típica de Gekkonidae. Desgraciadamente, el escaso material colectado así como su estado de fragmentación, impiden toda comparación con otras formas fósiles o actuales. En este trabajo, solo podemos indicar la presencia de la familia en el Plioceno de Menorca, hecho que constituye la única mención fósil de Gekkonidae, previa a la llegada del hombre al archipiélago balear.

El registro fósil europeo de Gekkonidae podría remontar al Jurásico medio de Gran Bretaña (Evans, 1998), mientras que durante el Eoceno, la presencia de la familia está definitivamente atestada en Europa: Gekkonidae del Eoceno inferior de Belgica (Augé, 2003) y de las islas Británicas (Milner *et al.*, 1982), *Rhodanogekko vireti* del Eoceno medio (Hoffstetter, 1946) y *Cadurcogekko piveteaui* del Eoceno superior, los dos en Francia

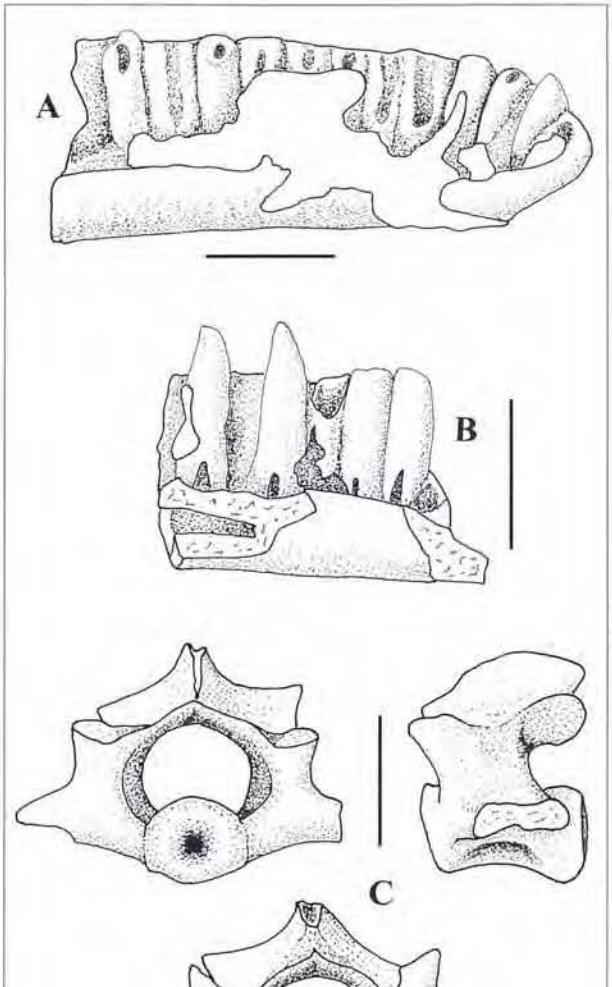

Fig. 1. Gekkonidae indeterminado. A y B, dentarios izquierdos; C, vértebra sacra, normas anterior, lateral izquierda y posterior. Punta Nati 3. Escala = 1mm.

Fig. 1. *Gekkonidae indeterminat. A i B, dentaris esquerres; C, vèrtebra sacra, normes anterior, lateral esquerra i posterior. Punta Nati 3. Escala = 1mm.*

Fig. 1. *Indeterminate Gekkonidae. A and B, left dentaries; C, sacral vertebra, anterior, left lateral and posterior views. Punta Nati 3. Scale bar = 1mm.*

(Hoffsteter, 1946; Augé, 1986). En la península ibérica, la más antigua mención de la familia data del Mioceno inferior de Córcoles (Alférez Delgado & Brea Lopez, 1981).

Las especies *Tarentola mauritanica* y *Hemidactylus turcicus* que pueblan actualmente la isla de Menorca han sido introducidas recientemente por el hombre en las islas Baleares. *T. mauritanica* podría haber sido introducida por los comerciantes cartagineses (Mayol, 1985) o incluso anteriormente, por la poblaciones talaióticas (Pleguezuelos, 2002), mientras que la llegada de *Hemidactylus turcicus* a las islas puede deberse a transporte pasivo por los pueblos comerciantes de la antigüedad, como los navegantes egeos, en la ruta del estaño (Mayol, 1985; Pleguezuelos, 2002).

Serpentes Linnaeaus, 1758
Famila Colubridae Oppel, 1811
Coluber sp. (grupo *C. dolnicensis*-*C. pouchetii*) (Fig. 2).

Material: un fragmento de maxilar, un dentario y cuatro vértebras dorsales (Punta Nati 12)

Descripción

El fragmento de maxilar corresponde a la extremidad distal de un maxilar derecho caracterizado por la presencia, sobre el borde dorsal del hueso, de una impresión del ectopterigoides marcada y bien delimitada posteriormente. En norma medial, el proceso ectopterigoides está roto y no puede conocerse su morfología, aunque parece poseer una base corta y robusta. En norma lateral, la superficie posterior del hueso es ligeramente cóncava y perforada por un foramen situado sobre la antepenúltima posición dental. Los dientes son relativamente robustos e isodontos, con bases circulares y muy próximos entre ellos, sin que ningún espacio interdental o diastema sean visibles.

El dentario presenta un aspecto relativamente corto y posee una marcada inflexion anteromedial en la que se sitúa una masiva sínfisis mandibular. Posteriormente, el hueso se encuentra fracturado y no podemos conocer su longitud total. Los dientes, en número de 16, presentan una morfología y una disposición parecidas a las descritas para el maxilar. En norma lateral, el foramen dental, relativamente corto, se abre bajo la novena posición dentaria mientras que el límite anterior de la escotadura posterior se encuentra bajo el diente número doce. En norma medial, el dentario rodea completamente el canal de Meckel a nivel de la octava posición dentaria pero no llega a fusionar completamente y se prolonga en un débil sillón hasta la cuarta posición dentaria.

Las vértebras dorsales son más largas que anchas: longitud del centro vertebral comprendida entre 5.2 mm y 4.32 mm; anchura a nivel del estrangulamiento interzigapofisario entre 4 mm y 3.44 mm y relación longitud/anchura entre 1.35 y 1.24. Las variaciones observadas pueden ser atribuidas a la diferente posición ocupada por cada una de las vértebras a la largo de la columna vertebral.

En norma dorsal, el borde anterior del zigosfeno es trilobulado, con un lóbulo central ancho y menos avanzado que los lóbulos laterales. La superficie articular de las prezigapófisis es de aspecto subrectangular y el único proceso prezigapofisario conservado es cónico, con una extremidad distal roma y ligeramente más corto que las prezigapófisis. La espina neural es larga, con una extremidad anterior bastante avanzada sobre el zigosfeno. Distalmente, dos pequeñas espinas epizigapofisarias son presentes.

En norma lateral, la arista interzigapofisaria es poco prominente y la espina neural se encuentra fracturada en todos los ejemplares. Los forámenes laterales se localizan, de cada lado de la vértebra, en una depresión moderadamente profunda y prolongada anteriormente en un estrecho sillón ubicado por encima de la diapófisis correspondiente y bien limitado dorsalmente por una pequeña excrecencia ósea. Las diapófisis son más pequeñas que las parapófisis y ocupan una posición más atrasada que estas últimas. La arista subcentral es recta y larga, aunque sin alcanzar el cóndilo. El límite ventral de la carena hemal es recto en sus dos tercios posteriores, mientras que el tercio anterior es variable y parece depender del rango vertebral: recto (vértebra media), ligeramente inclinado hacia delante (vértebra medio-posterior) o con un escalón anterior bien marcado (vértebra posterior).

En norma ventral, los sillones subcentrales son profundos y ocupan la casi totalidad del centro vertebral en las dos vértebras más posteriores, mientras que en las vértebras de rango medio estos sillones se atenúan. La carena hemal es ligeramente ancha, con una superficie ventral débilmente convexa y con límites laterales cada vez mejor marcados conforme la vértebra es más posterior. La vértebra más posterior presenta una neta interrupción anterior en forma de escalón. En corte transversal, la carena hemal presenta de cada lado, un estrangulamiento basal que se acentúa en profundidad y altura a medida que la vértebra se hace más posterior. Dos pequeños tubérculos subcotilares son visibles en todos los ejemplares.

En norma posterior, el arco neural es moderadamente abombado y posee unos bordes posteriores convexos y en norma anterior, el techo del zigosfeno es bastante recto y los forámenes paracotilares, bien visibles, se sitúan en depresiones relativamente profundas. El cótilo y el cóndilo son pequeños y circulares.

Comentarios

Sobre el maxilar, la morfología general de los dientes, así como la presencia de una impresión del ectopterigoides bien limitada posteriormente corresponden al modelo observado generalmente en *Coluber* y *Coronella*. Entre estos dos géneros, sólo en *Coronella* la diastema falta, como es el caso en el fósil, mientras que la implantación, relativamente corta y robusta del proceso ectopterigoides lo relaciona con *Coluber*.

El aspecto general del dentario, así como la morfología y la disposición de los dientes evocan los representantes de los géneros *Coluber* y *Coronella*. La presencia de una extremidad anterior del dentario masiva es un carácter utilizado por Ivanov (2002) para diferenciar *Coluber dolnicensis* Szyndlar, 1987, del Mioceno inferior de la República Checa, del resto de representantes del género *Coluber* (aunque pensamos que debe considerarse la posibilidad de que este tipo de estructura tenga un origen patológico y por lo tanto desprovisto de valor sistemático). El dentario de Punta Nati difiere del atribuido a esta especie por la menor dimensión del foramen dental.

El gran parecido observado en la morfología y la disposición de los dientes en el maxilar y en el dentario, permiten pensar que estos dos elementos óseos pertenecen a individuos de un mismo taxón.

La ausencia de hipapófisis en las vértebras dorsales permite atribuirlas a un colúbrido no natricino. Dentro de este grupo de colúbridos, la morfología vertebral es bastante homogénea y resulta difícil una diferenciación incluso a nivel genérico. No obstante, teniendo en cuenta el alargamiento vertebral y de los procesos prezigapofisarios, así como la presencia de un arco neural abombado, de forámenes paracotilares et de una carena hemal bien definida estas vértebras pueden adscribirse al modelo general presentado por los diferentes representantes del género *Coluber*.

Durante el Neógeno, el género *Coluber* se encuentra representado en Europa central y del oeste por *C. dolnicensis* del Mioceno inferior (MN 3 y MN 4) de la República Checa (Szyndlar, 1987; Ivanov, 2002), *C. caspioides* del Mioceno inferior de la República Checa (MN 3, Ivanov, 2002), de Alemania (MN4, Szyndlar & Schleich, 1993) y probablemente de Austria (MN 4, Szyndlar, 1998), *C. pouchetii* del Mioceno medio (MN 6, Rage, 1981, Augé & Rage, 2000) y aparentemente también en el mioceno inferior (MN 4) de Francia (Rage & Bailon, en prensa), *C. suevicus* del Mioceno medio de Alemania (MN 7+8, Szyndlar & Böhme, 1993) y aparentemente del Mioceno inferior de la República Checa (MN 3, Ivanov, 2002), *C. planicarinatus* del Mioceno superior de Austria (MN 11, Bachmayer & Szyndlar, 1985 y 1987), *C. hungaricus* del Mioceno superior (MN 13 de Hungría, Venczel, 1994 y 1998) y *C. viridiflavus* del Plioceno de Polonia (MN 16, Szyndlar, 1984). En la Península Ibérica, un representante de la familia a morfología vertebral similar a *C. dolnicensis* y *C. caspioides* (cf. *Coluber* sp.) es señalado en el Mioceno inferior (MN 5) de Portugal (Szyndlar, 2000).

Las vértebras de Punta Nati presentan dos caracteres comunes con *C. dolnicensis y C. pouchetii*: diapófisis desplazadas posteriormente con respecto a las parapófisis y carena hemal con un escalón anterior. Sin embargo, este último carácter se encuentra en todas las vértebras de *C. dolnicensis*, mientras que en *C. pouchetii* y las vértebras de Punta Nati esta estructura aparece sólo en las vértebras posteriores. El fósil balear difiere de *C. pouchetii* por su más pequeña talla; el zigosfeno posee un lóbulo central, mientras que en *C. pouchetii* esta estructura es recta o ligeramente cóncava; el cóndilo y el cótilo son más pequeños que en el fósil francés; la carena hemal aparece mejor limitada lateralmente y menos ensanchada posteriormente que en *C. pouchetii* y los bordes posteriores del arco neural de nuestro material son convexos y no rectos como en esta última. Este último carácter parece ser compartido con las vértebras atribuidas a *Coluber* aff. *C. pouchetii* por Augé & Rage (2000), no obstante, la ausencia de figura acompañando la descripción de estas últimas impide una comparación más detallada con nuestro material.

En cualquier caso, la presencia de un estrangulamiento basal a nivel de la carena hemal y de un sillón lateral situado por encima de las diapófisis, parecen constituir dos caracteres aún no descritos en el registro fósil europeo y que podrían justificar la creación de un nuevo taxón [un sillón lateral parecido al de las vértebras de Punta Nati, puede observarse en la figura 6 I de Szyndlar & Schleich (1993) correspondiente a una vértebra posterior de *C. caspioides* (Mioceno inferior de Alemania), pero esta carácter no es observable (figura 6 D) ni señalado por estos autores en la descripción de las vértebras ocupando una posición más avanzada]. No obstante, consideramos que una nueva revisión del material que se encuentra actualmente en el Institut de Paleontologia Miquel Crusafont de Sabadell, España, es necesaria afín de establecer de forma más precisa la descripción del material, el valor taxonómico de los caracteres y las posibles relaciones filogenéticas del fósil balear. El material es atribuido temporalmente a *Coluber* sp., estrechamente relacionado con el grupo de especies *C. dolnicensis-C. pouchetii.*

Como es el caso para la familia Gekkonidae, la presencia de un colúbrido en los yacimientos de Punta Nati constituye la primera mención fósil de la familia anterior a la colonización del hombre en las Islas Baleares. Actualmente, la familia Colubridae se encuentra representada en el archipiélago por *Macropotodon mauritanicus, Elaphe scalaris* y *Natrix maura*, todas ellas introducidas recientemente por al hombre en las islas (Pleguezuelos, 2002).

CONCLUSIÓN

Aunque escasos, los restos de reptiles escamosos estudiados hasta ahora en el conjunto de yacimientos de Punta Nati indican la existencia de una fauna variada y de carácter marcadamente exótico para este grupo de reptiles y sin equivalente actual en el conjunto balear. A la presencia ya conocida de al menos dos representantes de la familia Viperidae (Viperidae indeterminado del Mioceno medio de Punta Nati 2 y *Vipera* sp. y *V. natiensis* del Plioceno de Punta Nati 3 y Punta Nati 12, Bailon *et al.*, 2002), de un anfisbénido (*Blanus* sp., del Plioceno de Punta Nati 12, Garcia Porta *et al.* en prensa) y de un lacértido (*Podarcis* aff. *P. lilfordi*, probablemente ancestro del actual *P. lilfordi*, del Plioceno de Punta Nati 3 y Punta Nati 12, Bailon, 2004), cabe añadir a partir de este trabajo la presencia en el archipiélago de un Gekkonidae (Punta Nati 3 y Punta Nati 12) y de un colúbrido representado solamente en Punta Nati 12.

Bien que la presencia de Gekkonidae en Menorca se encuentra bien atestada por elementos a morfología característica de la familia (dentarios y vértebras), el estado fragmentario de estos no permite una comparación con las formas conocidas del Neógeno europeo ni con los representantes actuales. El material es atribuido a la familia Gekkonidae sin que una atribución más precisa pueda ser avanzada.

Con respecto al colúbrido, la morfología general de los elementos estudiados (dentario, maxilar y vértebras) corresponde bien a la encontrada en el género *Coluber*. Por otro lado, la presencia de una región anterior masiva, relaciona el dentario, en el caso que esta estructura no tenga un origen patológico, con la forma del Mioceno inferior *C. dolnicensis*. En el caso de las vértebras, la posición más retrasada de las diapófisis con respecto a las parapófisis y la presencia de un escalón anterior sobre la carena hemal son caracteres que se encuentran en la especie del Mioceno medio *C. pouchetii* y en menos medida con *C. dolnicensis* (la presencia de escalón sobre la carena hemal es un carácter constante en esta última especie, mientras que en la vértebras de Punta Nati, así como en *C. pouchetii* es un carácter que solo existe en las vértebras posteriores). Sin embargo, la talla de las vértebras de nuestro material, más

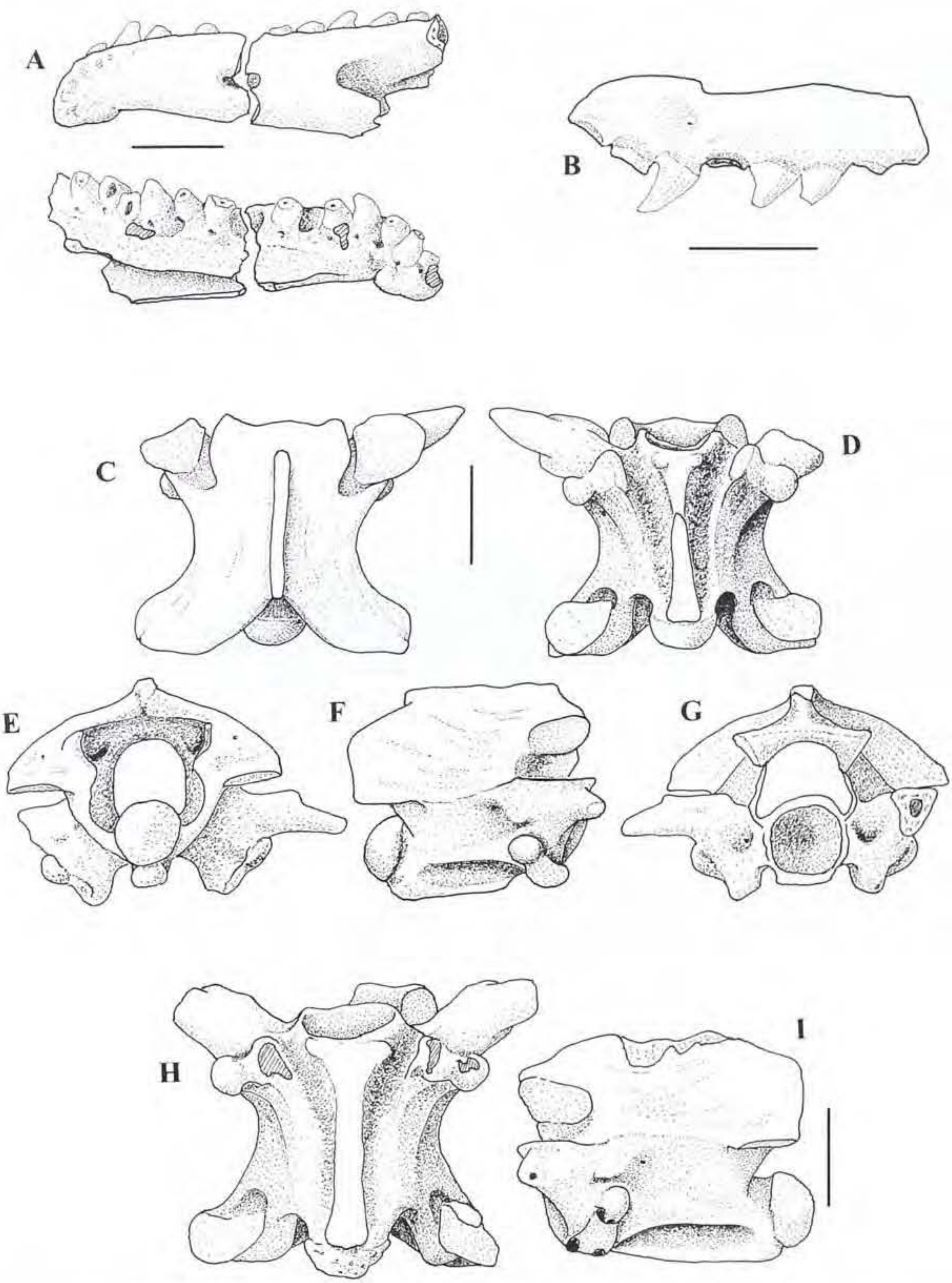

Fig. 2. *Coluber* sp. (grupo *C. dolnicensis-C. pouchetii*). A, dentario izquierdo, vistas lateral y medial; B, maxilar derecho, fragmento posterior, vista lateral; C, D, E, F y G, vértebra dorsal posterior, normas dorsal, ventral, posterior, lateral derecha y anterior; H e I, vértebra dorsal medio-posterior, vistas ventral y lateral izquierda. Punta Nati 12. Escala = 2mm.

Fig. 2. Coluber *sp. (grup* C. dolnicensis-C. pouchetii*). A, dentari esquerre, vistes lateral i medial; B, maxil·lar dret, fragment posterior, vista lateral; C, D, E, F i G, vèrtebra dorsal posterior, norma dorsal, ventral, posterior, lateral dreta i anterior; H i I, vèrtebra dorsal medio-posterior, vistes ventral i lateral esquerra. Punta Nati 12. Escala = 2mm.*

Fig. 2. Coluber *sp. (*C. dolnicensis-C. pouchetii *group). A, left dentary, lateral and medial views; B, right maxilla, posterior fragment, lateral view; C, D, E, F and G, posterior dorsal vertebra, dorsal, ventral, posterior, right lateral and anterior views; H and I, postero-medial vertebra, ventral and left lateral views. Punta Nati 12. Scale bar = 2mm.*

pequeña, así como la presencia de un lóbulo central a nivel del zigosfeno, la menor dimensión del cóndilo y del cótilo y la presencia de bordes posteriores del arco neural convexos, diferencian nuestro material de *C. pouchetii* y lo relacionan con *C. dolnicensis*. Por último, tanto la dimensión vertebral como la presencia de un arco neural abombado parecen corresponder a los señalados por Augé & Rage (2000) para *Coluber* aff. *C. pouchetii*.

Las afinidades del colúbrido de Punta Nati 12 con las especies fósiles *C. dolnicensis* y *C. pouchetii* parecen ser estrechas, aunque la presencia de un estrechamiento basal a nivel de la carena hemal y de un sillón lateral situado por encima de las diapófisis constituyen dos caracteres exclusivos de las vértebras de Punta Nati.

La situación geográfica de las yacimientos (Menorca, islas Baleares), así como las dos diferencias morfológicas indicadas, podrían parecer suficientes para definir una nueva especie. No obstante, antes de dar este paso, pensamos que una nueva revisión del material fósil es necesaria para poder establecer una descripción precisa de los caracteres morfológicos así como sus relaciones con las formas ya establecidas. En espera de este estudio, el material de Punta Nati 12 es atribuido a *Coluber* sp. grupo *C. dolnicensis-C. pouchetii* para indicar la relación con estas dos especies.

Por otro lado, las afinidades del colúbrido fósil con las especies del Mioceno *C. dolcinensis* y *C. pouchetii*, muestra bien el origen relativamente antiguo avanzado en otros trabajos para la fauna de Punta Nati 3 y Punta Nati 12: Mioceno superior (Mesiniense).

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05

Sistemática de las Jutías de las Antillas (Rodentia, Capromyidae)

Rafael Borroto-Páez, Charles A. Woods & C. William Kilpatrick

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Resum

S'estudia la sistemàtica dels capromïids vivents amb mètodes fenètics i filogenètics, en base a caràcters externs i del crani, i a la seqüència de nucleòtids del citocrom b. L'anàlisi de la variació morfològica i de similitud indiquen que *Mysateles garridoi* és una espècie vàlida i que *Capromys pilorides* es diferencia de la resta d'espècies de capromïids. El volum cranial discrimina els taxa i ha evidenciat un baix Quoficient d'Encefalització, el qual s'interpreta com a resultat d'una evolució sense pressions selectives i/o com a un caràcter primitiu. La divergència en la seqüència de nucleòtids va apuntar *Plagiodontia aedium* com l'espècie més basal. S'ha descobert un nou taxon (una espècie críptica). *Mysateles* es parafilètic i es proposa la nova combinació *Mesocapromys melanurus.* Les dades moleculars i morfològiques recolzen el retorn de *M. gundlachi* a la seva categoria subespecífica (=*M. prehensilis gundlachi*) i la validesa dels cinc gèneres. La major similitud es dona entre *Mysateles* i *Mesocapromys*. El temps de divergència estimat fou de 23 Ma (milions d'anys) per a *Plagiodontia* i *Geocapromys,* i entre 17 i 19 Ma per a *Capromys, Mysateles* y *Mesocapromys.* Les subespècies de *Capromys* i *Mysateles* varen divergir fa només 2,4 Ma i 0,8 Ma respectivament. Les anàlisis morfològiques i moleculars permeteren establir relacions fenètiques i filogenètiques que justifiquen els canvis taxonòmics proposats.

Paraules clau: Sistemàtica, Capromyidae, Antilles, morfometria, citocrom b, juties.

Resumen

La sistemática de los caprómidos vivientes se estudia en base a métodos fenéticos y filogenéticos, caracteres externos y del cráneo y la secuencia de nucleótidos del gen citocromo b. El análisis de la variación morfológica y de similitud indican que *Mysateles garridoi* es una especie válida y *Capromys pilorides* se separa del resto de las especies de caprómidos. El volumen craneal discrimina a los taxones y demostró el bajo Coeficiente de Encefalización, interpretándose como resultado de una evolución sin presiones selectivas y/o como carácter primitivo. La divergencia en la secuencia de nucleótidos apunta a *Plagiodontia aedium* como la especie más basal. Se descubre un nuevo taxón (una especie críptica). *Mysateles* es parafilético y se propone la nueva combinación *Mesocapromys melanurus.* Los datos moleculares y morfológicos avalan retornar *M. gundlachi* a su posición subespecífica (=*M. prehensilis gundlachi*) y confirman la validez de los cinco géneros, con la mayor similitud entre *Mysateles* y *Mesocapromys.* El tiempo de divergencia calculado fue 23 Ma (millones de años) para *Plagiodontia* y *Geocapromys,* y entre 17 y 19 Ma para *Capromys, Mysateles* y *Mesocapromys.* Las subespecies de *Capromys* y *Mysateles* divergieron hace sólo 2,4 Ma y 0,8 Ma, respectivamente. Los análisis morfológicos y moleculares establecieron relaciones fenéticas y filogenéticas que justifican el arreglo taxonómico propuesto.

Palabras clave: Sistemática, Capromyidae, Antillas, morfometría, citocromo b, jutías.

Abstract

The systematics of the recent capromyids were studied with phenetics and phylogenetic methods of external and cranial characters and nucleotide sequence of cytochrome b. Analyses of morphological variation and similarity indicate the validity of *Mysateles garridoi* as a valid species and separate *Capromys pilorides* from the rest of the species of capromyids. Cranial volume discriminated the taxa and demonstrated low encephalization coefficients that could be interpreted as evolution without selective pressures and/or a primitive character state. Analysis of sequence divergence identified *Plagiodontia aedium* as the most basal species and discovered a new taxon (a cryptic species). *Mysateles* was paraphyletic and the new combination *Mesocapromys melanurus* was proposed. Molecular and morphologic data support the return of *M. gundlachi* to subspecific level (=*M. prehensilis gundlachi*) and the validity of five genera, with *Mysateles* and *Mesocapromys* being very similar. Divergence times were estimated to be 23 My for *Plagiodontia* from *Geocapromys* and between 17 and 19 My for the divergence among *Capromys, Mysateles* and *Mesocapromys.* The subspecies of *Capromys* and *Mysateles* were estimated to have diverged 2,4 My and 0,8 My, respectively. Morphologic and molecular analyses established phenetics and phylogene-tics relationships that justify the taxonomic arrangement.

Key Words: Systematics, Capromyidae, Antilles, morphometrics, cytochrome b, hutias.

Introducción

La fauna antillana y su origen, evolución, especiación, adaptaciones, taxonomía y relaciones biogeográficas, entre otros, han sido objeto de interés investigativo, de polémicas y de criterios diversos (Darlington, 1938; Williams, 1989; Woods, 1989a; Iturralde-Vinent & MacPhee, 1999; Hedges, 2001; Woods & Sergile, 2001). Un grupo focal de estas controversias son los mamíferos, en particular los roedores, por sus peculiaridades morfológicas, su discutida clasificación taxonómica a los distintos niveles y las diferentes hipótesis sobre su origen, biogeografía y relaciones evolutivas (Simpson, 1956; Morgan & Woods, 1986; Woods, 1989 b; 1989c; 1990; Woods *et al*, 2001).

El orden Rodentia está representado en las Antillas por un gran número de especies endémicas (64), en su mayoría extinguidas (76,6%), que pertenecen a 19 géneros, 8 subfamilias y 4 familias. De estas especies endémicas, 68,8% corresponden a la familia Capromyidae (conocidas comúnmente como jutías), la única familia con especies vivientes (13), la mayoría de ellas en Cuba (10) y las restantes (3) en Jamaica, Bahamas y La Hispaniola. En tiempos recientes se extinguió la especie de la Islas Swan y es discutida la posible existencia de *Isolobodon portoricensis* en La Hispaniola (Woods *et al.*, 1986). Esto elevaría a un total de 15 las especies que han llegado hasta tiempos recientes. Sin embargo, el número de especies y géneros está en constante cambio debido a la descripción de nuevos taxones, la cuestionada validez de algunos y las sinonimias de otros.

Históricamente la mayor controversia se ha relacionado con los arreglos sistemáticos que han tratado de dar una explicación a la relación y afinidad entre las especies de Capromyidae (fósiles y recientes) de Cuba, así como con la validez dudosa de algunas de ellas (especialmente las fósiles). Algunos han considerado monotípica a la subfamilia Capromyinae, con un solo género (*Capromys*) (Allen, 1911; Varona, 1974), mientras que otros agruparon a las especies en *Capromys* y *Geocapromys* (Hall & Kelson, 1959). Mohr (1939) y Kratochvíl *et al.* (1978; 1980) revisan la sistemática de la familia y estos últimos propusieron separar a las especies cubanas vivientes en los géneros *Capromys, Mesocapromys* y *Mysateles,* de manera que la subfamilia Capromyinae en Cuba estaría formada por cuatro géneros (incluyendo los representantes fósiles pertenecientes a *Geocapromys*). Miembros de esta subfamilia se encuentran, además, en Jamaica, Bahamas e Islas Caimán. Más recientemente MacPhee & Iturralde-Vinent (1995) describieron del Mioceno temprano la especie fósil *Zazamys veronicae,* primer representante cubano de la subfamilia Isolobodontinae, expandiendo al oeste de las Antillas la distribución de esta subfamilia. Teniendo en cuenta todo lo anterior, Capromyidae tendría 9 géneros en cuatro subfamilias (cuatro en Capromyinae, dos en Plagiodontinae, dos en Isolobodontinae y uno en Hexolobodontinae).

En base a los análisis fenético, a diferentes niveles de integración morfológica, y filogenético, en el análisis molecular del gen citocromo b, se estudia la sistemática de las especies recientes de la familia Capromyidae, lo que permite un mejor entendimiento de las relaciones de afinidad y de la variación morfológica, importantes para lograr un conocimiento más objetivo de los numerosos taxones, especialmente los fósiles.

MATERIALES Y MÉTODOS

La Tabla 1 muestra los taxones estudiados, acrónimos y tamaños de muestras en adultos. Los animales eran pesados, medidos y se les tomaban muestras de vísceras y músculos, que eran congelados o conservadas en alcohol 70%. Las colectas de especimenes cubanos fueron depositadas en la Colección de Mamíferos del IES. Las mediciones fueron realizadas con calibrador Vernier y cinta métrica de 0,1 y 1 mm de precisión respectivamente, en dependencia de la magnitud de la medida.

Las 5 medidas externas (en mm) se realizaron en 11 especies y fueron las longitudes: total (LT), cuerpo y cabeza (CU), cola (CO), altura de la oreja (AO), pie posterior (LP). El peso fue tomado con dinamómetros Homs de 2 kg y 10 kg (20 g y 100 g de precisión respectivamente). Los datos externos de especies no cubanos fueron tomados de colecciones de EEUU (Borroto, 2002).

Las 33 medidas de cráneo (mm) se ilustran en Borroto (2002). Se tomaron en 14 especies y fueron: **Longitudes:** COND- condilobasal; PAL- palatilar; PBN- parte basal del neurocráneo; D- diastema maxilar; R- rostral; HAM- hilera alveolar maxilar; B- bula; N- nasal; F- frontal; DHP- horizontal del preorbital; DHO- horizontal de la órbita; FI- foramen incisivo; BA- bulas a la hilera alveolar; PLT- palatino. **Anchuras:** NC- neurocráneo; PZ- postcigomática; PO- postorbital; AF- frontal; IO- interorbital; RO- rostral; NP- nasal posterior; NA- nasal anterior; AP- arco preorbital; AZ- arco cigomático; DHF- foramen magno; ANCOA- coana; ANPA- palatino; CIGO- cigomática; ANORB- orbital. **Alturas:** BU- bula; AR- rostral; VFP- preorbital; DVF- del foramen magno. No se utilizaron las medidas de la mandíbula para poder incluir a *M. garridoi,* descrita a partir de un cráneo sin mandíbula, y porque análisis previos con caracteres craneales y mandibulares no cambian la distribución de las especies en el espacio morfológico de los Componentes Principales (Borroto, 2002). Además, la forma de la mandíbula de los caprómidos muestra similitud entre las distintas especies (Woods & Howland, 1979).

Se calcularon la media, desviación estándar (DE) y la amplitud, se comprobó la normalidad por la Prueba D de Kolmogorov-Smirnov y se realizon pruebas *t* de Student y pruebas F para comparar las medias y las varianzas (Sokal & Rohlf, 1995), utilizando el programa Statmost, Versión 3.0. Con el programa NTSYS-PC (Rohlf, 1994), se estudió la variación multivariada con los Análisis de Agrupamientos, de Componentes Principales (CP) y del método de Burnaby para el ajuste de tamaño (Burnaby, 1966). El análisis de CP se realizó a partir de dos tipos de matrices: de correlación, para la variación intraespecífica y de varianza-covarianza, para los análisis alométricos, previa transformación logarítmica de los datos. Las matrices fueron estandarizadas cuando fue necesario. Los agrupamientos fueron por el método de pares asociados al azar sin peso aritmético (UPGMA) a partir del índice de Distancia Taxonómica Promedio y se calcularon los Coeficientes de Correlación Cofenéticos (Sneath & Sokal, 1973; Marcus, 1990).

Para el análisis del volumen craneal (VC) se utilizó el método empleado por Eisenberg & Wilson (1978). El coeficiente de encefalización (E.Q.) se calculó como el cociente del VC observado (Eo) entre el VC esperado (Ev) (Jerison, 1973). Ev se calculó partir de la fórmula alométrica, que se deriva de la regresión entre VC contra peso del cuerpo. Se calcularon tres E.Q.: E.Q. (Mammalia) a partir de la fórmula $Ev=0,055 \text{ (Peso del Cuerpo)}^{0,74}$, derivada de 300 mamíferos (Eisenberg & Wilson, 1978); E.Q. (Rodentia) a partir de la fórmula $Ev=0,102 \text{ (Peso del Cuerpo)}^{0,63}$, derivada de 45 roedores (Eisenberg, 1981), y el que se obtuvo en este trabajo para 11 taxones de Capromyidae.

Se usaron análisis de regresión, pruebas F, transformación logarítmica y análisis bivariado.

El análisis molecular fue a partir del ADN mitocondrial del gen citocromo b, muy útil para estudio entre especies estrechamente relacionadas (Irwin *et al.*, 1991). Se tomaron muestras de tejidos de 26 especímenes de jutías (Tabla 1). Se incluyó la secuencia de dos grupos externos, *Octodon degus*, (Lessa & Cook, 1998) y *Thrichomys apereoides* (Lara *et al.*, 1996). El ADN fue extraído por el método de la proteinasa K/fenol/cloroformo (Blin & Stafford, 1976; Sibley & Ahlquist, 1981). Los tejidos se lavaron con agua destilada y buffer de lisis y se homogeneizaron según Longmire *et al.* (1991). Este fue rehidratado en un microtubo de 1,5 ml con 700 ml de agua destilada y el ADN fue liberado con la adición de 70 ml de SDS 10% y 5 ml de proteinasa K (20mg/ml); entonces fue incubado a 55 °C de 10 a 48 horas y el tejido se destruyó mecánicamente. Las componentes celulares fueron tomadas mediante dos extracciones con 700 ml de una mezcla tamponeada de fenol/cloroformo (1:1) y cloroformo/alcohol isoamílico (24:1), seguidas de otras dos extracciones de esta última. El ADN fue precipitado con la adición de 20 ml de cloruro de sodio 0,5 M y al menos 900 m l de etanol frío 100%; enfriado a -70 °C durante 10 min. y colectado por centrifugación a 9000 rpm a temperatura ambiente por 1 min. y posteriormente lavado con 1 ml de etanol frío 70% y secado al aire, después de lo cual fue resuspendido en 100 ml de agua destilada y almacenado a 4 °C.

Una porción del gen citocromo b fue amplificada por la reacción en cadena de la polimerasa (PCR) (Saiki *et al.*, 1988) usando: 35 ciclos de 94 °C (1 min.) desnaturalización, 50 °C (1 min.) temperatura de unión, y 72 °C (1 min. 10 seg.) extensión. La reacción de amplificación fue realizada en 25 ml usando esferas PCR , 0.5 mM de cada cebador y 2.5 ml de ADN muestra y con el uso de los cebadores (referido a la secuencia de *Mus*, Bibb *et al.*, 1981) L-14115 GATATGAAAAACCATCGTTG y H-14541 CAGAATGATATTTGTCCTCA (Sullivan *et al.*, 1997). Los productos de amplificación fueron purificados usando precipitación con polietilenglicol (Maniatis *et al.*, 1982). La secuencia de ADN fue realizada automáticamente por un equipo Applied Biosystems 373, utilizando terminadores de color y siguiendo el método de secuenciado cíclico. Excesos de terminadores marcados con color fueron eliminados con columnas de centrifugación G-50 Sephadex y los productos de esta secuencia fueron secados en un SpeedVac y almacenados a -80°C.

El análisis de la secuencia de nucleótidos se realizó a partir de la del género *Mus* (Bibb *et al.*, 1981). El porcentaje de la divergencia en la secuencia y las distancias genéticas se hallaron por el método de Kimura (1980) y Tamura & Nei (1993). Estas distancias facilitan la comparación de los niveles de divergencia con otros roedores histricognatos (Lara *et al.*, 1996; Lessa & Cook, 1998) y otras especies de mamíferos (Johns & Avise, 1998). Para estimar los árboles más parsimoniosos fueron usadas al menos 20 búsquedas heurísticas. Se obtuvo el árbol consenso a partir de los árboles igualmente parsimoniosos, empleando la opción estricto. La confiabilidad de los nodos se determinó empleando el método de *bootstrap* (Felsenstein, 1985) y el índice o soporte de Bremer (Bremer, 1994). Se usaron los programa PAUP (Versión 4.0b4, Swofford, 1999) y Autodecay (Eriksson, 1997).

RESULTADOS Y DISCUSIÓN

Caracteres Externos

La exploración de los datos reveló que todos se distribuyen normalmente (D entre 0.85 y 1, P<0.001) y no se detectó diferencia entre sexo ni para las medias, ni para las varianzas. En la Tabla 2 se dan los valores de los caracteres externos, la relación cola-cuerpo (CO/CU) y el peso de las especies estudiadas. Otros caracteres de la morfología externa se presentan en Borroto (2002). En la Fig. 1 se

	Tamaño de muestras por análisis			
Taxones utilizados	**MEP**	**MC**	**VC**	**M**
Capromys pilorides (sensu lato), **Cp**	**235**	**68**	**37**	-
C. p. pilorides, Cpp	147	-	18	2
C. p. relictus, Cpr	16	-	7	2
C. p. ciprianoi, Cpc	59	-	12	2
C. p. doceleguas, Cpd	-	-	-	-
C. pilorides ssp. Cpss	13	-	-	-
Capromys sp. Csp	-	-	-	1
Mysateles garridoi, Mgar	-	1	-	-
Mysateles prehensilis, Mp	118	33	25	2
Mysateles gundlachi, Mg	42	27	15	4
Mysateles melanurus, Mm	43	45	15	5
Mysateles meridionalis, Mmer	-	2	-	-
Mysateles sp. Msp	3	3	-	1
Mesocapromys auritus, Meau	6	17	3	-
Mesocapromys sanfelipensis, Mesa	-	7	-	-
Mesocapromys angelcabrerai, Mean	24	14	6	2
Mesocapromys nanus, Mena	10	7	-	-
Geocapromys browni, Gb	30	31	5	1
Geocapromys thoracatus, Gt	10	9	-	-
Geocapromys ingrahami, Gi	21	24	7	2
Plagiodontia aedium, Pa	14	21	2	2
TOTALES	556	309	115	26

Tabla 1. Especies y subespecies estudiadas en los diferentes análisis. MEP, medidas externas y peso; MC, medidas craneales; VC, volumen craneal; M, estudio molecular. En la suma de totales se considera a *Capromys pilorides* en *sensu lato*. *Capromys* sp. es un espécimen de Cayo Ballenato del Medio, Bahía de Nuevitas, al Norte de Camaguey, localidad que esta fuera de la distribución de *C. p. gundlachianus*. *Mysateles* sp. son especimenes de las localidades de Monte Verde, Yateras y Baracoa, Guantánamo, con variaciones en el color del pelaje.

Taula 1. *Espècies i subespècies estudiades a les diferents anàlisis. MEP, mesures externes i pes; MC, mesures cranianes; VC, volum cranià; M, dades moleculars. A la suma de totals es considera* Capromys pilorides *en* sensu lato. Capromys *sp. és un espècimen de Cayo Ballenato del Medio, Badia de Nuevitas, al Nord de Camaguey, localitat que es troba fora de l'àrea de distribució de* C. p. gundlachianus. Mysateles *sp. són espècimens de les localitats de Monte Verde, Yateras i Baracoa, Guantánamo, amb variacions en el color del pelatge.*

presenta la proyección bivariada de los valores medios del peso respecto LT y la relación CO/CU. La media del peso varía entre 3782,7 g en *Capromys pilorides* y 483 g en *Mesocapromys angelcabrerai*. Dentro de este intervalo caen los pesos de las especies de los otros tres géneros; *Mysateles* con especies que promedian entre 1231,4 y 1799,4 g; *Geocapromys* que varía entre 737,9 y 1741,9 g y *Plagiodontia* promedia 936,5 g. Los valores medios y las amplitudes de los caracteres morfológicos externos coinciden con los de otros autores (Varona, 1970a, 1979, 1986; Varona en Varona & Garrido, 1970; Kratochvíl *et al.*, 1978; Anderson *et al.*, 1983; Morgan, 1985, 1989; Woods & Ottenwalder, 1992).

Capromys pilorides ocupa el extremo de la distribución con mayor LT y *Mesocapromys nanus* es la más pequeña dentro de la familia. Las especies de *Mysateles* y *C. pilorides* se separan en este carácter; mientras que *Mesocapromys*, *Geocapromys* y *Plagiodontia* solapan algo sus distribuciones. La cola (CO) es uno de los caracteres de mayor importancia taxonómica, con variación en los 5 géneros tanto en su valor absoluto, como en su valor relativo al tamaño de la longitud cabeza-cuerpo (CO/CU). Solamente *Mysateles* y *Mesocapromys* tienen una relación muy semejante en esta proporción que les confiere similitud en su aspecto externo (Fig. 1). La cola también difiere en los diferentes géneros en cuanto a su carácter prensil: *Mysateles* y *Mesocapromys* muestran este carácter, en *Capromys* y *Plagiodontia* la cola es "semiprensil" y en *Geocapromys* la cola es muy pequeña y no prensil.

Hay especies de las que se tienen pocos ejemplares en colecciones y los datos disponibles son escasos. En *M. garridoi*, los únicos datos de la morfología externa que existen son los del holotipo y estos valores están dentro de la amplitud del género *Mysateles*, excepto la relación CO/CU que está por debajo; esta relación CO/CU y el color negruzco de la piel fueron caracteres importantes para ubicarla en *Capromys*, aunque con algunas reservas (Varona, 1970b). Los datos ofrecidos en la descripción de *M. meridionalis* (Varona, 1986), están dentro de la amplitud de *M. prehensilis* y *M. gundlachi*, pero la relación CO/CU está muy por debajo para *Mysateles* y fue un carácter importante al describir la especie. De *M. sanfelipensis* se conocen 4 especimenes y sus medidas están dentro de la variación de *Mesocapromys*.

En el análisis multivariado las contribuciones de las variables a cada componente principal (CP) son: en el CP-I la mayor variación (48,8%) la aportan las variables LT, CU y Peso; mientras que en el CP-II (24,2%) son las variables CO, LP y AO. Las medidas más representativas del tamaño de una especie son el peso corporal, la longi-

X ± DE Amplitud (N)							
Especies	Peso	LT	CO	CU	CO/CU	AO	LP
Cp	3 782,7±986,9 1 880-6 903 (228)	740,7±56,8 561-960 (226)	244,9±25,9 131-315 (226)	495,8±43,0 336-625 (233)	0,50±0,05 0,34-0,69 (226)	36,9±3,2 25,0-46,2 (230)	98,1±6,8 78,2-125,0 (229)
Mp	1 799,4±348,8 1 120-2 800 (118)	691,7±34,2 603-780 (117)	303,5±20,3 250-355 (116)	388,0±22,6 334-452 (117)	0,78±0,06 0,66-0,94 (117)	29,0±2,7 22,3-38,8 (108)	80,6±4,6 69,4-90,0 (109)
Mg	1 660,5±354,8 1 000-2 280 (42)	650,1±35,3 580-707 (40)	281,6±18,8 240-322 (40)	370,0±24,9 329-439 (42)	0,77±0,05 0,61-0,87 (40)	29,6±2,9 21,0-41,5 (42)	77,7±3,9 66,5-84,3 (42)
Mm	1 231,4±160,2 1 000-1 640 (45)	615,6±31,9 541-687 (46)	273,3±20,6 212-322 (46)	343,6±17,3 309-378 (46)	0,80±0,05 0,61-0,90 (46)	25,9±2,32 21,6-34,5 (46)	73,1±4,1 65,0-80,6 (46)
Meau	632,8±103,2 450-800 (14)	485,2±24,7 430-513 (14)	197,5±13,5 175-220 (14)	265,3±21,6 235-299 (14)	0,74±0,10 0,64-0,94 (14)	24,4±2,5 20,0-28,1 (14)	60,0±3,2 53,0-65,0 (14)
Mean	483,0±60,1 340-570 (24)	425,9±21,9 399-499 (20)	175,5±11,4 158-208 (20)	251,9±13,1 223-291 (24)	0,70±0,04 0,64-0,81 (19)	24,0±1,6 20,5-27,3 (24)	53,1±2,3 48,9-58,4 (24)
Mena	- -	359,4±40,3 293-395 (5)	163,8±25,9 119-182 (5)	204,7±26,7 174-250 (6)	0,83±0,09 0,69-0,92 (5)	16,5±2,6 14,0-19,0 (4)	43,0±5,8 36,3-46,9 (3)
Gb	1 741,9±576,0 780-2 610 (14)	418,3±60,9 286-514 (31)	52,1±12,4 27-81 (31)	367,3±63,7 250-470 (31)	0,15±0,05 0,07-0,25 (31)	20,5±3,3 15,0-24,0 (6)	70,9±5,1 60,0-78,0 (17)
Gt	850 -	400,9±19,0 375-429 (10)	64,9±4,2 57-70 (10)	336,0±15,2 314-359 (10)	0,19±0,01 0,18-0,20 (10)	- -	65,7±2,6 63,5-69,8 (5)
Gi	737,9±314,7 400-1 240 (10)	387,5±42,7 323-484 (20)	67,8±9,7 52-85 (20)	319,8±36,7 265-399 (20)	0,21±0,03 0,15-0,26 (20)	22,0±4,49 15,0-30,0 (13)	56,0±4,61 51,0-65,0 (13)
Pa	936,5±189,7 720-1 130 (4)	466,5±34,7 378-496 (15)	137,9±9,3 125-156 (14)	330,8±27,1 268-358 (15)	0,4±0,05 0,35-0,53 (14)	21 - (2)	67,7±2,9 65,0-72,0 (4)

Tabla 2. Media (en mm), desviación estándar, amplitud y tamaño de muestra de las medidas externas tradicionales en 11 especies de jutías vivientes. Simbología de las especies en Tabla 1 y caracteres externos definidos en el capítulo de Materiales y Métodos.

Taula 2. Mitjana (en mm), desviació típica, valors màxims i mínims i mida de la mostra de mesures externes tradicionals a 11 espècies de juties vivents. Símbols de les espècies, com a la taula 1, i caràcters externs definits al capítol de materials i mètodes.

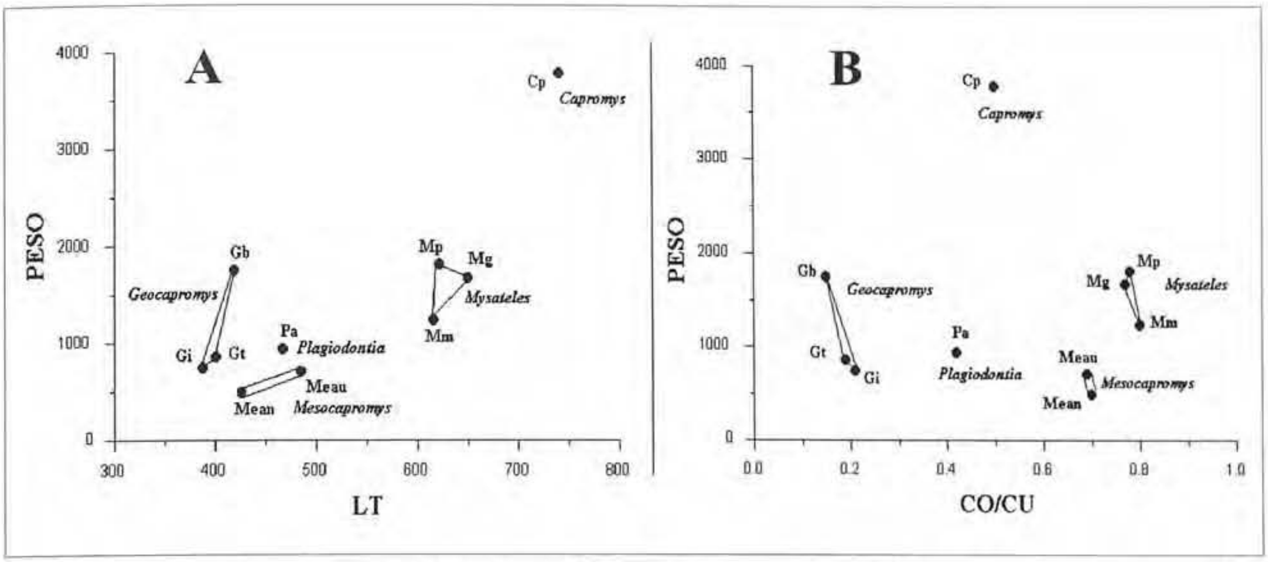

Fig. 1. Proyección bivariada de los valores medios del peso (g) con: A, las longitudes totales (LT) y B, la proporción CO/CU en 11 especies de jutías. Simbología de las especies en Tabla 1.

Fig. 1. Projecció bivariada dels valors mitjans del pes (g) respecte: A, les llargàries totals (LT) i B, la proporció CO/CU a onze espècies de juties. Sigles de les espècies com a la Taula 1.

tud del cuerpo (CU) y la longitud total (LT), ésta última muy influida por el tamaño de la cola. Estas medidas definen las variaciones morfológicas externas y tienen gran importancia como caracteres específicos. Es posible discriminar a los géneros y algunas especies en el análisis de CP (Fig. 2). En el CP-I la amplitud de variación es grande, con *C. pilorides* bien separada en el extremo superior, las tres especies de *Mysateles* en un agrupamiento bien definido y en los limites inferiores de la distribución se agrupan *Mesocapromys*, *Geocapromys* y *Plagiodontia aedium*. En el CP-II las tres especies de *Geocapromys* y *P. aedium*, junto a *C. pilorides*, se separan marcadamente de las especies de *Mysateles* y *Mesocapromys* las que ocupan el límite inferior, evidenciando dos tendencias morfológicas diferentes relacionadas con la robustez. El CP III representó muy poca variación.

En el análisis de agrupamiento a partir de una matriz de Distancia Taxonómica (Fig. 3), se pudieron observar dos agrupamientos mayores formados: uno por las especies del género *Mesocapromys* (pequeñas en tamaño), y el otro por las restantes especies. Dentro de este último se formaron tres subgrupos, el primero compuesto por las especies *C. pilorides* y *G. browni*, el segundo por las especies del género *Mysateles*, con una similitud muy grande entre *M. gundlachi* y *M. prehensilis* y el tercero por dos especies de *Geocapromys* y *Plagiodontia aedium*. Estos grupos están influidos por el efecto del tamaño corporal.

Para extraer el posible efecto del tamaño en estos análisis, se realizó otro agrupamiento después del procesamiento de la matriz de datos por el Método de Burnaby

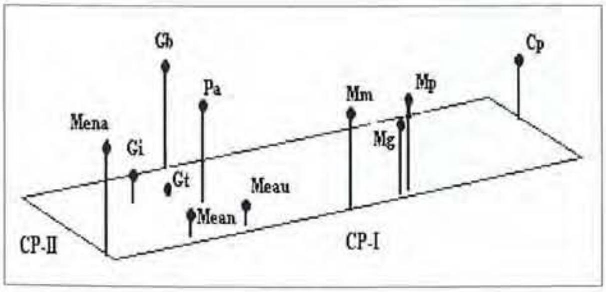

Fig. 2. Proyección tridimensional de los Componentes Principales a partir de la matriz de correlación. Datos estandarizados de la morfología externa en las 11 especies de caprómidos recientes. Se muestran datos promedios. Simbología de las especies en Tabla1.

Fig. 2. Projecció tridimensional dels Components Principals a partir de la matriu de correlació. Dades estandaritzades de la morfologia externa a les 11 espècies de capromiids recents. Es mostren les dades mitjanes. Sigles de les espècies, com a la Taula 1.

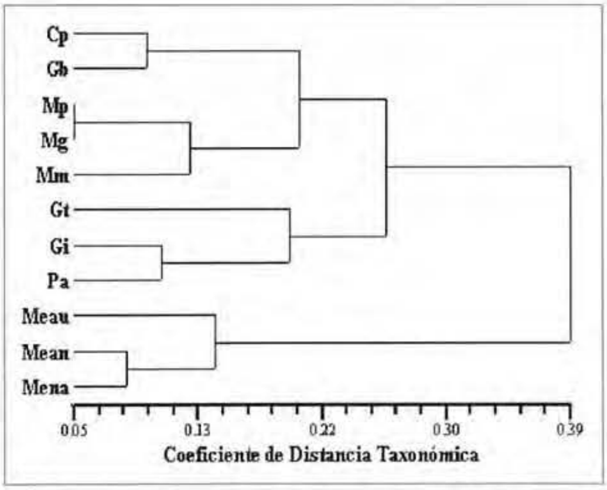

Fig. 3. Dendrograma calculado a partir de la matriz del Coeficiente de la Distancia Taxonómica (opción UPGMA) y 6 variables morfológicas externas en 11 especies de caprómidos. El Coeficiente de Correlación Cofenética (r) fue 0,81. Simbología de las especies en Tabla 1.

Fig. 3. Dendrograma calculat a partir de la matriu del Coeficient de la Distància Taxonòmica (opció UPGMA) i 6 variables morfològiques externes a 11 espècies de capromiids. El Coeficient de Correlació Cofenètica (r) va ser 0,81. Sigles de les espècies com a la Taula 1.

(Fig. 4). Se forman dos agrupamientos, uno con *C. pilorides*, *P. aedium* y las tres especies de *Geocapromys*; mientras que el otro lo conformaron las especies de los géneros *Mysateles* y *Mesocapromys*, que muestran una estructura corporal y proporciones semejantes, y refleja la estrecha relación fenética entre estos dos géneros con respecto a la forma corporal. En la nueva matriz sin efecto del tamaño los nuevos dos primeros componentes principales explican 81,1% y 15,3% de la variación.

Al extraer el efecto del tamaño corporal las especies se agrupan en cuanto a su forma y ambos grupos representan las dos tendencias en las formas morfológicas que se observan en los caprómidos: las especies robustas, de cola más corta y poco prensil, de hábitos más terrestres; y las especies menos robustas, con cuerpos más estilizados, cola larga y prensil, de hábitos más arborícolas. El primer grupo es más diverso por los miembros que lo componen, mientras que, *Mysateles* y *Mesocapromys* muestran afinidades estrechas en la forma de su morfología externa y sólo varían en el tamaño.

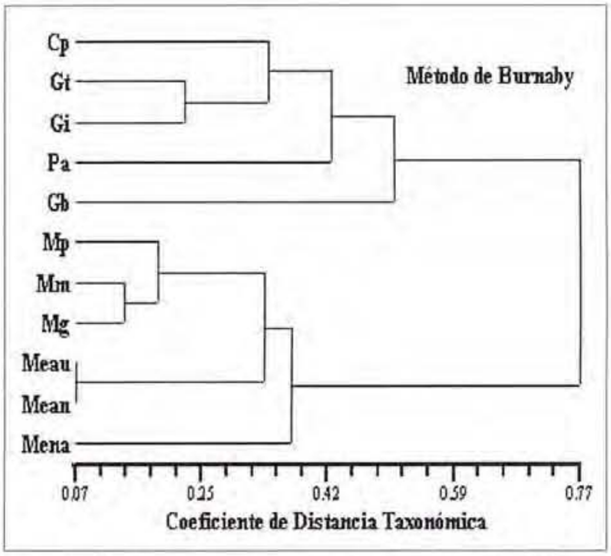

Fig. 4. Dendrograma calculado a partir de la matriz ajustada del Coeficiente de la Distancia Taxonómica (opción UPGMA) obtenida por el Método de Burnaby, para 6 variables morfológicas externas en 11 especies de caprómidos. El Coeficiente de Correlación Cofenética (r) fue 0,86. Simbología de las especies en Tabla 1.

Fig. 4. *Dendrograma calculat a partir de la matriu ajustada del Coeficient de la Distància Taxonòmica (opció UPGMA) obtinguda pel Mètode de Burnaby, per a 6 variables morfològiques externes a 11 espècies de capromïids. El Coeficient de Correlació Cofenètica (r) va ser 0,86. Sigles de les espècies com a la Taula 1.*

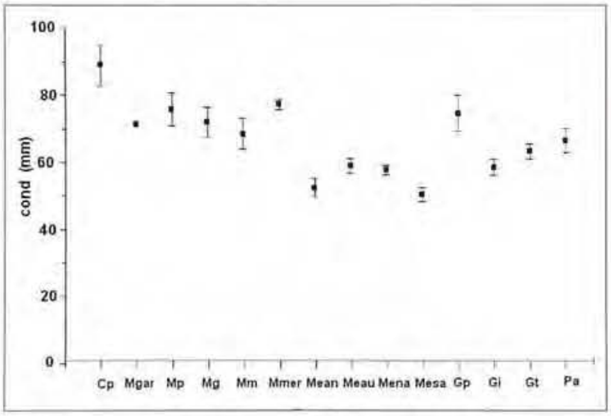

Fig. 5. Media (en mm) y desviación estándar de la longitud condilobasal (COND) en las 14 especies de caprómidos. Simbología de las especies en Tabla 1.

Fig. 5. *Mitjana (en mm) i desviació típica de la llargària condilobasal (COND) a les 14 espècies de capromïids. Sigles de les espècies com a la Taula 1.*

Los análisis bivariados y multivariados de la morfología externa de los caprómidos discrimina bien a la mayoría de las especies y géneros. *M. gundlachi* y *M. prehensilis* son las especies que tienen una mayor similitud en casi todos sus caracteres, y ocupan posiciones muy cercanas en las proyecciones de ambos tipos de análisis. La separación morfológica de estas especies no es lo suficientemente amplia, como era de esperar, para especies diferentes y más bien presentan una diferenciación de nivel subespecífico, como fueron descritas inicialmente. En todos los análisis los tres ejemplares denominados como *Mysateles* sp. se ubicaron dentro de la dispersión de *M. melanurus* y deben ser reconocidos dentro de discha especie. *G. ingrahami* y *G. thoracatus* también mostraron afinidad morfológica. A nivel de género, *Mysateles* y *Mesocapromys* son estructuralmente muy semejantes y esta relación de similitud aumenta al extraer el efecto de tamaño en los análisis.

Caracteres del cráneo

En la Tabla 3 se muestran las medidas de los 33 caracteres craneales utilizados. En el análisis de comparación de medias (Prueba t) y de varianza (prueba F) entre sexo para las 33 variables, solamente 2 caracteres presentan diferencias significativas entre las medias y ninguno para las varianzas y en las dos variables los mayores valores correspondieron a las hembras. El dimorfismo sexual en tamaño no fue apreciable y para el resto de los análisis se combinan los sexos.

Con excepción del arco preorbital (AP) que fue mayor en *G. browni*, *G. thoracatus* y *P. aedium* (criterio taxonómico importante respecto a los otros géneros cubanos) en el resto de las medidas craneales *C. pilorides* tiene los valores mayores. *M. garridoi* tiene la mayoría de los valores de las medidas craneales dentro de la amplitud de variación morfológica craneal que define a *Mysateles*. La dimensión condilobasal (COND) es unas de las más importantes en taxonomía ya que refleja bien el tamaño corporal. La Fig. 5 muestra cómo varía en los caprómidos y las similares dimensiones para los miembros de un mismo género. La mayoría del resto de las variables del cráneo tienen la misma tendencia de variación entre las especies.

El análisis multivariado de los caracteres craneales se realizó en las 14 especies y con las 33 variables craneales. El CP-I aportó 75,8% de la variación, CP-II y CP-III lo hicieron en 5,8 y 2,3% de variación, respectivamente. Dado que el CP-I es considerado como un componente de tamaño corporal, tiene implícito las variaciones basadas en diferencias de tamaño. Una gran cantidad de caracteres contribuyeron con la variación del CP-I, evidenciado por las altas cargas de muchos de ellos, pero los principales aportes fueron: COND, AR, R, IO, CIGO, D y VFP. Para el CP-II los principales aportes fueron de AP, B, BU, ANORB, DHO y N; mientras que en el CP-III los caracteres ANCOA, ANPA, ANORB, DHF y NP son los más importantes.

	X±DE Amplitud													
Caract.	Cp (N=68)	Mgar (N=1)	Mp (N=33)	Mg (N=27)	Mm (N=48)	Mmer (N=2)	Meau (N=17)	Mesa (N=7)	Mean N=14)	Mena (N=7)	Gb (N=31)	Gi (N=24)	Gt (N=9)	Pa (N=21)
CON	89,5±5,3 79,9-102,3	71,2	76,2±4,6 68,0-83,9	72,1±4,4 63,0-78,0	68,5±4,5 56,8-77,1	77,3±1,4 76,3-78,4	59,1±2,2 55,4-62,2	57,8±1,4 55,9-59,7	52,6±2,7 48,5-60,5	50,5±2,0 48,0-54,0	74,6±5,3 62,2-81,9	58,6±2,4 51,4-62,8	63,3±2,2 59,9-66,4	66,5±3,6 58,9-71,6
PAL	44,8±2,8 39,9-52,0	34,7	35,5±2,0 31,5-39,8	33,4±2,4 28,2-39,5	33,6±3,1 29,5-41,7	38,8±1,2 38,7-39,0	29,2±1,3 26,2-31,2	29,0±0,6 28,1-30,2	26,3±1,4 24,0-30,0	24,8±1,2 23,3-26,8	38,5±3,4 30,0-45,9	29,6±1,5 26,2-32,9	32,4±1,4 30,0-34,6	34,3±2,4 30,0-38,1
PBN	34,0±2,4 28,0-41,8	27,8	30,0±1,9 26,9-32,9	28,1±1,8 23,8-31,0	26,3±1,6 22,1-30,7	31,4±1,5 30,3-32,5	22,6±1,2 20,0-25,2	21,7±1,1 20,0-23,1	19,1±1,3 18,0-23,0	20,6±1,7 18,6-23,3	27,3±2,2 22,8-31,9	20,7±1,4 17,6-23,3	23,2±1,2 21,9-25,5	23,1±1,2 20,2-25,0
D	26,1±1,8 22,8-29,9	21,0	20,1±1,1 18,2-22,6	18,8±1,4 15,5-20,9	18,7±1,6 15,2-21,6	21,4±0,6 21,0-21,9	17,3±0,7 16,3-18,5	14,6±0,6 15,9-17,4	14,6±0,7 13,5-16,3	14,1±0,8 13,0-15,1	19,6±1,8 14,3-23,6	15,5±0,9 13,1-17,1	15,9±0,7 15,4-17,8	15,7±1,1 13,5-17,3
R	36,4±2,6 31,1-42,4	27,0	29,8±2,6 25,6-34,7	27,3±2,4 22,2-30,0	26,8±2,5 20,3-31,3	28,6±0,6 28,1-29,0	22,7±1,2 20,7-24,7	22,2±0,4 21,5-22,9	20,2±1,4 17,6-23,6	19,0±1,3 17,2-20,5	30,9±2,8 24,6-37,3	23,3±1,5 19,3-27,4	24,6±1,3 22,6-26,3	25,6±1,6 23,0-28,8
HAM	21,4±1,3 18,6-24,1	17,2	16,7±0,9 15,0-18,2	16,3±1,1 14,5-19,2	15,9±0,8 13,6-17,8	17,2 17,2-17,2	12,7±0,4 11,7-13,3	12,7±0,5 12,1-13,5	11,7±0,7 10,8-13,3	11,6±0,5 10,9-12,5	19,5±1,5 15,9-23,7	15,7±0,7 13,6-16,9	15,5±0,8 14,3-17,6	19,8±1,1 17,6-21,7
B	15,9±1,2 12,7-18,5	14,1	13,2±0,8 11,5-14,8	13,1±0,7 11,9-14,8	12,5±0,6 10,3-14,0	13,9±0,5 13,6-14,3	13,9±0,5 12,9-15,2	13,2±0,5 12,5-14,2	12,0±0,6 10,8-13,4	11,8±0,6 10,5-11,3	12,1±0.8 10,7-14,5	11,4±0,45 10,6-12,1	11,2±0,5 10,0-11,6	11,0±0,6 10,0-12,4
N	28,2±2,4 24,2-34,2	22,2	23,0±2,1 19,2-27,2	20,9±1,9 25,3-16,9	22,2±2,4 15,6-26,5	20,5±1,3 19,6-21,5	19,1±0,8 17,9-20,7	18,9±1,0 17,2-20,3	16,7±0,9 15,3-18,5	15,9±1,0 14,8-17,7	27,3±2,1 22,6-32,0	22,0±1,6 18,5-25,0	22,9±0,8 21,3-23,9	23,3±1,6 19,9-25,9
F	32,4±2,7 26,7-38,0	23,9	28,3±2,0 24,5-32,4	26,3±1,9 21,7-30,5	23,6±2,1 19,2-29,3	27,3±0,6 26,9-27,8	21,6±1,1 19,6-23,5	21,0±1,3 19,6-23,8	19,5±1,6 17,7-23,9	19,6±0,6 18,7-20,5	27,9±2,1 22,8-31,4	20,7±1,5 16,2-23,3	21,9±0,9 20,6-23,8	25,3±1,5 22,5-27,6
DHP	22,1±2,1 17,7-27,2	15,0	16,7±1,0 15,0-18,8	15,9±1,4 12,8-18,3	16,4±1,7 12,2-20,0	17,2±0,28 17,0-17,4	13,6±1,2 10,9-16,4	11,8±1,1 10,5-13,8	11,3±0,8 9,4-13,1	11,5±0,6 10,5-12,3	16,5±1,6 13,7-19,3	12,7±1,5 8,5-14,6	13,7±1,3 10,8-15,4	15,9±1,9 9,8-18,5
DHO	14,0±0,8 12,2-16,8	12,4	12,5±0,8 10,9-14,3	12,7±0,8 10,9-13,9	11,6±1,1 8,2-14,6	13,2±0,5 12,8-13,6	11,9±0,6 11,3-13,4	12,1±0,2 11,8-12,5	11,4±0,5 10,6-12,1	11,5±0,6 11,0-12,7	11,8±1,1 10,0-14,3	10,6±0,6 9,6-12,2	9,8±0,5 9,2-10,9	12,6±2.0 10,1-20,0
FI	10,8±1,3 8,1-15,0	9,3	8,3±0,9 6,5-10,0	7,4±0,6 5,9-9,0	7,9±0,9 4,8-9,8	7,8±1,6 6,7-9,0	8,0±0,6 6,8-9,1	8,0±0,4 7,5-8,8	7,1±0,8 5,8-8,8	8,1±2,7 5,4-12,0	8,9±0,9 5,9-10,5	6,4±1,0 4,5-9,4	7,6±0,7 6,7-9,2	6,3±0,82 5,0-7,6
BA	16,5±2,0 12,0-22,0	11,7	15,7±1,7 12,9-18,9	13,5±1,2 10,3-15,2	12,7±1,3 8,8-15,5	14,7±1,0 14,0-15,5	10,3±0,8 9,0-11,7	10,2±0,7 8,8-11,2	8,9±0,9 7,7-11,0	8,4±0,6 7,3-9,1	14, 3±1,5 9,7-16,7	9,3±0,9 7,6-11,7	11,4±0,8 10,3-12,7	11,9±1,6 9,1-13,9
NC	33,2±1,9 29,0-40,3	28,7	26,8±1,2 24,5-29,4	26,2±0,8 24,2-28,2	25,3±1,3 22,2-27,5	27,0±0,2 26,9-27,2	23,9±0,8 22,7-25,2	23,8±0,7 22,5-24,7	22,7±0,9 21,1-24,8	22,4±0,9 20,6-23,5	29,3±1,5 25,8-32,2	24,4-0,9 23,0-26,7	24,6±0,8 23,4-25,6	28,8±1,4 24,5-31,0
PZ	29,3±1,6 26,1-34,3	24,8	24,5±1,1 22,9-26,3	24,1±0,8 22,8-26,4	23,4±1,5 20,0-28,7	24,7±0,9 24,0-25,4	21,6±0,6 20,5-23,0	22,0±0,8 21,0-23,2	20,5±0,8 18,9-22,4	20,4±0,6 19,3-21,0	25,5±1,3 23,3-28,1	22,2±1,2 20,1-26,5	22,2±0,6 21,0-23,6	25,6±1,6 21,2-28,0
PO	26,4±2,1 22,0-32,7	24,7	21,5±1,3 19,4-23,8	22,0±1,4 19,2-24,5	20,9±1,3 18,3-28,2	22,1±1,9 20,7-23,5	17,4±0,7 15,5-19,2	18,8±0,5 18,3-19,6	17,9±0,9 16,8-20,1	17,7±0,6 16,9-18,6	18,4±1,4 15,5-21,2	18,1±0,9 16,5-20,0	19,4±0,7 18,5-20,8	18,9±1,7 16,0-22,3
AF	30,5±3,1 25,0-39,0	23,5	26,1±2,1 22,8-30,8	23,4±2,0 18,5-27,1	22,2±1,9 18,5-26,4	23,6±1,7 22,4-24,8	16,7±1,1 14,3-18,5	16,3±0,8 15,0-17,6	16,5±0,9 14,7-18,9	15,8±0,6 15,2-16,9	23,4±2,4 18,4-28,2	19,5±1,4 16,1-21,7	20,8±1,27 19,1-22,6	22,1±2,1 17,9-24,6
IO	26,4±2,5 21,9-31,9	20,0	21,1±1,7 18,0-24,5	19,2±1,7 15,3-21,5	18,9±1,6 15,7-22,6	21,2±0,3 21,0-21,5	14,3±0,6 12,8-15,2	14,1±0,5 13,1-14,9	13,4±0,8 11,7-14,7	12,5±0,6 11,5-13,2	23,4±2,.2 19,1-28,0	16,9±1,0 15,0-19,0	17,7±0,8 16,5-19,1	18,1±1,6 14,5-20,4
RO	17,2±1,7 14,3-21,8	14,2	14,4±1,4 12,2-17,9	13,2±1,5 10,1-15,7	12,4±1,5 9,2-15,6	13,2±0,2 13,0-13,4	9,9±0,8 8,5-11,2	9,5±0,7 8,3-10,5	9,0±0,7 8,0-10,6	8,7±0,6 8,1-9,7	16,0±1,5 12,4-18,8	11,3±1,3 9,3-15,6	12,3±0,6 10,9-13,1	12,5±0,9 10,8-13,6
NP	10,9±1,4 8,6-15,5	9,2	9,8±0,9 8,2-11,9	8,7±1,0 6,5-10,4	8,2±1,2 6,0-12,0	10,1±0,1 10,0-10,2	5,8±0,4 5,1-6,7	6,3±0,2 6,1-6,7	5,3±0,5 4,5-6,5	6,1±0,9 4,5-9,1	10,6±1,2 8,1-13,8	7,0±0,8 5,1-8,6	9,6±0,4 9,1-10,3	6,9±0,8 5,6-8,6
NA	14,5±1,6 10,6-18,6	10,9	11,4±0,8 10,0-13,2	11,1±1,2 8,3-13,0	10,9±1,2 8,9-14,1	11,5 11,5-11,5	8,0±0,6 6,5-9,0	7,7±0,4 7,3-8,4	7,0±0,8 5,6-8,7	7,4±0,7 6,6-8,5	11,2±1,2 7,9-13,7	9,3±0,6 8,5-10,1	10,7±0,8 9,5-11,9	9,1±0,8 7,9-10,8
AP	3,9±0,6 2,8-5,8	3,3	2,7±0,6 1,5-3,9	2,5±0,4 1,8-3,5	2,3±0,4 1,6-3,7	3,0±0,4 2,7-3,3	1,8±0,2 1,5-2,4	2,3±0,3 1,7-2,7	1,7±0,2 1,4-2,5	1,3±0,2 1,0-1,8	5,5±1,0 4,0-7,6	3,3±0,4 2,5-4,5	4,9±1,7 4,0-9,5	4,6±1,1 3,4-9,4
AZ	10,6±1,2 8,4-13,7	7,1	7,9±0,9 5,6-9,6	7,6±0,9 5,4-9,1	6,9±1,2 4,6-12,0	8,4±0,7 7,9-9,0	5,8±0,4 5,3-7,0	6,0±0,3 5,5-6,8	5,1±0,5 4,4-6,5	5,0±0,6 4,0-5,9	10,4±1,1 6,6-12,9	6,9±0,8 4,9-9,0	7,9±0,4 7,4-8,5	6,9±0,7 5,6-8,3
BU	12,6±1,0 9,1-14,4	11,6	10,4±1,2 7,8-12,9	10,1±0,9 8,2-11,5	10,0±0,9 7,3-11,3	11,1±0,1 11,0-11,2	10,3±0,7 8,8-11,6	10,0±0,5 9,3-10,6	9,8±0,4 9,1-10,8	8,8±0,9 7,4-10,3	9,5±0,8 8,1-11,3	8,6±0,7 7,2-9,9	8,3±0,3 7,7-8,8	9,1±1,4 4,3-11,1
AR	22,1±2,0 17,6-27,6	17,4	18,1±1,2 16,3-20,5	16,7±1,3 14,0-19,0	15,8±1,2 11,9-17,8	18,6±1,1 17,8-19,4	13,3±0,7 11,7-14,3	12,9±0,6 12,0-13,6	8,8±0,7 10,9-13,8	11,7±0,3 11,0-12,0	19,4±15,4 15,4-22,2	14,4±0,6 13,3-15,6	15,2±0,6 14,2-16,8	16,3±1,1 14,3-18,2
VFP	17,2±1,4 14,2-20,9	12,9	12,9±0,6 11,1-14,4	12,9±0,9 10,7-14,5	11,7±1,1 8,2-14,2	13,7±0,3 13,5-14,0	10,6±1,8 8,1-14,6	10,1±0,6 9,3-11,2	9,1±0,5 8,0-10,2	10,1±1,1 8,4-11,9	14,8±1,5 10,4-18,2	11,3±0,7 9,9-13,1	11,1±0,9 9,3-12,4	10,9±0,8 9,2-12,2
DHF	11,6±1,0 9,7-14,5	11,4	9,4±0,8 7,8-11,0	8,7±0,6 7,1-11,0	8,7±0,5 7,1-9,9	9,5±0,7 9,0-10,0	8,2±0,4 7,4-9,3	8,5±0,3 8,1-9,0	7,3±0,3 7,0-8,4	7,7±0,5 6,6-8,3	9,9±0,6 8,2-10,9	9,0±0,5 8,0-10,0	7,7±0,3 7,1-8,2	9,1±0,6 8,2-11,1
DVF	11,2±0,8 9,8-13,1	10,7	9,0±0,6 7,4-10,9	8,6±0,7 7,4-11,2	8,2±0,8 6,5-9,8	9,0±0,2 8,8-9,2	8,0±0,5 6,6-9,0	8,7±0,4 8,2-9,6	7,4±0,4 6,7-8,3	7,5±0,4 6,8-8,2	9,1±0.8 7,1-10,7	8,8±0,6 7,8-9,9	7,5±0,6 6,5-8,5	8,6±0,5 7,4-10,0
PLT	24,5±1,8 19,8-29,0	16,8	19,6±1,9 16,0-23,4	18,8±1,4 15,3-21,4	18,3±1,7 14,3-22,9	21,1±1,1 19,0-23,3	14,9±0,7 13,8-16,3	14,9±0,3 14,3-15,5	14,8±1,1 12,4-16,8	13,4±1,7 10,1-15,7	19,8±2,5 14,9-23,8	17,3±2,0 12,0-19,6	19,2±1,0 17,9-20,9	21,1±1,1 19,0-23,3
ANCO	5,4±0,8 2,8-7,2	5,2	4,2±0,7 3,0-6,2	4,0±0,6 2,2-5,6	4,2±0,4 3,4-5,4	3,5±0,4 2,9-4,1	3,7±0,3 2,9-4,5	4,4±0,3 4,1-5,0	3,7±0,5 2,8-5,0	3,5±0,4 2,9-4,1	4,4±0,6 3,2-5,9	3,7±0,6 2,1-4,7	3,9±0,2 3,5-4,5	3,9±0,2 3,5-4,5
ANPA	4,5±0,6 3,5-5,9	3,6	3,9±0,4 3,1-4,5	3,7±0,3 3,1-4,3	3,4±0,5 1,8-4,5	4,4±0,2 4,3-4,6	2,7±0,3 2,0-3,1	2,5±0,4 1,7-3,0	2,5±0,2 2,1-3,0	2,5±0,3 2,1-3,0	3,5±0,9 1,7-5,5	2,6±0,4 2,0-4,1	2,8±0,5 1,8-3,8	2,9±0,4 3,5-4,5
CIGO	47,5±3,3 42,1-56,4	37,3	40,9±2,8 35,1-46,5	38,6±2,9 32,1-42,8	36,5±2,4 28,6-40,7	44,2±2,1 40,7-43,7	31,9±1,3 30,0-35,1	31,9±0,7 31,2-33,5	28,6±2,1 24,8-33,5	28,5±1,3 26,6-30,0	43,6±3,8 33,7-51,5	32,6±2,4 24,4-34,8	34,6±1,4 32,4-36,9	40,3±3,0 33,7-44,5
ANOR	14,8±0,9 13,2-16,9	13,6	14,0±0,8 12,3-15,6	13,5±0,9 11,7-15,1	12,5±0,8 10,4-14,5	14,3±0,1 14,3-14,4	12,9±0,8 11,5-14,4	12,2±0,6 11,5-13,4	11,9±0,6 10,8-13,6	12,4±0,4 11,8-13,0	12,7±0,8 10,8-14,4	10,9±0,5 10,2-12,0	11,6±0,6 10,7-12,6	12,4±0,8 11,0-14,5

Tabla 3. Media (en mm), desviación estándar, amplitud y tamaño de muestra de las medidas craneales en 14 especies de jutías. Simbología de las especies en Tabla 1 y de los caracteres craneales en Materiales y Métodos.

Taula 3. *Mitjana (en mm), desviació típica, amplària i mida de la mostra de les mesures cranianes a 14 espècies de jutíes. Sigles de les espècies, com a la Taula 1, i dels caràcters cranians, com s'indica a Materials i Mètodes.*

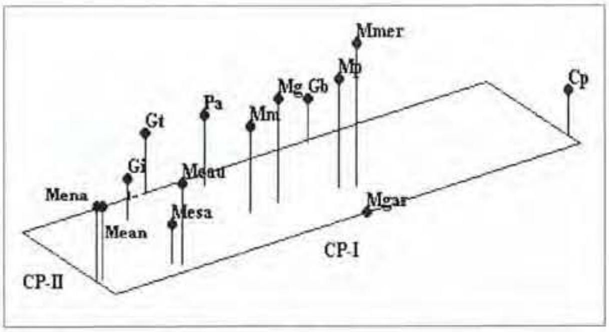

Fig. 6. Proyección tridimencional de los tres primeros Componentes Principales (CP) de 33 caracteres craneales. Datos estandarizados y matriz de correlación. Simbología de las especies en Tabla 1.

Fig. 6. *Projecció tridimencional dels tres primers Components Principals (CP) de 33 caràcters cranians. Dades estandaritzades i matriu de correlació. Sigles de les espècies com a la Taula 1.*

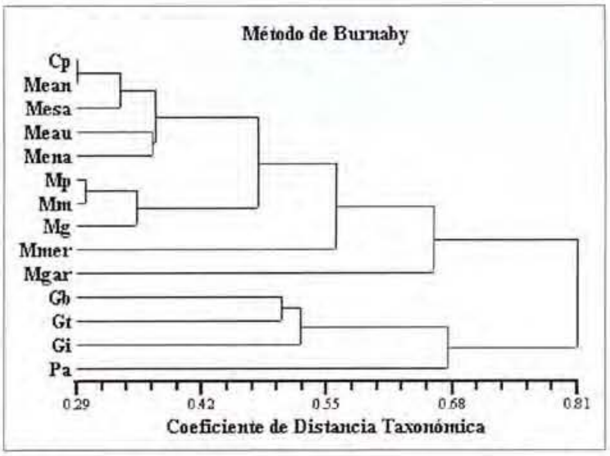

Fig. 8. Dendrograma calculado a partir de la matriz ajustada del Coeficiente de la Distancia Taxonómica (opción UPGMA) obtenida por el Método de Burnaby para 33 caracteres craneales (sin caracteres de la mandíbula) en 14 especies de caprómidos. El Coeficiente de Correlación Cofenética (r) fue 0,87. Simbología de las especies en Tabla 1.

Fig. 8. *Dendrograma calculat a partir de la matriu ajustada del Coeficient de la Distància Taxonòmica (opció UPGMA) obtinguda pel Mètode de Burnaby per a 33 caràcters cranians (sense els caràcters de la mandíbula) a 14 espècies de capromiids. El Coeficient de Correlació Cofenètica (r) fou 0,87. Sigles de les espècies com a la Taula 1.*

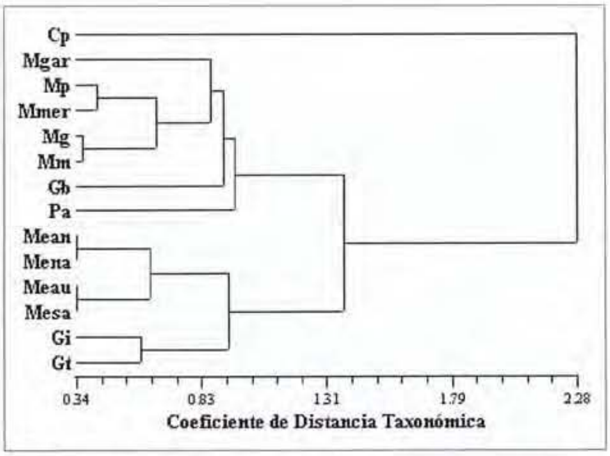

Fig. 7. Dendrograma calculado a partir de la Distancia Taxonómica de 33 caracteres craneales (sin caracteres de mandíbula) en 14 especies de caprómidos (opción UPGMA). El Coeficiente de Correlación Cofenética (r) fue 0,83. Simbología de las especies en Tabla 1.

Fig. 7. *Dendrograma calculat a partir de la Distància Taxonòmica de 33 caràcters cranians (sense els caràcters de la mandíbula) a 14 espècies de capomiids (opció UPGMA). El coeficient de Correlació Cofenètica (r) fou 0,83. Simbología de las especies en Tabla 1.*

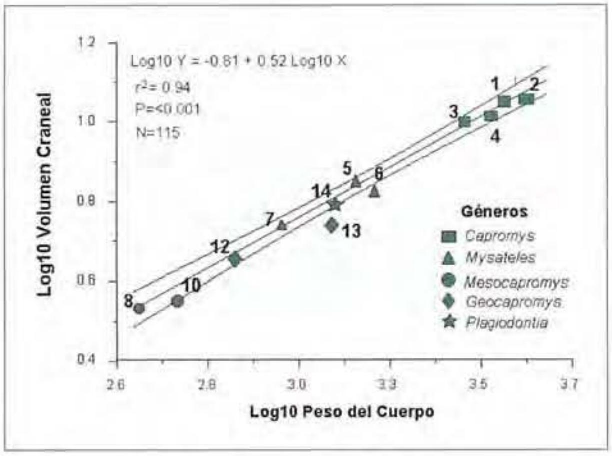

Fig. 9. Regresión del log$_{10}$ del volumen craneal (cm^3) contra los log$_{10}$ del peso corporal (g) para roedores caprómidos. Los puntos representan la media de las especies y los símbolos los géneros. *1, Capromys p. pilorides; 2, Capromys p. ciprianoi; 3, Capromys p. relictus; 4, Capromys pilorides (sensu lato); 5, Mysateles prehensilis; 6, Mysateles gundlachi; 7, Mysateles melanurus; 8, Mesocapromys angelcabrerai; 10, Mesocapromys auritus; 12, Geocapromys ingrahami; 13, Geocapromys browni; 14, Plagiodontia aedium.*

Fig. 9. *Regresió del log$_{10}$ del volum cranià (cm^3) respecte els log$_{10}$ del pes corporal (g) per a rosegadors capromiids. Els punts representen les mitjanes de les espècies i els símbols els gèneres. 1,* Capromys p. pilorides; *2,* Capromys p. ciprianoi; *3,* Capromys p. relictus; *4,* Capromys pilorides (sensu lato); *5,* Mysateles prehensilis; *6,* Mysateles gundlachi; *7,* Mysateles melanurus; *8,* Mesocapromys angelcabrerai; *10,* Mesocapromys auritus; *12,* Geocapromys ingrahami; *13,* Geocapromys browni; *14,* Plagiodontia aedium.

La proyección tridimensional de los tres CP (Fig. 6) revela que en el eje del CP-I se extienden las especies de acuerdo con su dimensión corporal, por lo que se observa un gradiente bien definido en el que las especies del género *Mesocapromys* y *C. pilorides* ocupan los valores extremos de la distribución. Las especies de *Mysateles*, *Geocapromys* y *P. aedium* ocuparon el centro de este eje; y dentro de los géneros mantuvieron su relación. En el eje CP-II hay una marcada separación de las especies de *Mesocapromys*, *Mysateles* y *C. pilorides*, con relación a *Geocapromys* y *P. aedium* que ocupan el extremo superior de CP-II, expresando la variación en forma del cráneo. En la dimensión CP-III se observó que *M. garridoi* se separó del resto de la especies.

En la Fig. 7 se muestra el análisis de agrupamiento a partir de la Distancia Taxonómica y se evidencia que los agrupamientos tienen un alto componente de tamaño pues los tres grupos están asociados al tamaño grande, mediano y pequeño del cráneo de las especies. Las variables que definen estos agrupamientos son las identificadas en el análisis de componentes principales para el CP I. Al aplicar el Método de Burnaby se obtuvo el dendrograma de la Fig. 8, que agrupó a las especies de acuerdo con la forma. Ahora las especies se separan en dos grandes grupos: las especies cubanas por un lado, con dos subgrupos, uno con *C. pilorides* y las especies de *Mesocapromys* y el otro con las especies de *Mysateles*. Al igual que en el análisis de la morfología externa, al extraer el efecto de tamaño la relación fenética entre *Mysateles* y *Mesocapromys* fue mayor. Las especies del resto de las Antillas formaron el otro grupo, con las especies de *Geocapromys* en un subgrupo y con *P. aedium* por el otro. El Coeficiente de Correlación Cofenético fue adecuado (0,87). Este nuevo componente principal explica el 77,7% y el 10,2% de la variación en los primeros dos componentes.

También desde el punto de vista de la morfometría de los caracteres del cráneo, los 3 ejemplares denominados como *Mysateles* sp., se deben considerar como *M. melanurus*.

Volumen Craneal

Para 11 taxones y 115 especimenes de jutías con pesos conocidos, el tamaño del cerebro (expresado en volumen craneal) y el tamaño del cuerpo están funcionalmente relacionados por una tendencia lineal positiva (Fig. 9), expresada por la ecuación: Log_{10} Volumen=-0,81 + 0,523 Log_{10} Peso (coeficiente de determinación de 0,88 y una correlación de 0,94). La distribución de las especies mostró la separación de *Capromys* con respecto a las otras especies, con los valores más altos de volumen craneal para un tamaño del cuerpo dado. Los valores menores correspondieron a *Mesocapromys* y en el medio de la dispersión se ubican los otros géneros. La separación entre especies de diferentes géneros fue marcada.

Esta distribución avala la separación de las especies cubanas en más de un género, contrario al criterio de considerar a *Capromys* como único género para expresar la variación existente en la subfamilia Capromyinae en Cuba (Varona, 1974). Según Lande (1979), dentro de grupos de especies muy relacionadas el principal modo de evolución es, en principio, a través de las dimensiones del cerebro y del cuerpo, recalcando el valor adaptativo del cerebro y su relación con la inteligencia y la significación selectiva del tamaño del cuerpo con respecto a la tasa metabólica, fecundidad, habilidad competitiva, etc.

En la Tabla 4 se muestran los datos de peso, longitud del cuerpo y volumen craneal de los taxones de caprómidos analizados, y los correspondientes valores del coeficiente de encefalización (E.Q.). Las tres subespecies de *C. pilorides*, *Mysateles prehensilis* y *M. melanurus* mostraron valores de E.Q. (Capromyidae) mayores a 1. Estas tres especies son las más abundantes y con mayor distribución entre los caprómidos cubanos y de las Antillas. Pudiera interpretarse que valores altos de encefalización entre los caprómidos, permiten a las especies un mayor éxito por la supervivencia ante factores ecológicos a que tienen que enfrentarse.

	X ± DE (N)		X ± DE	E.Q.		
Especies	Peso (g)	Cabeza+Cuerpo (mm)	Volumen Endocraneal (cm^3)	Mammalia	Rodentia	Capromyidae
1- Capromys pilorides pilorides	3 908,9±1 161,1 (18)	497,7±56,7 (24)	12,74±1,9	0,509	0,682	1,114
2- Capromys pilorides ciprianoi	4 377,5±1 147,0 (12)	495,9±50,6 (12)	12,28±1,5	0,451	0,612	1,013
3- Capromys pilorides relictus	3 060,0±723,1 (7)	473,8±30,4 (7)	11,29±0,7	0,541	0,705	1,122
4- Capromys pilorides (s. lato)	3 913,2±1 147,2 (37)	489,4±31,1 (43)	12,10±1,7	0,483	0,647	1,075
5- Mysateles prehensilis	1 632,0±509,3 (25)	389,4±31,1 (27)	7,45±0,8	0,568	0,691	1,026
6- Mysateles gundlachi	1 757,3±406,7 (15)	370,2±37,7 (24)	7,02±0,	0,507	0,622	0,930
7- Mysateles melanurus	1 172,7±209,1 (15)	343,5±13,4 (17)	6,22±0,4	0,606	0,711	1,017
8-Mesocapromys angelcabrerai	436,7±77,4 (6)	259,5±19,8 (6)	3,59±0,8	0,726	0,764	0,981
9- Mesocapromys nanus	-	201,8±28,7 (5)	3,59±0,3	-	-	-
10- Mesocapromys auritus	726,7±87,4 (3)	290,7±7,2 (3)	4,41±0,3	0,612	0,681	0,925
11- Geocapromys thoracatus	-	333,3±17,1 (6)	4,55±0,5	-	-	-
12- Geocapromys ingrahami	784,1±243,9 (7)	320,6±44,7 (10)	4,81±0,3	0,631	0,708	0,970
13- Geocapromys browni	1 776,4±392,1 (5)	388,7,±46,9 (14)	6,40±0,6	0,459	0,564	0,844
14- Plagiodontia aedium	1 409,5±112,4 (2)	356,2±73,2 (5)	6,63±0,3	0,563	0,675	0,986
15- Dasyprocta fuliginosa	3 900,0±1 555,6 (3)	521,0±23,2 (3)	24,37±3,6	0,975	1,305	-
16- Proechimys guyannensis	220,0±84,8 (2)	247,5±55,8 (2)	2,51±0,1	0,843	0,823	-
17- Proechimys longicaudatus	307,6±88,5 (3)	218,3±34,0 (3)	3,02±0,03	0,791	0,802	-
18- Cavia porcellus	575,7±107,7 (3)	262,5±23,2 (3)	4,45±0,6	0,733	0,796	-

Nota : E.Q. (Mammalia) calculado a partir de la línea de regresión de la clase Mammalia; E. Q. (Rodentia) calculado a partir de la línea de regresión del orden Rodentia ; E. Q. (Capromyidae) calculado a partir de la línea de regresión de la familia Capromyidae.

Tabla 4. Peso corporal , longitud corporal y coeficientes de encefalización en roedores caprómidos y en 4 especies de roedores histricomorfos sudamericanos.

Taula 4. *Pes corporal, llargària corporal i coeficients d'encefalització a rosegadors capromïids i a quatre espècies de rosegadors histricomorfs sudamericans.*

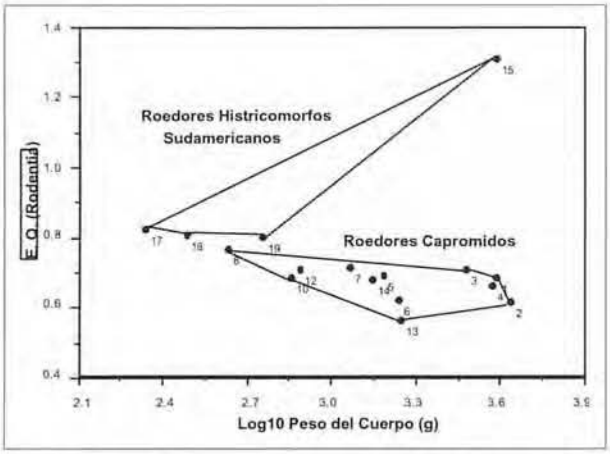

Fig. 10. Diagrama de dispersión del cociente de encefalización [E. Q. (Rodentia)] contra peso corporal en g ($\log_{10}$) para 4 histricomorfos sudamericanos y los roedores caprómidos. Simbología de las especies como en Figura 9 y *15, Dasyprocta fuliginosa; 16, Proechimys guyannensis; 17, P. longicaudatus; 18, Cavia porcellus.*

Fig. 10. Diagrama de dispersió del coeficient d'encefalització [E. Q. (Rodentia)] respecte el pes corporal en g ($\log_{10}$) per a 4 histricomorfs sudamericans i els rosegadors capromiids. Sigles de les espècies com a les Figures 9 i 15, Dasyprocta fuliginosa; *16,* Proechimys guyannensis; *17,* P. longicaudatus; *18,* Cavia porcellus.

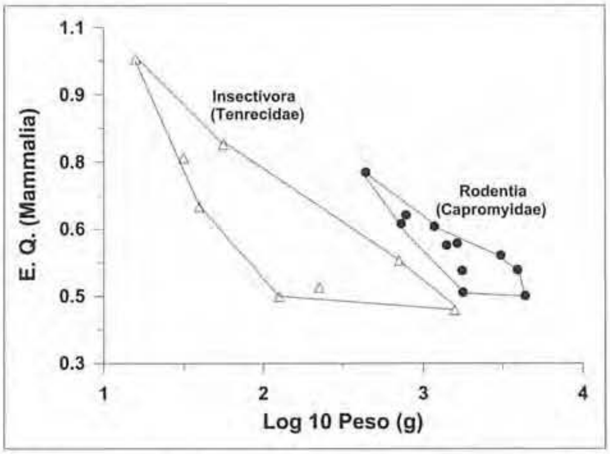

Fig. 11. Diagrama de dispersión del coeficiente de encefalización [E.Q. (Mammalia)] contra peso corporal (log10) para insectívoros tenrécidos en comparación con roedores caprómidos. Los datos de Tenrecidae obtenidos de Eisenberg & Wilson (1981).

Fig. 11. Diagrama de dispersió del coeficient de encefalització [E.Q. (Mammalia)] respecte el pes corporal (log10) per a insectívors tenrècids en comparació amb els rosegadors capromiids. Les dades de Tenrecidae provenen d'Eisenberg & Wilson (1981)

Entre los caprómidos, *Capromys pilorides* es la especie que muestra mayor plasticidad ecológica, habita en una gran variedad de tipos de vegetación, se alimenta de una gran variedad de plantas y es la más abundante y mejor distribuida. Todas estas características pueden estar relacionadas con las presiones de selección que han favorecido un mayor tamaño relativo del cerebro en *C. pilorides.*

Al analizar los valores de E.Q. sobre la base de la ecuación para la clase Mammalia, Capromyidae muestra valores entre los más bajos dentro del orden Rodentia y definitivamente los más bajos dentro de Hystricognathi. Esto significa que los caprómidos tienen un tamaño del cerebro mucho menor que el valor promedio hipotético de la clase Mammalia, en comparación con otros roedores. Los valores de E.Q. (Rodentia) contra peso del cuerpo para cuatro histricomorfos de Sudamérica y los caprómidos, mostraron que estos últimos presentan una menor proporción de tamaño del cerebro para su peso corporal (Fig. 10). Al hacer el análisis de los valores de E. Q. (Mammalia) y el peso corporal de los caprómidos y los insectívoros de la familia Tenrecidae (Fig. 11), se ve que los caprómidos también muestran una relación del tamaño del cerebro con su peso corporal, semejante a la mostrada por esta familia de insectívoros primitivos (considerados como un grupo típico por su estructura cerebral básica o primitiva), y que muestran los menores valores de E.Q. para un peso del cuerpo dado entre los mamíferos. Los histricomorfos han sido considerados, en sentido general, como roedores con altos coeficientes de encefalización (Eisenberg, 1981; Pagel & Harvey, 1989). Los resultados en caprómidos muestran que los histricomorfos tienen una mayor amplitud de variación y los caprómidos (que viven en islas) una tendencia evolutiva diferente.

Los valores bajos de encefalización en los caprómidos con respecto a otros histricomorfos, pueden deberse a su evolución aislada en las Antillas, donde actuó la presión selectiva de evolución sin la presencia de muchos depredadores, más abundantes en zonas continentales. El aislamiento produce especialización del nicho ecológico porque ayuda a evitar la posible competencia directa entre especies relacionadas. Resultados similares se han encontrado al comparar mamíferos de zonas continentales con los de islas (Jerison, 1973; Mace & Eisenberg, 1982). La baja encefalización también puede ser considerada como un carácter primitivo del grupo, comparable en valor a los insectívoros tenrécidos. El tamaño relativo del cerebro tiende a incrementarse durante el tiempo filogenético, en las formas actuales se demuestra que tienden a poseer un grado de encefalización mayor que sus formas ancestrales (Jerison, 1973; Eisenberg, 1981).

Los caprómidos presentan un nicho trófico especializado, con modificaciones en la anatomía del aparato digestivo, que favorecen su alimentación casi exclusivamente a partir de las hojas de una gran variedad de plantas (disponibles de forma continua). Esto puede haber actuado también como presión selectiva para mantener los pequeños tamaños relativos del cerebro en los caprómidos, en comparación con otros roedores de mayor diversidad dietaria. Mace *et al.* (1981) han encontrado que en pequeños mamíferos (roedores y lagomorfos), las especies folívoras tienden a tener menor encefalización que las frugívoras, insectívoras, granívoras y generalistas, que involucran una estrategia de forrajeo más compleja para recursos menos disponibles todo el año y requieren de un gasto energético mayor.

Análisis Molecular

Los resultados aquí mostrados son la continuación y actualización de análisis moleculares previos (Woods *et al.*, 2001). Alguna información será repetida para mantener la integración de este trabajo. Las estimas de la divergencia de secuencia de las primeras 415 bases del gen citocromo b mitocondrial se dan en la Tabla 5, con el índice 2-parámetros de Kimura (Kimura, 1980) y la distancia genética de Tamura –Nei, dentro y entre todos los taxones de caprómidos examinados. La Tabla 6 muestra las estimas de los porcentajes de divergencia de secuencia y de distancia genética (Tamura & Nei, 1993) dentro y entre los principales grupos y géneros.

La divergencia de secuencia entre los taxones de Capromyidae osciló entre 0,4 y 21,7 %, con el nivel más bajo (0,4%) entre dos subespecies de *Capromys pilorides* (*ciprianoi* y *relictus*) de la Isla de la Juventud y similar al que fue observado dentro de las subespecies de *C. pilorides* (X = 0,2%, amplitud 0-0,5%). Entre la subespecie de la Isla de Cuba, *Capromys pilorides pilorides* y las formas de la Isla de la Juventud la divergencia fue 1,8%. Un nivel similar (1,2%) fue observado entre la población de *Mysateles prehensilis* de la región occidental de Cuba y *Mysateles gundlachi* de la Isla de la juventud. Entre los caprómidos que viven en diferentes islas, la divergencia fue de 6,5% entre *Geocapromys browni* y *G. ingrahami*, mientras que la divergencia de *Plagiodontia aedium* con *G. browni* y *C. pilorides* fue de 21,7 y 12,6 % respectivamente (Tablas 5 y 6).

La divergencia entre *Mesocapromys angelcabrerai* y *Mysateles melanurus* fue 3,2%, pero fue 8,8 y 8,3% cuando se comparó esta última con *M. prehensilis* y *M. gundlachi*, respectivamente. El nivel de divergencia entre *C. pilorides* y las especies del género *Mysateles* varió entre 8,6 y 8,7% para *prehensilis* y *gundlachi* y 11,5% para *M. melanurus*, mientras que el nivel de divergencia entre *Capromys* y *M. angelcabrerai* fue 11,5% .

El espécimen referido *a priori* como *Capromys* sp. muestra una tendencia diferente y el grado de divergencia, con respecto a las otras subespecies de *Capromys* (entre 5,5 y 6,4%), es mayor que el esperado. Estos valores son muy altos si se tiene en cuenta que entre las subespecies de *C. pilorides* la variación fue entre 1,9 y 0,4%, por lo que deben ser considerados indicativos de especie diferente. El árbol que muestra las transversiones separa completamente a este taxón de las subespecies de *Capromys*

Taxon	Cpp	Cpc	Cpr	Csp	Mp	Mg	Gi	Gb	Pa	Mean	Mm	Msp
Cpp	0,000	0,017	0,018	0.061	0,095	0,095	0,140	0,153	0,144	0,137	0,137	0,134
Cpc	0,017	0,005	0,004	0.053	0,095	0,092	0,137	0,130	0,138	0,128	0,127	0,125
Cpr	0,019	0,004	0,002	0.055	0,093	0,093	0,138	0,131	0,142	0,129	0,128	0,125
Cpg^1	0.064	0.055	0.056	——-	0.081	0.075	0.140	0.143	0.137	0.094	0.111	0.106
Mp	0,099	0,100	0,097	0.084	——	0,012	0,133	0,142	0,134	0,086	0,081	0,077
Mg	0,099	0,096	0,097	0.077	0,012	0,003	0,139	0,148	0,140	0,089	0,086	0,077
Gi	0,145	0,142	0,143	0.147	0,136	0,142	0,000	0,064	0,180	0,158	0,144	0,139
Gb	0,140	0,138	0,139	0.153	0,150	0,157	0,065	——-	0,204	0,142	0,131	0,132
Pa	0,148	0,142	0,147	0.142	0,136	0,143	0,188	0,217	——	0,166	0,165	0,158
Mean	0,147	0,137	0,138	0.099	0,088	0,091	0,165	0,151	0,174	0.030	0,030	0,035
Mm	0,147	0,136	0,137	0.118	0,083	0,088	0,149	0,138	0,172	0,030	0,011	0,013
Msp	0,143	0,134	0,134	0.112	0,079	0,079	0,143	0,139	0,164	0,035	0,013	

Tabla 5. Estimas de la divergencia en la secuencia basada en las primeras 415 bases del citocromo b para las especies y subespecies, con el Índice 2-parámetros de Kimura encima de la diagonal y la distancia Tamura–Nei debajo de la diagonal. Simbología de las especies en Tabla 1.

Taula 5. *Estimes de la divergència en la seqüència de les primeres 415 bases del citocrom b per a les espècies i subespècies analitzades: l'índex 2-paràmetres de Kimura damunt la diagonal i la distància Tamura-Nei sota la diagonal. Simbologia de les espècies com a la Taula 1.*

Taxones	*Capromys*	*Mesocapromys*	*Mysateles* A	*Mysateles* B	*Geocapromys*	*Plagiodontia*
Capromys	2,3	9,8	8,3	11,2	12,1	12,6
Mesocapromys	0,115	2,9	7,1	3,0	12,5	13,6
Mysateles A	0,095	0,078	1,2	7,5	12,4	12,5
Mysateles B	0,135	0,031	0,082	1,2	12,2	14,2
Geocapromys	0,143	0,149	0,146	0,142	6,0	16,2
Plagiodontia	0,145	0,160	0,142	0,167	0,198	------

Tabla 6. Estimas de la divergencia en las primeras 415 bases del citocromo b dentro y entre géneros y para los clados de *Mysateles*. El porcentaje de la divergencia en la secuencia entre taxones está encima de la diagonal, dentro de los taxones está en la diagonal y la distancia genética de Tamura-Nei (Tamura & Nei, 1993) está debajo de la diagonal. *Mysateles* A incluye *M. prehensilis* y *M. gundlachi* y *Mysateles* B incluye *M. melanurus* y un espécimen *Mysateles* sp.

Taula 6. *Estimes de divergència a les primeres 415 bases del citocrom b, dintre i entre gèneres i als clades de* Mysateles. *El percentatge de divergència a la seqüència entre taxa és a damunt la diagonal, dintre dels taxa és a la diagonal, i la distància genètica de Tamura-Nei (Tamura & Nei, 1993) és per sota de la diagonal.* Mysateles *A inclou* M. prehensilis *i* M. gundlachi, *i* Mysateles *B inclou* M. melanurus *i un espècimen de* Mysateles *sp.*

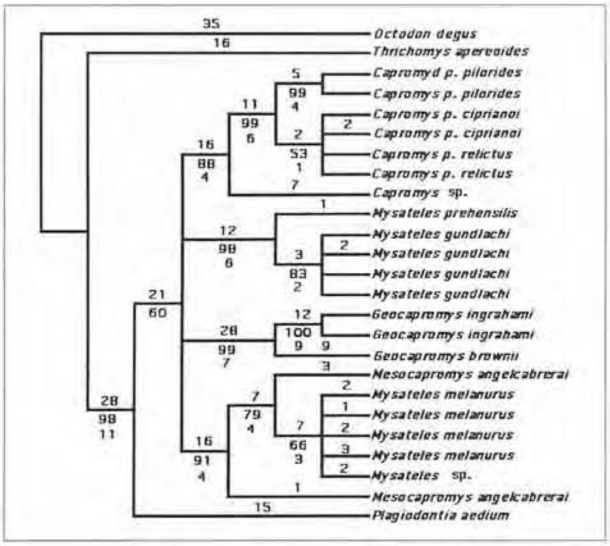

Fig. 12. Árbol consenso estricto de 48 árboles igualmente parsimoniosos de 258 pasos (CI = 0.554; RI= 0.786) de la relación entre caprómidos (se usaron los 110 caracteres filogenéticamente informativos de la secuencia de nucleótidos del gen citocromo b) y *Octodon degus* y *Thrichomys apereoides* como grupos externos. Valores de la longitud de las ramas mostradas encima de las ramas y los índices bookstrap y Bremer debajo.

Fig. 12. Arbre de consens estricte de 48 arbres igualment parsimoniosos de 258 pases (CI = 0.554; RI= 0.786) de la relació entre els capromiids (es varen emprar els 110 caràcters filogenèticament informatius de la seqüència de nucleòtids del citocrom b), emprant Octodon degus *i* Thrichomys apereoides *com a grups externs. Valors de la llargària de les branques situades a damunt de les mateixes i valors de bookstrap a davall.*

(Fig. 13). Se le denominará *Capromys* sp. nov.; sin embargo, para la definición de este posible taxón es necesario esperar la obtención de nuevos ejemplares y de información más precisa sobre el mismo. Este ejemplar, que es morfológicamente igual a *Capromys pilorides*, fue colectado en Cayo Ballenato del Medio, en el extremo este del Archipiélago Sabana-Camagüey. En su captura el cráneo fue deteriorado y hay referencias de que parte de las poblaciones de este cayo son introducidas.

El análisis de máxima parsimonia de los 110 sitios filogenéticamente informativos permitió obtener 48 árboles igualmente parsimoniosos, con una longitud de árbol de 258 pasos. *Plagiodontia* es el único miembro en el clado basal y todos los otros taxones son incluidos en una politomía de cuatro clados. *Capromys* y *Geocapromys* forman clados monofiléticos; *Mysateles*, sin embargo se ubica en dos clados diferentes, uno que contiene a *M. prehensilis y M. gundlachi* y el segundo a *M. melanurus*, el espécimen identificado como *Mysateles* sp. y a *Mesocapromys angelcabrerai*. Los cuatro clados están bien soportados por los índices de *bootstrap* y de Bremer (Fig. 12).

La Fig. 13 es el árbol consenso estricto de 5 árboles igualmente parsimoniosos de 50 pasos, usándose sólo todas las transversiones con información filogenética, mostrando a *Capromys pilorides* como la más basal de las especies cubanas y la que divergió de *Plagiodontia*. El hecho de que *Capromys pilorides* y *Plagiodontia aedium* compartan el tipo de hígado multilobulado (único en mamíferos), avala la posible relación de filogenética entre ambas especies.

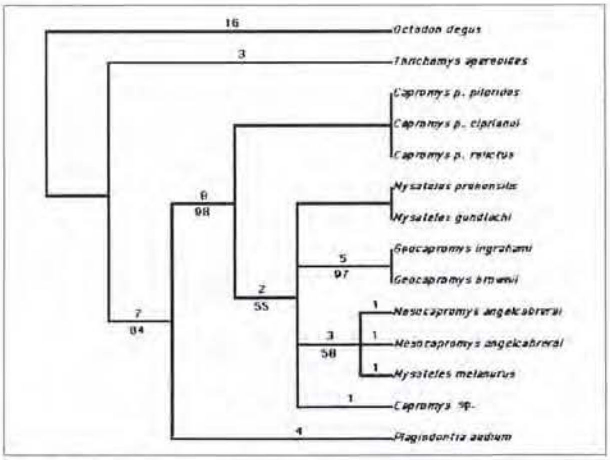

Fig. 13. Árbol consenso estricto de 5 árboles igualmente parsimoniosos de 50 pasos (CI = 0.780; RI= 0.823) de la relación entre caprômidos (se usaron solo las transversiones filogenéticamente informativas de la secuencia de nucleótidos del gen citocromo b) y *Octodon degus* y *Thrichomys apereoides* como grupos externos. Valores de la longitud de las ramas mostradas encima de las ramas y los índices bookstrap debajo.

Fig. 13. Arbre de consens estricte de 5 arbres igualment parsimoniosos de 50 pases (CI = 0.780; RI= 0.823) de la relació entre els capromiids (emprant només les transversions filogenèticament informative de la seqüència de nucleòtids del citocrom b), emprant Octodon degus *i* Thrichomys apereoides *com a grups externs. Valors de la llargària de les branques situades a damunt de les mateixes i valors de bookstrap a davall.*

Aunque morfológica y conductualmente hay diferencias que soportan el reconocimiento de *C. pilorides ciprianoi* y *C. p. relictus* como distintas subespecies del *N* y del *S* de la Isla de la Juventud (Borroto *et al*, 1992), genéticamente hay muy poca divergencia entre estas subespecies. Evaluar la divergencia molecular en subespecies, donde es posible el intercambio genético, es complicado. La categoría subespecífica muchas veces se considera como una categoría geográfica, ecológica e incluso de conservación, pero carece de la objetividad de la categoría de especie y por tanto su significado evolutivo debe ser evaluado con cuidado.

Las estimas de divergencia de secuencia y el análisis de parsimonia soportan el reconocimiento de las dos especies de *Geocapromys* vivientes. Sin embargo *Mysateles prehensilis* del occidente de Cuba y *M. gundlachi* de la Isla de la Juventud tienen ligeramente menos divergencia de secuencia que la observada entre *C. p. pilorides* de Cuba y *C. p. relictus* de la Isla de la Juventud. Estos dos taxones de *Mysateles* forman un clado monofilético y deberían ser reconocidas como subespecies de *Mysateles prehensilis* (*M. p. prehensilis y M. p. gundlachi*). Igualmente, el espécimen *Mysateles* sp. genéticamente es *M. melanurus*, cosa que concuerda con los resultados morfológicos.

El análisis de parsimonia ubicó las formas de *Mysateles* en dos clados distintos. *Mesocapromys angelcabrerai* es el taxón hermano de *Mysateles melanurus* en un clado; mientras que las dos subespecies de *Mysateles prehensilis* están en el otro (Fig. 12). El nivel de divergencia observado entre *Mesocapromys* y *Mysateles melanurus* (3,2%) sugiere que estos taxones son congenéricos, siendo incluso de nivel semejante al de poblaciones de una misma especie, a pesar de distinguirse perfectamente desde el punto de vista morfológico. Teniendo en cuenta este nivel de divergencia sería conveniente ubicar a *melanurus* en el género *Mesocapromys* y la similitud existente entre esta especie y *Mysateles prehensilis* sería explicada por un proceso de convergencia evolutiva. La amplitud de la variación morfológica del género *Mesocapromys* sería mayor, al mismo tiempo se acotaría la variación de *Mysateles*.

Plagiodontia aparece como el linaje basal de los caprómidos (Figs. 12 y 13) y los niveles de divergencia de secuencia soportan su reconocimiento como un género distinto. Una cuestión por dilucidar es cuántos otros géneros de roedores caprómidos están representados entre los taxones muestreados en este estudio. Una posibilidad pudiera ser que cada uno de los cuatro clados representa un género distinto (*Capromys, Mysateles, Geocapromys* y *Mesocapromys*, incluyendo a *Mysateles melanurus* en este último) la mayoría de los cuales son monotípicos. Sin embargo, el nivel de divergencia de secuencia observado en los 2-parámetros de Kimura (Tabla 5) están bien dentro de la amplitud y cerca de la media de 0,112 para especies de mamíferos congenéricas reportada por Johns & Avise (1998). Adicionalmente, el nivel de la distancia de Tamura–Nei observados entre *Capromys* y *Mysateles prehensilis* están dentro de la observada entre especies de *Ctenomys* (Lessa & Cook, 1998) y están bien por debajo del nivel visto entre géneros de roedores equímidos (Lara *et al.*, 1996). No obstante, los procesos evolutivos, para alcanzar un cierto nivel de divergencia genética, son muy particulares de cada grupo y es de esperar que la naturaleza de las presiones de selección sean diferentes en las islas y en los continentes (Grant, 1998).

Los caprómidos, al igual que otros roedores histricognatos, tienen tasas metabólicas bajas, bajos coeficientes de encefalización, largos períodos de gestación, tasa reproductiva baja con crías en estado precocial y son longevos; por lo que, es probable que el reloj molecular en los caprómidos corra más despacio que en otros roedores. Aparentemente, en los roedores caprómidos existen diferencias entre la evolución molecular y la morfológica. Esto se evidenció previamente en los análisis enzimáticos y morfológicos (Camacho *et al.*, 1995) y ha sido hallado en otras especies de roedores (Zimmerman *et al.*, 1978; Nevo & Cleve, 1978; Avise & Aquadro, 1982; Nevo, 1985).

El nivel de divergencia genética observada en la transversión de la tercera posición entre todos los pares de comparaciones es usado para estimar la divergencia en el tiempo (Irwin *et al.*, 1991). Diferentes relojes moleculares para el citocromo b han sido sugeridos (Irwin *et al.*, 1991; Smith & Patton, 1993), pero la selección apropiada es problemática. Aquí se siguió el criterio de Smith & Patton (1993) de 1,8 %/millon de años, como la tasa que encontraron con mejor correspondencia con los datos fósiles para histricognatos de la familia Ctenomyidae (Lessa & Cook, 1998).

Estos datos moleculares sugieren que *Plagiodontia* en La Hispaniola divergió de otros roedores caprómidos hace alrededor de 20 Ma (millones de años) y *Geocapromys* se separó aproximadamente hace 17 Ma. *Mesocapromys* (incluyendo *melanurus*), *Mysateles* y *Capromys* divergieron entre 17 y 19 Ma. Entre especies, la menor divergencia se da entre *Mesocapromys angelcabrerai* y *M. melanurus* (4,3 ma) y la mayor entre *Plagiodontia* y las dos especies de *Geocapromys* (23,3 y 21,7 Ma). La divergencia entre las formas de *Capromys* pertenecientes a la Isla de la Juventud y de la Isla de Cuba ocurrió hace alrededor de 2,4 Ma; mientras que entre los taxones de *Mysateles* de la Isla de Cuba y la Isla de la Juventud la separación ocurrió hace alrededor de 0,8 Ma.

Nuevo arreglo taxonómico para las especies recientes

No obstante que el análisis morfológico y molecular se realizó en las especies de caprómidos recientes de las subfamilias Plagidontinae y Capromyinae, y sobre esta última recaen las novedades del arreglo taxonómico, es conveniente incluir todas las especies y los géneros (fósiles y vivientes) de la Familia Capromyidae, así como la actualización de la sinonimia de géneros y subgéneros, parcialmente referida en Woods (1993). En letras negras se señalan las novedades de este nuevo arreglo taxonómico.

Familia Capromyidae Desmarest, 1822
Subfamilia Capromyinae Smith, 1842

Género *Capromys* Desmarest, 1822
(incluye *Procapromys* Chapman, 1901;
Macrocapromys Arredondo, 1958 y
Paleocapromys Varona & Arredondo, 1979)

†*Capromys acevedo* Arredondo, 1958
†*Capromys antiquus* Varona & Arredondo, 1979
†*Capromys arredondoi* Varona, 1984
†*Capromys latus* Varona & Arredondo, 1979
†*Capromys pappus* Varona, 1984b
†*Capromys robustus* Varona & Arredondo, 1979
Capromys pilorides (Say, 1822).
C. pilorides pilorides (Say, 1822).
C. pilorides relictus G. M. Allen, 1911.
C. pilorides ciprianoi Borroto, Camacho & Ramos, 1992.
C. pilorides gundlachianus Varona, 1983.
C. pilorides doceleguas Varona, 1980.
***Capromys* sp.** 1 (Cayo Ballenato del Medio, Camaguey, Cuba)
†*Capromys* sp. 2 (Islas Caimán)

Género *Mysateles* Lesson, 1842
(incluye *Brachycapromys* Varona & Arredondo, 1979 y
Leptocapromys Kratochvíl, Rodríguez & Barus, 1978)

Mysateles garridoi (Varona , 1970)
†*Mysateles jaumei* (Varona & Arredondo, 1979)
Mysateles meridionalis (Varona, 1986)
Mysateles prehensilis (Poeppig, 1824)
M. prehensilis gundlachi* (Chapman, 1901). *stat. nov.
M. prehensilis prehensilis (Poeppig, 1824)

Género *Mesocapromys* (Varona 1970)
(incluye *Paracapromys* Kratochvíl, Rodríguez & Barus, 1978; *Pygmaeocapromys* Varona, 1979 y *Stenocapromys* Varona & Arredondo, 1979)

Mesocapromys angelcabrerai (Varona, 1979)
Mesocapromys auritus (Varona, 1970)
†*Mesocapromys barbouri* (Varona & Arredondo, 1979)

†*Mesocapromys beatrizae* (Varona & Arredondo, 1979)
†*Mesocapromys delicatus* (Varona & Arredondo, 1979)
†*Mesocapromys gracilis* (Varona & Arredondo, 1979)
†*Mesocapromys kraglievichi* (Varona & Arredondo, 1979)
Mesocapromys melanurus* (Poey en Peters, 1865). *comb. nov.
†*Mesocapromys minimus* (Varona & Arredondo, 1979)
Mesocapromys nanus (G. M. Allen, 1917)
Mesocapromys sanfelipensis, (Varona en Varona & Garrido, 1970)
†*Mesocapromys silvai* (Varona & Arredondo, 1979)

Género *Geocapromys* Chapman, 1901
(incluye *Synodontomys* Allen, 1917)

Geocapromys browni (Fischer, 1830)
†*Geocapromys columbianus* (Chapman, 1892)
†*Geocapromys megas*[1] (Varona & Arredondo, 1979)
†*Geocapromys pleistocenicus* (Arredondo, 1958)
Geocapromys thoracatus (True, 1888)
Geocapromys ingrahami (J. A. Allen, 1891)
G.i. abaconis Lawrence, 1934
G.i. ingrahami (Allen, 1891)
G.i. irrectus Lawrence, 1934
†*Geocapromys* sp. (Islas Caimán)

Subfamilia Plagiodontinae Ellerman, 1949

Género *Plagiodontia* F. Cuvier, 1836
(incluye *Hyperplagiodontia* Rimoli, 1976)

Plagiodontia aedium F. Cuvier, 1836.
P. a. aedium F. Cuvier, 1836
P. a. hylaeum (Miller, 1927)
†*Plagiodontia araeum* Ray, 1964
†*Plagiodontia ipnaeum* Johnson, 1948
†*Plagiodontia spelaeum* Miller, 1929
†*Plagiodontia velozi* Rímoli, 1976
Genero *Rhizoplagiodontia* Woods, 1989

†*Rhizoplagiodontia lemkei* Woods, 1989
Subfamilia Isolobodontinae Woods, 1989

Género *Isolobodon* Allen, 1916
(incluye *Aphaetreus* Miller, 1922 y
Ithydontia Miller, 1922)

†*Isolobodon portoricensis* Allen, 1916
†*Isolobodon montanus* (Miller, 1922)

Género *Zazamys* MacPhee e Iturralde-Vinent, 1995

†*Zazamys veronicae* MacPhee & Iturralde-Vinent, 1995

Subfamilia Hexolobodontinae Woods, 1989
Género *Hexolobodon* Miller 1929

†*Hexolobodon phenax* Miller, 1929
†*Hexolobodon poolei* Rímoli, 1976
†*Hexolobodon* sp. (La Hispaniola)

Discusión General

Integración de los resultados morfológicos

Por primera vez la sistemática de los caprómidos es estudiada en todas las especies vivientes, con tamaños de muestras grandes y con varios métodos de análisis. La utilización de diferentes caracteres de la morfología permite conocer el grado de variación a distintos niveles de integración morfológica, y sometidos a diferentes presiones selectivas (en naturaleza, intensidad y dirección). Los caracteres de la morfología externa están sometidos más fácilmente a la acción directa de los factores del ambiente que el cráneo, el cual soporta elaboradas estructuras tróficas (musculatura masticatoria y dentición), el cerebro y los órganos de los sentidos, todos de importancia vital para los organismos y su interacción con el ambiente. Según Harvey & Bennett (1983) el tamaño del cuerpo responde más fácilmente a la selección que el tamaño del cerebro, en el tiempo evolutivo. Cambios en el volumen craneal, vinculan al sistema nervioso central y tienen un gran significado evolutivo. Otros caracteres anatómicos y sus diferencias entre especies (hígado, cuerpos lúteos, número de vértebras caudales, báculo) abordados en Borroto (2002), representan otro nivel de integridad que es considerado de importancia en la sistemática de taxones superiores (Mayr & Ashlock, 1991). Esta representatividad de diferentes niveles de integración morfológica, analizados por diferentes métodos, resultó en un grado alto de congruencia taxonómica, que permite llegar a conclusiones sólidas y objetivas con respecto a la sistemática de los caprómidos y justifican reevaluar algunos *status* específicos y mantener los géneros *Capromys*, *Mesocapromys*, *Mysateles*, *Geocapromys* y *Plagiodontia* para las especies vivientes de caprómidos.

Capromys, tal y como se evidencia en todos los análisis morfométricos realizados, es una entidad taxonómica bien definida y diferenciada de los otros géneros, que ocupa los extremos superiores de las distribuciones en el espacio morfológico. Actualmente este género tiene una sola especie viviente (*C. pilorides*), pero han sido descritas otras 6 especies fósiles para Cuba. Una forma fósil de *Capromys* se ha reportado para las Islas Caimán y está en proceso de ser descrita como una especie nueva (Morgan, 1994). Aquí se descubre otro nuevo taxón viviente, pendiente de descripción, que por sus características, puede ser considerada una especie críptica, con morfología semejante a *C. pilorides*, pero molecularmente divergente.

Capromys pilorides ha sido considerada por mucho tiempo como la especie más representativa de la familia Sin embargo, lejos de mostrar caracteres que son comunes en el resto de las especies de la misma familia, muestra peculiaridades. Más generalizados son los caracteres presentes en *Mysateles* y *Mesocapromys*, que agrupan un mayor número de especies con una mayor relación fenética.

Mysateles ocupa una posición intermedia en el espacio morfológico y solo muestra los valores mayores en caracteres relacionados con la cola. En algunos análisis comparte esa posición con *Geocapromys* y *Plagiodontia* (volumen craneal) y en aspectos más relacionados al

[1] Según Diaz-Franco (2001) *G. megas* es sinónimo de *Capromys pilorides*.
† Especie descrita como fósil

tamaño que a la forma. La gran similitud de *Mysateles* y *Mesocapromys* en aspectos morfológicos y anatómicos justifica el criterio de su relación fenética estrecha, auque deben ser considerados como géneros distintos por sus diferencias en hábitos y conducta, así como algunos caracteres craneales importantes.

Las especies de *Mysateles* mostraron una estrecha relación. La afinidad entre *M. prehensilis* y *M. gundlachi* (descrita como subespecies de *prehensilis*) es grande en caracteres externos, cráneo y volumen craneal. Varona (1986) propuso su separación, basado en caracteres de báculo. *M. meridionalis* tiene estrecha afinidad con *M. prehensilis* en caracteres craneales, aunque el pequeño tamaño de muestra disponible puede influir en estos resultados y es necesario profundizar en el conocimiento de esta especie.

M. garridoi es una especie con grandes incógnitas, por haber sido descrita como del género *Capromys*, a partir de un animal muerto momificado, encontrado en un cayo sin nombre al NW de Cayo Largo, cuyo cráneo no tenía mandíbula. Sin embargo, en los análisis de los caracteres craneales ocupa una posición bien definida que avala su *status* específico y su posición en el género *Mysateles*. De ser cierta esta posición genérica, sería la primera especie de *Mysateles* descrita para un cayo, fuera de la Isla de Cuba y de la Isla de la Juventud. No fue posible evaluar la encefalización por no disponer de los datos de peso corporal y talla, pero Kratochvíl *et al.* (1980) dan el valor del volumen craneal de *M. garridoi* en 9,0 cm^3, mayor que la amplitud mostrada por las especie de *Mysateles* (5,5-8,0 cm^3).

Mesocapromys agrupa las especies de menor talla y peso corporal, muestra los valores menores en la mayoría de los caracteres craneales y ocupa el límite inferior de la distribución espacial en todos los análisis morfológicos realizados. Morfológicamente *Mesocapromys* y *Mysateles* son los géneros más relacionados, sobre todo en caracteres externos, número de vértebras de la cola y anatomía, mientras que en caracteres craneales existe un solapamiento menor entre ambos géneros. El espacio morfológico entre las especies de *Mesocapromys* fue mayor que el observado en *Mysateles*. *Mesocapromys melanurus* (*comb. nov.*) aumenta la amplitud de los caracteres morfológicos del género.

Geocapromys ocupó un espacio morfológico intermedio en casi todos los caracteres y análisis. Sin duda constituye un género diferente; aunque sus especies estuvieron agrupadas en *Capromys* por mucho tiempo. Desde el punto de vista del tamaño comparten el espacio morfológico de los caracteres craneales con *Mesocapromys*, *Mysateles* y *Plagiodontia* en los diagramas bivariados, por lo que muestran la mayor amplitud de variación. En el espacio multivariado ocupan una posición intermedia (CP-I) entre *Mesocapromys* y *Mysateles*, solapándose ligeramente en los extremos de la distribución de estos dos géneros cubanos y siempre relativamente cerca de *Plagiodontia;* en el otro componente mostraron un definida separación. Las tres especies de *Geocapromys* se separan perfectamente en todos los análisis, mientras que, contrario a lo que se ha considerado, *G. thoracatus* es más afín fenéticamente a *G. ingrahami* que a *G. browni*, de la que fue considerada una subespecie (Morgan, 1985).

Plagiodontia presenta caracteres cualitativos diferenciales marcados, principalmente el patrón de los pliegues del esmalte en los molares, que muestra un ángulo de 45° con respecto al eje del cuerpo, mientras que en el resto de los géneros este ángulo es de 90° (Woods & Howland, 1979). Este carácter es muy importante para ubicar a *Plagiodontia* en otra subfamilia (Plagiodontinae). Su mayor afinidad fenética, en la mayoría de los análisis, es con las especies de *Geocapromys*, coincidiendo con los resultados de Woods (1989b) en un análisis cladístico de caracteres craneales, dentales y musculares. No obstante, la similitud en el tipo de hígado reticulado con *Capromys* es una incógnita por resolver.

A nivel de subgénero se propone simplificar la sistemática de Capromyinae, teniendo en cuenta el carácter subjetivo de este nivel taxonómico y porque dentro de los géneros no existe la suficiente variación morfológica como para hacer subdivisiones.

Implicaciones de los datos de secuencia en el arreglo sistemático, la biogeografía y la historia evolutiva

En las novedades del arreglo taxonómico propuesto, la divergencia de la secuencia de nucleótidos del gen citocromo b fue muy importante. La divergencia de secuencia encontrada entre las formas de *Mysateles* de la Isla de Cuba (*prehensilis*) y la de la isla de la Juventud (*gundlachi*) no soporta mantenerlas como especies distintas, al igual que su similitud morfológica, por lo que deben ser reconocidas como dos subespecies de *M. prehensilis*. En el arreglo taxonómico se considera a *Mysateles prehensilis gundlachi* como *status novus* teniendo en cuenta que por años fue considerada como especies y el cambio constituye una nueva alteración del rango taxonómico (Winston, 1999).

Se propone *Mesocapromys melanurus* (*combinatio nova)* sobre la base del bajo nivel de divergencia en la secuencia de nucleótidos con respecto a *Mesocapromys angelcabrerai* (3,2 %) que sugiere que son especies congenéricas y forman un clado monofilético bien soportado. La similitud morfológica entre *Mesocapromys melanurus* (*comb. nov.*) y *Mysateles prehensilis* se explicaría por procesos de convergencia al explotar hábitats muy similares y estaríamos en presencia de otra especie críptica, sólo detectada molecularmente.

Los datos moleculares son los únicos analizados para *Capromys sp. nov.*, pero el nivel de divergencia en la secuencia con respecto a *Capromys pilorides* (*sensu lato)* es lo suficientemente grande como para que no existan dudas de que constituye un nuevo taxón. Este espécimen mostró dos transversiones más que el resto de las subespecies de *Capromys*, compartidas con el resto de los géneros. Las transversiones ocurren con menos frecuencia que las transiciones y toma más tiempo acumular divergencia por transversión (Hillis & Moritz, 1990; Lara *et al.*, 1996).

La politomía de 4 clados monofiléticos a partir de *Plagiodontia*, bien soportados estadísticamente, justifica molecularmente que se consideren los géneros *Capromys*, *Mysateles*, *Mesocapromys* y *Geocapromys* (la diferenciación morfológica obtenida en los análisis fenéticos también apoya este criterio), aunque el nivel de divergencia es menor que en otros grupos de roedores y mamíferos (Lara *et al.*, 1996; Lessa & Cook, 1998; Johns & Avice, 1998), y es difícil hacer comparaciones cuando la tasa de divergencia varía entre los diferentes grupos (Hillis & Moritz, 1990).

El origen y dispersión de los caprómidos desde el sur, con La Hispaniola y Puerto Rico como centros de irradiación adaptativa fue propuesto por Woods (1989b, 1989c), mientras que el descubrimiento de *Zazamys veronicae* en Cuba confirma la presencia de caprómidos bien definidos en la parte más occidental de las Antillas en épocas tan lejanas como el Mioceno Temprano (MacPhee & Iturralde-Vinent, 1995).

Iturralde-Vinent & MacPhee (1999) proponen una nueva distribución e interrelación de las tierras del Caribe durante el Cenozoico y plantean que hace 33-35 millones de años la Cresta de Aves estaba emergida y conectaba a las Grandes Antillas con el norte de Sudamérica. A esta unidad de tierra, que pudo llegar hasta la parte central de Cuba, la denominan GAARlandia. Woods (1989 b) propuso una unión similar basada en la interpretación geológica de Holcombe & Moore (1977) y Holcombe & Edgar (1990), quienes sugieren que la Cresta de Aves estuvo emergida hasta el Mioceno Temprano. Esta unión de las Antillas con Sudamérica pudo haber representado una oportunidad para la dispersión de los proto-caprómidos hacia las Antillas (Woods, 1989b e Iturralde-Vinent & MacPhee, 1999). Hedges (2001) plantea que es polémico y especulativo el hecho de considerar a la Cresta de Aves como un cinturón continuo de tierra o un collar de islas separadas por el mar y al mismo tiempo que fuera la vía principal o única para la dispersión de la biota antillana, sin tener en cuenta la dispersión por el mar.

La hipótesis de que el centro de la evolución de los caprómidos fue la región de la Cresta de Aves, Puerto Rico y La Hispaniola, se confirma con el hecho de que *Plagiodontia* es la especie más basal de los caprómidos vivientes y es exclusiva de La Hispaniola.

La calibración del reloj molecular para el citocromo b es problemática. En base al reloj de Smith & Patton (1993), *Plagiodontia* divergió del resto de los caprómidos aproximadamente 20 millones de años atrás. Si la estima de los eventos vicariantes de GAARlandia (Iturralde-Vinent & MacPhee, 1999) es correcta, la estima de esta divergencia sería algo más de 12 o 13 millones de años más tardía. Si colocamos el reloj molecular para los caprómidos sobre la base de la vicarianza de La Hispaniola en GAARlandia (Iturralde-Vinent & MacPhee, 1999) en 33 millones de años, entonces se puede recalibrar el reloj molecular del citocromo b y recalcular el tiempo de divergencia. Asumiendo que *Plagiodontia* se separara del resto de los caprómidos hace 33 millones de años, entonces *Geocapromys*, con una mayor distribución geográfica, divergió del resto de las formas aproximadamente al mismo tiempo. Al igual que *Plagiodontia*, *Geocapromys* es un clado distinto y bien definido de acuerdo con los datos moleculares, a pesar de la similitud morfológica encontrada entre ambos grupos en un análisis filogenético (Woods, 1989b).

Dentro de la radiación de las jutías cubanas la separación ocurrió en diferentes momentos. Por un lado el clado *Capromys* (*sensu lato*) y por el otro el de las jutías del género *Mesocapromys* se apartaron del resto de los caprómidos hace alrededor de 16,5 millones de años. Estos clados son fácilmente discernibles.

La jutía carabalí del norte de la Isla de la Juventud (*Mysateles gundlachi*) divergió de la forma representada en la Isla de Cuba (*Mysateles prehensilis*) hace menos de 1,32 millones de años, pero este tiempo no parece suficiente como paraque pueda ser considerada una especie válida, por lo que debe ser denominada como *Mysateles prehensilis gundlachi*. Esto puede implicar que entre Cuba y la Isla de la Juventud los eventos vicariantes fueron incompletos durante el Pleistoceno Medio al Tardío, cuando el nivel del mar fluctuó y esta forma de jutía pudo ocupar una zona de bosque continuo en los momentos de bajos niveles del mar. Sin embargo, *Capromys pilorides* (*relictus* + *ciprianoi*) de la Isla de la Juventud divergió de la forma de Cuba (*C. p. pilorides*) hace 3,96 millones de años, lo que indica un evento vicariante más completo.

Congruencia entre los análisis morfológicos y moleculares

Una de las grandes polémicas de los estudios sistemáticos contemporáneos es el grado de congruencia entre los análisis morfológicos y moleculares (Patterson, 1987; Moritz & Hillis, 1990; Patterson *et al.*, 1993). En este análisis de la sistemática de Capromyidae se observa congruencia entre los resultados morfológicos y los moleculares. Los cinco géneros de Capromyidae, la similitud entre las especies congenéricas y la posición subespecífica de *Mysateles prehensilis gundlachi* se justifican por ambos tipos de análisis. Solamente en la nueva combinación *Mesocapromys melanurus* se pudiera decir que hay incongruencia, teniendo en cuenta la similitud morfológica de esta especie con *Mysateles prehensilis* y los criterios taxonómicos existentes hasta ahora para definir a este último género. Sin embargo,la inclusión de *melanurus* en *Mysateles* ampliaba el diagnóstico del género y ocupaba el límite inferior de la distribución de los caracteres morfológicos, pero en contacto con el extremo superior de la distribución del género *Mesocapromys*. Con esta nueva combinación y con respecto a la distribución de los caracteres morfológicos, se reduce la amplitud del género *Mysateles* en sus límites inferiores y se incrementa la de *Mesocapromys* en sus límites superiores.

CONCLUSIONES

Para las especies vivientes de la familia Capromyidae deben ser reconocidos los géneros *Capromys*, *Mysateles*, *Mesocapromys*, *Geocapromys* y *Plagiodontia*, como entidades bien definidas morfológica y molecularmente y sin separación subgenérica.

La especie críptica *Capromys sp. nov.* a partir del estudio molecular se identifica como un nuevo taxón. Los resultados moleculares justifican la nueva combinación *Mesocapromys melanurus* y puede ser considerada también como una especie críptica. *Mysateles prehensilis gundlachi* debe retomar el *status* de subespecie de *M. prehensilis*, por no existir suficiente divergencia fenética y filogenética que justifiquen su condición específica. *Mysateles garridoi* es una especie bien definida en varios aspectos craneales y debe ser reconocida como tal y en esta posición genérica. *Mysateles meridionalis* debe mantenerse como una especie válida. *Capromys pilorides* es una entidad morfológica y molecular bien definida, con una gran divergencia del resto de las especies. La relaciones fenéticas justifican mantener las subespecies de *C. pilorides*. Las tres especies de *Geocapromys* (*browni*, *ingrahami* y *thoracatus*) están bien definidas morfológica y molecularmente. Filogenéticamente, *Plagiodontia* es la forma más basal de los caprómidos y confirma la hipótesis de que los caprómidos evolucionaron a partir de la parte Central de las Antillas Mayores (La Hispaniola).

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06

CATÀLEG DELS JACIMENTS AMB *MYOTRAGUS* A LES ILLES BALEARS

Pere BOVER & Josep Antoni ALCOVER

BOVER, P. & ALCOVER, J.A. 2005. Catàleg dels jaciments amb *Myotragus* a les Illes Balears. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 51-58.

Resum

El darrer catàleg general de jaciments de *Myotragus* va ser publicat l'any 1981. Posteriorment s'ha publicat un llistat de jaciments de l'espècie a Menorca. Llevat d'aquests treballs sintètics, diversos articles fan referència a nous jaciments de *Myotragus* de les Illes Gimnèsies. A aquestes illes l'exploració de les coves s'ha desenvolupat de forma notable durant aquests darrers 20 anys, amb la realització de descobriments paleontològics importants. Conseqüentment, la quantitat de jaciments amb *Myotragus* s'ha incrementat de manera significativa. El nombre més alt de nous jaciments descoberts correspon als de *M. balearicus*. El nombre de dipòsits coneguts d'aquesta espècie s'ha incrementat des dels 79 jaciments coneguts l'any 1981 fins devers 140 l'any 2004. Pel que fa les espècies més antigues, no s'ha incrementat molt el nombre absolut de jaciments (9 coneguts l'any 1981, 15 el 2004), però hi ha hagut algunes addicions interessants, tals com dos jaciments atribuïts a *M. batei* a l'avenc Socarrat (Calvià, Mallorca) i al cap Pinar (Alcúdia, Mallorca) i dos jaciments de *Myotragus* cf. *antiquus* a la talaia Moreia (Artà, Mallorca) i al Racó de s'Homo Mort (Manacor, Mallorca). Quasi tots els nous descobriments s'han realitzat a la serra de Tramuntana de Mallorca i a la costa Nord de Menorca, gràcies al treball d'alguns grups d'exploració espeleològica i de paleontòlegs de cada illa. A més, s'han començat a realitzar nous descobriments gràcies a l'exploració, mitjançant tècniques d'espeleobusseig, de galeries submergides de diferents cavitats costaneres. Fins a la data, s'han descobert tres jaciments submergits amb ossos de *Myotragus balearicus* a la costa de Llevant de Mallorca.

Paraules clau: *Myotragus*, jaciments, Illes Balears, espeleologia.

Abstract

The last general catalogue of *Myotragus* deposits was published in 1981. From Menorca, a list of deposits has been recently published. Additionally, just several papers introduced a few new *Myotragus* deposits from the Gymnesic Islands in the literature. The exploration of caves in the Gymnesic Islands has been increasingly developed during the last 20 years, with noticeable palaeontological discoveries. Consequently, the amount of deposits with *Myotragus* fossils has increased in a significant number. The more important number of new deposits refers to *M. balearicus*. The number of known deposits of this species has increased from 79 in 1981 to near 140 in 2004. No a great number of additions have occurred in the number of earlier deposits (9 known in 1981, to 15 in 2004), although some important deposits, such as those containing *M. batei* in Avenc Socarrat (Calvià, Mallorca) and Cap Pinar (Alcúdia, Mallorca) and *Myotragus* cf. *antiquus*, in Talaia Moreia (Artà, Mallorca) and Racó de s'Homo Mort (Manacor, Mallorca) have been recently incorporated. Almost all the new discoveries have taken place in the northern mountains of Mallorca, Serra de Tramuntana, and in North coast of Menorca, due to the work of some speleological groups and of some local palaeontologists. Significant new discoveries have been started with the exploration of underwater caves through diving methods. Currently, three underwater sites containing *Myotragus balearicus* bones have been discovered in the Eastern coast of Mallorca.

Key words: *Myotragus*, fossiliferous deposits, Balearic Islands, speleology.

INTRODUCCIÓ

El darrer catàleg general de dipòsits de *Myotragus* va ser publicat fa més de vint anys (Alcover *et al.*, 1981). Aquest treball relacionava tant els jaciments de *Myotragus* explorats pels seus autors com els esmentats a bibliografia anterior, i feia referència a aquelles cavitats, en el cas de *M. balearicus*, en les que havia aparegut, com a mínim, un os de l'espècie. La gran majoria de vegades les restes de *Myotragus* estaven associades a restes osteològiques de fauna acompanyant diversa (*Hypnomys, Nesiotites, Podarcis, Alytes, Discoglossus* i ocells).

Fins l'any 1981 s'havien excavat a fons de forma sistemàtica, amb algun registre estratigràfic, només dos jaciments de *M. balearicus* (Waldren, 1982): la cova de Muleta (Sóller, Mallorca) i la balma de Son Matge (Valldemossa, Mallorca). De les espècies antigues de *Myotragus*, el fet de no disposar de quasi cap jaciment en sediments tous de l'interior de cavitats, i de trobar-se les restes englobades en una matriu més o menys dura, fou la causa què habitualment només es realitzessin extraccions mecàniques

Fig. 1. A. Cova Estreta (Pollença, Mallorca). Acumulació en superfície d'ossos de *M. balearicus.* **B.** Cova des Moro. Excavació del Sector 3. Foto G. Santandreu. **C.** Cova Genovesa. Extracció subaquàtica d'ossos de *M. balearicus.* Foto G. Santandreu. **D.** Racó de s'Homo Mort. Sèrie dentària superior de *M.* cf. *antiquus.* Escala 2 cm.

Fig. 1. A. Cova Estreta (Pollença, Mallorca). Surface accumulation of M. balearicus *bones. B. Cova des Moro. Excavation of Sector 3. Photo G. Santandreu. C. Cova Genovesa. Underwater obtaining of* M. balearicus *bones. Photo G. Santandreu. D. Racó de s'Homo Mort. Upper teeth series of* M. *cf.* antiquus. *Scale bar, 2 cm.*

de blocs de mida diversa de bretxes fossilíferes per a l'obtenció de materials destinats a estudis taxonòmics, habitualment mitjançant la seva extracció de la matriu amb l'ajut d'àcid acètic o mitjançant mètodes físics.

Més recentment s'ha publicat un llistat de dipòsits de vertebrats fòssils de Menorca (Quintana, 1998). Aquest autor relaciona tots els jaciments del Mio-Pleistocè en què apareixen vertebrats fòssils, entre els quals s'ha de destacar la importància del nombre de jaciments amb *Myotragus.* En molts d'aquests jaciments, l'assignació específica de les restes no s'ha pogut dilucidar, i són esmentades com a pertanyents a *Myotragus* sp.

Amb posterioritat al 1981, llevat de l'article esmentat al paràgraf anterior, només uns pocs articles presenten nous dipòsits de *Myotragus* de les Gimnèsies (e.g., Alcover *et al.*, 1997; Encinas & Alcover, 1997; Seguí *et al.*, 1998; Arnau *et al.*, 2000; Trias *et al.*, 2001). Es tracta no només de jaciments paleontològics de rellevància, sinó de localitats que tenen també una importància espeleològica afegida, ja que, almenys en alguns casos, han estat trobats be a cavitats de difícil accés, be a cavitats amb entrades segellades o be a cavitats amb peculiaritats espeleogènetiques notables.

La troballa de nombrosos jaciments amb restes fòssils de *Myotragus* que romanen inèdits a la bibliografia fa que sigui pertinent l'elaboració d'un catàleg actualitzat.

METODOLOGIA

Aquest treball s'ha basat en la recopilació de les dades publicades, així com en la incorporació de dades inèdites disponibles per l'equip de paleontologia de l'IMEDEA. Els materials inèdits als que fan referència aquestes dades es conserven a la col·lecció de vertebrats "Museu de la Naturalesa de les Illes Balears" (Palma de Mallorca). Aquestes darreres dades de jaciments de *Myotragus* provenen de fonts diverses. Amb l'equip de paleontologia col·laboren habitualment diferents espeleòlegs que estan actualment explorant i/o topografiant cavitats de diferents indrets de Mallorca i Menorca. Gràcies a aquesta col·laboració s'han localitzat diferents jaciments.

A les Balears, els jaciments paleontològics estan localitzats majoritàriament a l'interior de les coves, bàsicament enterrats en els sediments del trispol. La troballa de bretxes fossilíferes exteriors és menys freqüent. La freqüència de troballes reflecteix probablement que la quantitat real de jaciments en sediments de l'interior de coves és superior al nombre de bretxes exteriors.

S'ha considerat com a jaciment susceptible de ser inclòs en aquest treball aquella cavitat o bretxa en què ha aparegut, com a mínim, un os sencer o un fragment d'os de

Myotragus, o be restes de copròlits de l'espècie. No s'han tingut en compte aquells jaciments en els que, encara que hagin aparegut ossos de la fauna fòssil acompanyant de *Myotragus*, no s'hagi trobat cap os d'aquest bòvid.

Normalment, als pocs jaciments on han aparegut copròlits també apareixen ossos de *Myotragus* i per tant, aquests estan també considerats en base a l'evidència osteològica. A l'actualitat només es coneixen dos jaciments a Mallorca i un a Menorca on només han sortit copròlits (Son Mulet a Llucmajor, Cuerda *et al.*, 1969; probablement, cap de Cala Figuera, a Calvià, inèdit, i l'illa de l'Aire a Maó, Mercadal *et al.*, 1972) i estan actualment en estudi i discussió.

En aquest treball no s'han inclòs els jaciments que han lliurat únicament petjades o rastres fossilitzats. Fornós *et al.* (2002) fan un recull d'eolianites que conserven restes de petjades de *Myotragus* a la costa de llevant de Mallorca, i Quintana (1993) documenta també la presència de petjades de *Myotragus* a l'illa de Menorca.

Els mapes dels jaciments s'han realitzat mitjançant el programa DMAP, amb les coordenades UTM subministrades pel catàleg espeleològic més recent (Encinas, 1997). D'aquells que no es tenien les coordenades o be s'han pres amb un GPS Magellan GPS 300 o be s'han pres a partir de la seva localització a mapes a escala 1:25000 de l'IGN.

JACIMENTS FOSSILÍFERS AMB *MYOTRAGUS*

L'exploració de coves a les Illes Gimnèsies s'ha desenvolupat molt durant aquests darrers 20 anys, amb descobriments realment importants de jaciments fossilífers. Aquest fet ha provocat que el nombre de dipòsits amb *Myotragus* s'hagi incrementat en nombre considerable. Alguns d'aquests nous jaciments han estat excavats de forma sistemàtica, com ara la cova Estreta (Pollença, Mallorca; Encinas & Alcover, 1997; Fig. 1A), la cova des Moro (Manacor, Mallorca; Trias, 2000; Fig. 1B) i la cova C-2 (Ciutadella, Menorca; Seguí *et al.*, 1998).

Pel que fa a Mallorca, l'increment en el nombre de jaciments ha estat important, en general, a la regió de la serra de Tramuntana. La tasca d'exploració de diferents espeleòlegs com Miquel Trias, Gabriel Santandreu, José Antonio Encinas, entre altres, ha permès la troballa de cavitats noves que contenien restes esquelètiques fòssils al seu interior (e.g., Encinas, 1994; Santandreu, 2002). Per altra banda, l'exploració sistemàtica i el treball de topografia de cavitats de la zona de la serra de na Burguesa (Calvià), ha fet incrementar el nombre de jaciments a aquest indret (Barceló, 1992; Gracia *et al.*, 1997; Barceló *et al.*, 1998; 2003; Vicens *et al.*, 2000; Crespí *et al.*, 2001; Bover *et al.*, 2004), el qual queda ben reflectit als

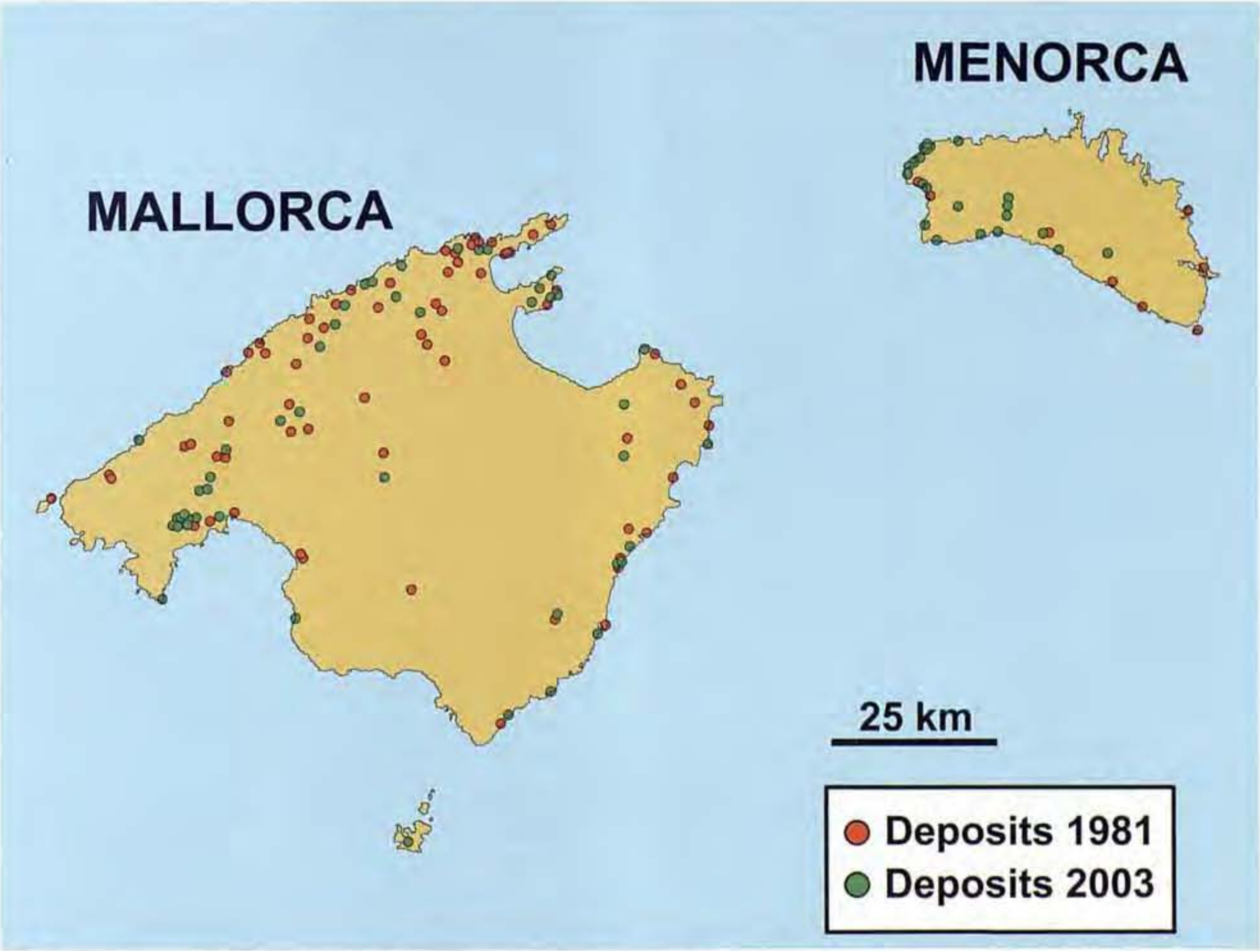

Fig. 2. Mapa de localització dels jaciments de *M. balearicus* i *Myotragus sp.* En vermell se situen els jaciments coneguts abans de 1981; en verd els que els coneguts fins l'any 2003.

Fig. 2. *Location map of* M. balearicus *and* Myotragus sp *deposits. In red, known deposits before 1981; in green, known deposits in 2003.*

mapes presentats. Mentre que a la serra de Tramuntana s'han trobat nous nombrosos jaciments de *M. balearicus* (espècie de cronologia Pleistocè superior-Holocè), a la zona del Llevant de Mallorca, s'han trobat dos nous jaciments amb restes de *Myotragus* antics. La serra de Llevant (Artà) i la costa de Llevant (Manacor) han lliurat dos nous jaciments amb *Myotragus* que podrien pertànyer, amb reserves, a l'espècie *M. antiquus* del Pliocè superior (inèdit). Ambdós jaciments estan actualment en estudi.

A més, a l'illa de Mallorca, s'han iniciat una sèrie de descobriments importants gràcies a l'exploració, mitjançant tècniques d'espeleobusseig, de cavitats que tenen sales total o parcialment submergides (Gracia & Clamor, 2002). Aquestes troballes ens permeten avaluar quin han estat els processos glacioeustàtics a l'illa, i estan aportant dades d'interés per a l'establiment de la cronologia dels jaciments. Actualment, s'han descobert tres cavitats amb restes de *M. balearicus* submergides a la costa Est de Mallorca (Gràcia *et al.*, 2000; 2001; 2003a). A la font de ses Aiguades (Alcúdia, Gràcia *et al.*, 2001b) ha aparegut un sol individu quasi complet, mentre que a la cova de Cala Varques B (Manacor, Gràcia *et al.*, 2000) ha aparegut només una mandíbula. La troballa més espectacular sota aigua, prové de la cova Genovesa (Manacor, Gràcia *et al.*, 2003b; Fig. 1C), on han aparegut restes d'un mínim de 40 individus (F. Gràcia, com pers.) amb zones d'elevada densitat d'ossos (Gràcia *et al.*, 2003a). El fet d'haver estar submergits durant milers d'anys sota aigua salobrosa, ha fet que s'hagin hagut d'emprar tècniques diferents a les habituals per a l'extracció i conservació dels ossos de *Myotragus* extrets d'aquesta cova (Crespí & Bover, en prep.).

La geologia de Menorca (Obrador, 1998) fa que la zona més procliu a contenir jaciments amb restes fòssils de *Myotragus* (i d'altres vertebrats del Plio-Pleistocè) sigui la plataforma miocènica de l'illa, la qual cobreix tot el Migjorn, així com la costa de Ponent situada al nord de Ciutadella. El nombre de jaciments espeleològics s'ha incrementat sobretot al municipi de Ciutadella, gràcies a les tasques d'exploració de diferents espeleòlegs, entre els que cal destacar Pere Arnau (descobridor de nombrosos jaciments paleontològics i de dos jaciments arqueològics importants, la cova des Mussol i la cova des Càrritx, Lull *et al.*, 1999), Bep Márquez (co-descobridor de la cova C-2 juntament amb l'anterior) i Josep Lluis Florit. L'elaboració d'una Tesi Doctoral sobre un conill gegant del Pliocè de Menorca per part del paleontòleg menorquí Josep Quintana, ha comportat una exploració a fons de diferents zones del municipi de Ciutadella. El resultat d'aquesta acurada exploració ha permès troballa de nombrosos dipòsits de fòssils, entre els que es troben nous dipòsits de *Myotragus*.

Taula 1. Llistat de jaciments amb *Myotragus* de Mallorca i Menorca. A Mallorca estan inclosos els jaciments de Cabrera (municipi de Palma) i Dragonera (municipi d'Andratx). (*) indica que es tracta d'un jaciment exclusivament de copròlits. La numeració dels jaciments de Menorca són els proposats per Quintana (1998).

Table 1. Myotragus *deposits list from Mallorca and Menorca. In Mallorca, the deposits of Cabrera (municipality of Palma) and Dragonera (municipality of Andratx) are included. (*) deposits exclusively of coprolites. The numbers of some deposits from Menorca are following Quintana (1998).*

NÚMERO	JACIMENT	MUNICIPI	ESPÈCIE
	MALLORCA		
1	Cala Morlanda	Manacor	*M. pepgonellae*
2	Vall de l'Arboçar	Pollença	*M. pepgonellae*
3	Crulls de Cap Farrutx	Artà	*M. antiquus*
4	Cova des Fum	Sant Llorenç	*M. antiquus*
5	Racó de s'Homo Mort	Manacor	*M.* cf. *antiquus*
6	Cap Farrutx 2	Artà	*M.* cf. *antiquus*
7	Al·luvions de Sencelles	Sencelles	*M. antiquus/ pepgonellae*
8	Pedrera de s'Ònix	Manacor	*M. kopperi*
9	Pedrera de Gènova	Palma	*M. batei*
10	Cap Pinar	Alcúdia	*M. batei*
11	Avenc Socarrat	Calvià	*M.* cf. *batei*
12	Cova innominada son Camps	Palma	*M.* cf. *batei*
13	Cova de Canet	Esporles	*M. antiquus,* *M. kopperi,* *M. balearicus*
14	Cala Bona	Manacor	*M. sp*
15	Far de Cala Figuera	Calvià	*M. sp**
16	Son Mulet	Llucmajor	*M. balearicus**
17	Cap de Menorca	Alcúdia	*M. balearicus*
18	Cova devora la cova de sa Bassa Blanca	Alcúdia	*M. balearicus*
19	Cova Tancada	Alcúdia	*M. balearicus*
20	Font de ses Aiguades	Alcúdia	*M. balearicus*
21	Cova des Garrover	Alcúdia	*M. balearicus*
22	Cova des Bastons	Alcúdia	*M. balearicus*
23	Cova des Bancalets	Alcúdia	*M. balearicus*
24	Covota de sa Penya Roja	Alcúdia	*M. balearicus*
25	Avenc des Vi	Andratx	*M. balearicus*
26	Cova de s'Olla	Andratx	*M. balearicus*
27	Cova des Moro o de s'Aigo (Dragonera)	Andratx	*M. balearicus*
28	Cova 2 del Cap Farrutx	Artà	*M. balearicus*
29	Cova des Tresor	Artà	*M. balearicus*
30	Avenc de na Corna	Artà	*M. balearicus*
31	Cova des Coloms	Artà	*M. balearicus*
32	Sa coveta de Can Canals d'en Puceta	Artà	*M. balearicus*
33	Al·luvions de Búger	Búger	*M. balearicus*
34	Sa Comuna	Bunyola	*M. balearicus*
35	Avenc des Picó	Bunyola	*M. balearicus*
36	Cova de ses Pasteretes	Calvià	*M. balearicus*
37	Avenc de s'Aigo Estiulada	Calvià	*M. balearicus*
38	Coves de Calvià	Calvià	*M. balearicus*
39	Cova des Màrmol	Calvià	*M. balearicus*
40	Covota del Puig Gros de Bendinat	Calvià	*M. balearicus*
41	Avenc des Vent	Calvià	*M. balearicus*
42	Avenc des Mort	Calvià	*M. balearicus*
43	Avenc de n'Andreu	Calvià	*M. balearicus*
44	Avenc de na Picassento	Calvià	*M. balearicus*
45	Cova dets Albons	Calvià	*M. balearicus*
46	Cova Estreta de Gabellí	Campanet	*M. balearicus*
47	Cova de so na Pacs	Campanet	*M. balearicus*
48	Cova de na Barxa	Capdepera	*M. balearicus*
49	Son Jaumell	Capdepera	*M. balearicus*
50	Cova de l'Ermita	Capdepera	*M. balearicus*
51	Cova Nova	Capdepera	*M. balearicus*
52	Avenc de sa Marineta	Deià	*M. balearicus*
53	Avenc de na Donzella	Escorca	*M. balearicus*
54	Cova de sa Campana	Escorca	*M. balearicus*

55	Avenc de Fra Rafel	Escorca	*M. balearicus*
56	Avenc des Gorg Blau	Escorca	*M. balearicus*
57	Comellar de l'Infern	Escorca	*M. balearicus*
58	Coves de la ctra. de Sóller al Puig Major	Escorca	*M. balearicus*
59	Cova Estreta d'Escorca	Escorca	*M. balearicus*
60	Avenc dels Voltors o de na Loli	Escorca	*M. balearicus*
61	Cova de sa Tossa Alta	Escorca	*M. balearicus*
62	Avenc de Muntanya	Escorca	*M. balearicus*
63	Cova Llunyana	Escorca	*M. balearicus*
64	Coveta des Gorgs	Escorca	*M. balearicus*
65	Coval Simó	Escorca	*M. balearicus*
66	Cova des Morro den Bordils	Escorca	*M. balearicus*
67	Avenc Corcat	Esporles	*M. balearicus*
68	Avenc de sa Pedra	Esporles	*M. balearicus*
69	Cova de sa Tanca	Estellencs	*M. balearicus*
70	Cova de Santueri	Felanitx	*M. balearicus*
71	Cova de sa Barbacana 1	Felanitx	*M. balearicus*
72	Cova de sa Barbacana 2	Felanitx	*M. balearicus*
73	Porto Colom	Felanitx	*M. balearicus*
74	Cova des Bous	Felanitx	*M. balearicus*
75	Cova Calenta	Felanitx	*M. balearicus*
76	Cova des Corral des Porcs	Lloseta	*M. balearicus*
77	Badia Blava	Llucmajor	*M. balearicus*
78	Cova Genovesa o d'en Bessó	Manacor	*M. balearicus*
79	Cova Marina des Pont	Manacor	*M. balearicus*
80	Cova de Cala Falcó	Manacor	*M. balearicus*
81	S'Abissament	Manacor	*M. balearicus*
82	Penya Moltona	Manacor	*M. balearicus*
83	Cova des Moro	Manacor	*M. balearicus*
84	Cova des Xots	Manacor	*M. balearicus*
85	Cova des Fumassos	Manacor	*M. balearicus*
86	Cova de Cala Varques B	Manacor	*M. balearicus*
87	Porto Cristo	Manacor	*M. balearicus*
88	Cala Varques	Manacor	*M. balearicus*
89	Cova des Caragol	Palma	*M. balearicus*
90	La Porciúncula	Palma	*M. balearicus*
91	Cova de son Bauçà	Palma	*M. balearicus*
92	Coves del Pilar	Palma	*M. balearicus*
93	Cova de son Maiol	Palma	*M. balearicus*
94	S'Arenal	Palma	*M. balearicus*
95	Coves de son Vida	Palma	*M. balearicus*
96	Cova des Coal	Palma	*M. balearicus*
97	Coves de Génova	Palma	*M. balearicus*
98	Cova del Ram	Palma	*M. balearicus*
99	Pedreres cementiri son Roca	Palma	*M. balearicus*
100	Cova des Penyal Blanc o des Mort (Cabrera)	Palma	*M. balearicus*
101	Cova del Boc	Pollença	*M. balearicus*
102	Cova de can Punxa	Pollença	*M. balearicus*
103	Cova Soleada	Pollença	*M. balearicus*
104	Avenc de la canal de la Coma Freda	Pollença	*M. balearicus*
105	Cova de devora la cova de cal Pesso	Pollença	*M. balearicus*
106	Cova Estreta	Pollença	*M. balearicus*
107	Cova de ses Rodes	Pollença	*M. balearicus*
108	Formentor	Pollença	*M. balearicus*
109	Cova de la Base	Pollença	*M. balearicus*
110	Cova de les Ortigues	Pollença	*M. balearicus*
111	Cala Molins	Pollença	*M. balearicus*
112	Avenc del pla de les Basses	Pollença	*M. balearicus*
113	Cova de can Sion	Pollença	*M. balearicus*
114	Avenc den Joan	Pollença	*M. balearicus*
115	Cova de Llenaire	Pollença	*M. balearicus*
116	Cova de les Quarterades	Pollença	*M. balearicus*
117	Cova del Caló	Pollença	*M. balearicus*
118	Avenc del Naviforme	Pollença	*M. balearicus*
119	Cova de Cornavaques	Pollença	*M. balearicus*
120	Cova dels Dos Canals	Pollença	*M. balearicus*
121	Es bufador de son Berenguer	Santa Maria	*M. balearicus*
122	Avenc de Coanegrina o de can Millo	Santa Maria	*M. balearicus*
123	Avenc de l'Hospital	Santa Maria	*M. balearicus*
124	Cala Figuereta	Santanyí	*M. balearicus*
125	Cova dels Amengual-Sastre	Sencelles	*M. balearicus*
126	Cova de Moleta	Sóller	*M. balearicus*
127	Coval den Pep Rave	Sóller	*M. balearicus*
128	Avenc de ses Formigues	Sóller	*M. balearicus*
129	Racó de s'Argentera I	Sóller	*M. balearicus*
130	Racó de s'Argentera II	Sóller	*M. balearicus*
131	Balma de son Matge	Valldemossa	*M. balearicus*
	MENORCA		
1	Barranc de Binigaus	Es Migjorn Gran	*M.batei*
2	Cales Coves	Alaior	*M. sp*
3	Punta Esquitxador 12	Ciutadella	*M. sp*
4	Punta Esquitxador 13	Ciutadella	*M. sp*
5	Punta Esquitxador 15 (Ses Truqueries)	Ciutadella	*M. sp*
6	Bajolí-Sa Segonya 19	Ciutadella	*M. sp*
7	Sa punta des Sac des Blat 23	Ciutadella	*M. sp*
8	Es Bol de ses Sírvies 24	Ciutadella	*M. sp*
9	Es Bol de ses Sírvies 25	Ciutadella	*M. sp*
10	Ses Capelles 31	Ciutadella	*M. sp*
11	Sa Caleta d'en Gorries	Ciutadella	*M. sp*
12	Son Bou 1	Es Mercadal	*M. sp*
13	Son Bou 2	Es Mercadal	*M. sp*
14	Es Colomar	Maó	*M. sp*
15	Illa de l'Aire	Maó	*M. sp**
16	Cala'n Blanes	Ciutadella	*M. balearicus, M. sp*
17	Cova Murada	Ciutadella	*M. balearicus*
18	Punta Esquitxador 16	Ciutadella	*M. balearicus*
19	Bajolí-Sa Segonya 20	Ciutadella	*M. balearicus*
20	Sa Punta des Gegant 21	Ciutadella	*M. balearicus*
21	Sant Joan de Missa 22	Ciutadella	*M. balearicus*
22	Cova C-2	Ciutadella	*M. balearicus*
23	Cova de les Tres Sales	Ciutadella	*M. balearicus*
24	Coveta de sa Colada	Ciutadella	*M. balearicus*
25	Coveta des Forat	Ciutadella	*M. balearicus*
26	Cova des Mussol	Ciutadella	*M. balearicus*
27	Cova des Càrritx	Ciutadella	*M. balearicus*
28	Cova des Myotragus	Ciutadella	*M. balearicus*
29	Cova des Tancats	Ciutadella	*M. balearicus*
30	Cala Morell	Ciutadella	*M. balearicus*
31	Cova des Bouer	Es Migjorn Gran	*M. balearicus*
32	Cova Bassera	Es Migjorn Gran	*M. balearicus*
33	Cova de na Polida	Es Migjorn Gran	*M. balearicus*
34	Cova de ses Tapareres	Ferreries	*M. balearicus*
35	Cova dels Estrangers	Ferreries	*M. balearicus*
36	Pas d'en Ravull-Sa Penya Fosca	Ferreries	*M. balearicus*
37	Illa del Llatzaret	Maó	*M. balearicus*
38	Cala de Binidalí	Sant Lluís	*M. balearicus*

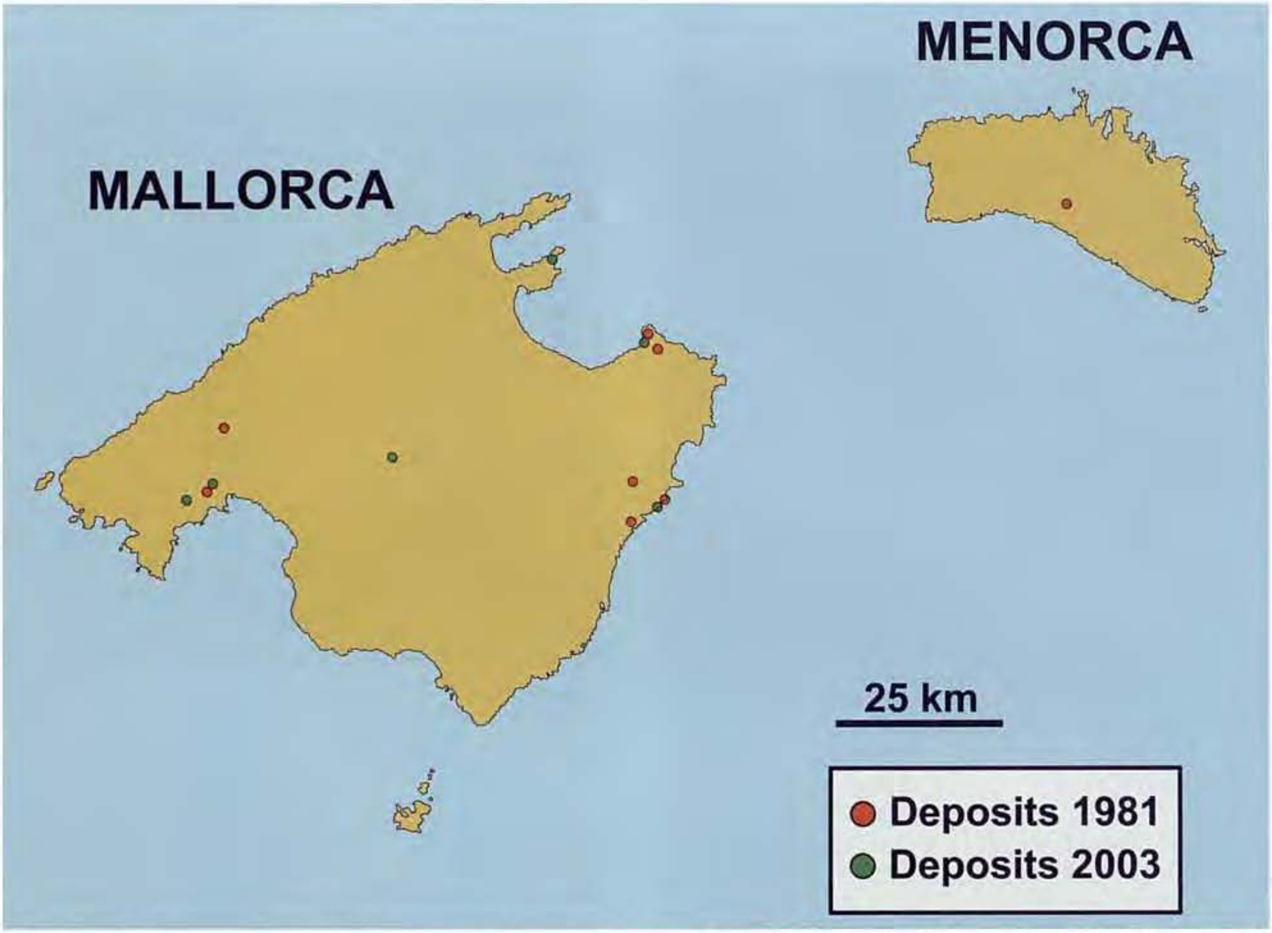

Fig. 3. Mapa de localització dels jaciments de les espècies primerenques de *Myotragus* antics. En vermell se situen els jaciments coneguts abans de 1981; en verd els coneguts fins l'any 2003. La cova de Canet és un jaciment de *M. antiquus* i *M. kopperi* i suposa un sol punt al mapa.

Fig. 3. *Location map of earlier* Myotragus *deposits. In red, known deposits before 1981; in green, known deposits in 2003. Cova de Canet is a* M. antiquus *and* M. kopperi *deposit and it is just drawn with one point in the map.*

D'altra banda, cal esmentar que durant aquests anys s'ha descobert, per primera vegada, la presència de fòssils de *M. balearicus* a l'illa gran de Cabrera, a la cova des Mort o des Penyal Blanc (Alcover *et al.*, 1997). La presència de l'espècie a aquesta illa havia estat deduïda prèviament en base a anàlisis biogeogràfiques i constatada mitjançant la troballa de petjades a eolianites.

El nombre més important de dipòsits nous és el dels que contenen *M. balearicus.* El nombre de dipòsits coneguts d'aquesta espècie s'ha incrementat des dels 79 l'any 1981 fins els 140 el 2004 (Taula 1 i Fig. 2).

En contrast (i per altra banda, per lògica), no s'ha descobert un gran nombre de dipòsits més antics. Dels 9 jaciments coneguts a l'any 1981, només s'ha passat als 15 l'any 2004 (veure Taules 2 i 3 i Fig. 3). La cova de Canet (Esporles) és un jaciment en què s'han trobat tres espècies de *Myotragus* (*antiquus, kopperi* i *balearicus*) (Pons-Moyà *et al.*, 1979), però s'ha comptabilitzat individualment com a jaciment de cada espècie.

Els sis nous dipòsits que aquí consideram inclouen dos jaciments amb restes atribuïbles, amb algunes reserves, a *M. batei* a l'avenc Socarrat (Calvià, Mallorca, Crespí *et al.*, 2001) i a una cavitat innominada de la serra de na Burguesa (Palma, Mallorca; inèdit), un jaciment de *M. batei* al cap Pinar (Alcúdia, Mallorca; Bover & Alcover,

Espècie	Jaciments 1981	Jaciments 2004
Myotragus balearicus	79	140
Myotragus batei	2	3
Myotragus cf. *batei*	0	2
Myotragus kopperi	2	2
Myotragus antiquus	3	3
Myotragus pepgonellae	1	2
Myotragus cf. *antiquus/pepgonellae*	0	3
Myotragus sp	7(*)	17

Taula 2. Comparació del nombre de jaciments de *Myotragus* de l'any 1981 respecte l'any 2004 a les Illes Gimnèsies. (*) Dels set jaciments de *Myotragus sp* de 1981 (cinc a Menorca i dos a Mallorca), sis han estat reubicats com a jaciments de *M. balearicus* i un com a jaciment de *M cf. antiquus/pepgonellae.* Els 17 jaciments de *Myotragus sp* del 2004 són nous.

Table 2. *Comparison of the amount of* Myotragus *deposits in 1981 in relation of those in 2004 in the Gymnesic Islands. (*) six of the seven deposits of* Myotragus sp *in 1981 (five in Menorca and two Mallorca), have been identified as* M. balearicus *deposits and one as M cf.* antiquus/pepgonellae *deposit. The 17 Myotragus sp deposits of 2004 are new.*

1999), dos dipòsit atribuïbles a *Myotragus* cf. *antiquus*, com s'ha citat abans, un a la talaia Moreia (Artà, Mallorca) i l'altre al racó de s'Homo Mort (Manacor, Mallorca; Fig. 1D). D'altra banda s'ha d'afegir a aquest grup el jaciment conegut com a " al·luvions de Sencelles", on inicialment s'havia registrat la presència de *M. balearicus* per Muntaner (1956). Aquest jaciment ha estat re-avaluat i s'ha identificat com a d'una espècie indeterminada de *Myotragus* antic (*antiquus* o *pepgonellae*; Trias *et al.*, 2001). L'únic fèmur que es conserva no permet una diagnosi específica més precisa.

Del registre antic (és a dir, previ a l'any 1981), els dipòsits que han lliurat mostres més abundants de *Myotragus* són la cova de Moleta (Sóller, Mallorca), les coves de Campanet (Campanet, Mallorca), el bufador de Son Berenguer (Santa Maria, Mallorca) i la cova de Son Maiol (Palma, Mallorca). A hores d'ara la cova de Moleta continua sent el jaciment més ric de *Myotragus* que es coneix a les Balears. El jaciment original es troba pràcticament exhaurit. Des de 1981, s'han trobat una sèrie de coves amb mostres molt abundants de *Myotragus*, molt més riques que els altres dipòsits prèviament esmentats, que han estat excavades per l'equip de paleontologia de l'Institut Mediterrani d'Estudis Avançats. Aquestes cavitats són la cova Estreta (Pollença, Mallorca) amb 12600 ossos de *M. balearicus* exhumats en 3 campanyes, la cova des Moro (Manacor, Mallorca) amb més de 9000 ossos exhumats en 6 campanyes i la cova C-2 (Ciutadella, Menorca) amb 1700 ossos extrets en una sola campanya. Aquestes tres coves presenten encara un gran potencial paleontològic. Es tracta de jaciments no exhaurits, ni prou fer-s'hi.

Les perspectives de futur semblen prometedores. A l'inici del segle XXI el registre de dipòsits diguem-ne "normals" és bastant complet. Degut al fet que el territori gimnèsic ha estat profundament explorat, en la nostra opinió, els nous dipòsits a descobrir s'han de reclutar a partir de l'exploració d'indrets que han passat desapercebuts, be per la seva dificultat o be per tenir l'accés enterrat. Són els considerats com a dipòsits "amagats". De fet, durant els darrers anys troballes més espectaculars provenen be de coves amagades (cova Estreta, cova remota en què se va haver de desbloquejar l'entrada per accedir a l'interior; la cova dels Amengual-Sastre, descoberta durant la construcció d'una casa, a Mallorca), be de coves a penya-segats (cova de les Tres Sales, cova de sa Colada i la cova des Forat, a Menorca) o be de coves subaquàtiques (cova Genovesa, cova de Cala Varques B i font de ses Aiguades, Mallorca). Sembla evident que la millora de les diferents tècniques d'exploració espeleològica juntament amb un esforç incrementat de mostreig han permès, i presumiblement també permetran en el futur, el descobriment de noves cavitats d'interès paleontològic. L'exploració de les zones costaneres amb poca coberta vegetal també pot permetre el descobriment d'antics reblits espeleològics amb potencial fossilífer de gran interès, ja que és probable trobar-hi restes de les espècies antigues de *Myotragus*.

AGRAÏMENTS

El nombre de dipòsits de *Myotragus* s'ha vist incrementat gràcies a la inestimable tasca de diversos espeleòlegs: Miquel Trias (Palma de Mallorca), Francesc Gràcia (Palma de Mallorca), Bernat Clamor (Pollença), Miquel A. Gual (Sencelles), Gabriel Santandreu (Marratxí), Damià Vicens (Palma de Mallorca), Damià Crespí (Lloseta), Miquel Àngel Barceló (Calvià), Mateu Vadell (Palma de Mallorca), Antelm Ginard (Llucmajor), José Antonio Encinas (Pollença), José A. Casas (Palma de Mallorca), Vicenç Pla (Palma de Mallorca), Pere Arnau (Ciutadella de Menorca), Bep Quintana (Ciutadella de Menorca), Josep Márquez (Ciutadella de Menorca), Josep Lluis Florit (Maó), Rosa Arregui (Palma de Mallorca) i a totes aquelles persones, que d'un vent o altre han aportat informació rellevant pel que fa a la troballa de nous jaciments. Volem agrair a Pere Arnau (Ciutadella) la localització cartogràfica de diferents nous jaciments inèdits de Menorca. En Gabriel Santandreu ens ha permès publicar fotografies seves a la figura 1. Un dels autors (PB) ha gaudit d'una beca predoctoral de la Direcció General de Recerca, Desenvolupament Tecnològic i Innovació del Govern de les Illes Balears. Aquest treball s'inclou dins del projecte BTE2001-0589 de la Dirección General de Investigación Científica y Técnica (Madrid), "Análisis de la Evolución y Extinción de *Myotragus balearicus* (II)".

Espècie	Mallorca (3620 km^2)	Menorca (694 km^2)	Cabrera (13,2 km^2)	Dragonera (2,6 km^2)
M. balearicus	115	23	1	1
M. batei	2	1	-	-
M. cf. *batei*	2	-	-	-
M. kopperi	2	-	-	-
M. antiquus	3	-	-	-
M. pepgonellae	2	-	-	-
M. cf. *antiquus/pepgonellae*	3	-	-	-
Myotragus sp	2	15	-	-

Taula 3. Nombre de jaciments de *Myotragus* per illes i per espècies. Entre parèntesis s'especifica la superfície de cada illa.

Table 3. *Number of* Myotragus *deposits by islands and species. In brackets, insular area.*

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07

CARPAL BONES, CARPAL FUSIONS AND FOOTPRINTS OF *MYOTRAGUS*: CLUES FOR LOCOMOTION AND BEHAVIOR

Pere BOVER, Joan J. FORNÓS & Josep Antoni ALCOVER

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Resum

Algunes de les característiques anatòmiques de les extremitat de *Myotragus balearicus* demostren que aquesta espècie presentava una locomoció anomenada de "marxes curtes". Entre aquestes característiques cal destacar la fusió del complexe naviculocuboide als cuneïforms gran i petit i al metatars, la pròpia morfologia del ossos de les extremitats, amb ossos molt robusts i amb àrees d'inserció muscular i lligamentosa molt importants. Totes aquestes característiques s'han interpretat com una forma d'establitzar les articulacions degut a un gran pes corporal en relació a l'alçada del cos, en detriment d'una locomoció més cursorial. A més, s'han obtingut alguns ossos procedents de l'excavació dels jaciments de la cova Estreta (Pollença, Mallorca) i la cova des Moro (Manacor, Mallorca) que presenten unes característiques que s'adiuen amb les interpretacions més a dalt presentades. En concret, s'ha obtingut un os resultant de la fusió de l'escafoide i el semilunar, i un os resultant de la fusió del pisiforme i el cuneïforme. Actualment, només es disposa de dos exemplars del primer tipus de fusió i un del segon tipus. Cap d'aquests ossos sembla ser patològic, i no presenten cap tipus de recreixement ossis a la zona de fusió. La fusió de l'escafoide i el semilunar, i la fusió del cuneïforme i el pisiforme semblen provocar una limitació de moviment, i juntament amb les característiques d'altres articulacions (bàsicament de l'extremitat anterior), demostren que les extremitats no estaven situades just davall del cos, tal com passa a quasi tots el bòvids actuals. De nou, sembla que aquestes fusions (juntament amb la robustesa dels ossos del carp) estan relacionades amb l'adquisició d'una major estabilitat de les articulacions.

Les petjades i els rastres poder ser importants fonts d'informació pel que fa a la locomoció i comportament d'espècies fòssil i actuals. A pesar de que es diposa d'una considerable quantitat de petjades de *Myotragus*, només es poden seguir i mesurar molts pocs rastres o pistes. En concret, els jaciments de s'Estret des Temps i ses Piquetes a Santanyí (Mallorca) han proporcionat tres rastres que s'han estudiat aquí en detall. La mesura de la longitud de passa, l'amplada entre extremitats (anterior i posterior) i l'orientació dels potons pot donar algunes pistes sobre la locomoció i el disseny corporal d'aquesta espècie. L'angle dels peus (cap a fora) de *M. balearicus* és considerablment superior a la dels altres espècies d'ungulats estudiades, com *Cervus elaphus* i *Ovis aries*. Aquesta mesura, juntament amb la relativa separació de les extremitats (relacionada amb la longitud de passa), indiquen que les extremitats d'aquesta espècie no estaven situades just davall del cos durant la marxa (com a quasi tots els bòvids actuals), tal com se pot inferir a partir d'altres característiques anatòmiques.

Paraules clau: *Myotragus* - locomoció - ossos del carp - fusions òssies - rastres - etologia.

Abstract

Some of the anatomical features of the *Myotragus balearicus* limb bones show that this species displayed a "low gear" locomotion. These features are the fusion of the nabiculocuboid complex to the large and small cuneiforms and to the metatarsal bone, limb bones morphology and very stout leg bones with important muscular and ligament insertions. All these features have been identified as a way to stabilise the joints due to a great body mass in relation with the body height, in detriment of a cursorial locomotion. From the excavation of deposits as Cova Estreta (Pollença, Mallorca) and Cova des Moro (Manacor, Mallorca) several bones have been obtained displaying undescribed features that agree with the above explained proposal. Specifically, it has been obtained a bone produced as the result of the fusion of scaphoid and lunar and a bone result of the fusion of pisiform and cuneiform. For the present, only have been obtained two specimens of the former case and just one of the later. None of the bones seem to be pathologic, and they do not show any kind of bone regrowth in the fusion zone. Fused scaphoid and lunar, and fused cuneiform and pisiform, seems to limit this movement, and together with anatomical characteristics of other joints (mainly in the fore leg), shows that the legs were not placed just under the body, as the almost all the extant bovids. Again, it seems that these fusions (together with the stoutness of the carpal bones) are also related with the stability of the joint.

Tracks and trackways can be important sources of information on locomotion and behaviour of fossil (and extant) species. Although a considerable amount of *Myotragus* footprints are available, just few trackways can be followed and measured. Particularly, the deposits of s'Estret des Temps and Ses Piquetes in Santanyí (Mallorca) have furnished three trackways that have been here studied in detail. The measurement of path length, width between limbs (fore and hind limbs) and feet orientation can give some clues on locomotion and body design of this species. The feet angle (outwards) of *M. balearicus* is considerably larger than in other ungulate species studied, as *Cervus elaphus* and *Ovis aries*. This measurement together with the relative separation of the limbs (related to the path length) show that the limbs of this species were not positioned just under the body during walking (as almost all the extant bovids), as can be inferred from other anatomical characteristics.

Key words: *Myotragus* - locomotion - carpal bones - bone fusions - trackways - ethology.

INTRODUCTION

The anatomic characteristics of *M. balearicus* bones have been studied by different authors. The main aim of these studies was to determine what the effects of the acquisition of derived characteristics were on locomotion and on the body design of *M. balearicus* (Leinders & Sondaar, 1974; Sondaar, 1977; Leinders, 1979; Moyà-Solà, 1979; Alcover *et al.*, 1981; Spoor, 1988a and b; Köhler, 1993; Köhler & Moyà-Solà, 2001). All the studies into the functional morphology of the limbs have reached conclusions along the same lines. The main inference consists of the fact that *M. balearicus* must have had a non-cursorial type of locomotion (*sensu* Gambaryan, 1974), more graviportal, characterized as slow locomotion, but with great power (called "low gear" locomotion by Sondaar, 1977). The short, robust metapodials seem to indicate great stability in the stride (Alcover, 1976; Sondaar, 1977), while the robustness of the long, proximal limb bones (femur, humerus, tibia and fibula) could be related to a greater resistance to breakage (Alcover *et al.*, 1981).

Similar adaptations to those observed in *M. balearicus* have been documented in other species. For instance, the insular fossil hippopotamus *Phanourios minutus* has an important reduction in the size of different distal limb bones (e.g., Sondaar, 1977). In the Pleistocene cervid fossil found in Crete, *Cervus cretensis*, short, robust metapodials have been observed, which must have given great stability to the stride (Sondaar, 1977).

One of the anatomical areas that has been most studied is the digital region of *M. balearicus*. The peculiar morphology of the articular areas between the metapodials and the proximal phalange (with very slightly marked sagittal crests on the distal articular facet of the metapodials, and articulations with a very small palmar-dorsal surface), and between the different phalanges (very flat surfaces, without a great articular surface), was interpreted as proof of limited flexion capacity in the metapodial-phalange and interphalangeal articulations. What is more, this anatomical characteristic also seems to indicate a reduction in the capacity to absorb the shock produced in this area during jumping or running (Leinders, 1979). For this reason, the capacity to jump would be very limited in the species, and locomotion would be of a much slower, more powerful and peaceful nature. This would be in agreement with other works (Köhler, 1993; Köhler & Moyà-Solà, 2001).

Another part of the hind limb of *M. balearicus* that has been studied is the tarsal region. One of the most singular features in *M. balearicus* is the fusion of the naviculocuboid complex with the small cuneiform and with the great cuneiform. The bone resulting from the fusion of the three distal tarsals is fused to the metatarsal in most of the adult specimens of *M. balearicus* (Bate, 1909; Andrews, 1915; Alcover *et al.*, 1981; Spoor, 1988b). The fusion of these bones has been interpreted as a way of stabilising the articulations in this area, with the consequent loss of the capacity to perform zigzag movements while running (Leinders & Sondaar, 1974). These movements are very important in bovids, so as to avoid being captured by a running predator. This zigzag movement is caused by the contraction of the *musculus peroneus longus*, which transmits a small rotation movement to the metatarsal caused by the small cuneiform. In an environment lacking in terrestrial predators, it seems that this type of fleeing mechanism is not necessary, thus evolutionally favouring the stabilisation of the articulations (Leinders & Sondaar, 1974).

In fact, as regards this bone, Howell (1944) had already interpreted the progressive fusion of the different elements of the distal tarsal bones during the evolution of artiodactyls as a mechanism to restrict movement to one plane alone. *M. balearicus* would represent the extreme case known of movement restrictions in this sense.

Fusions of the tarsal bones are known in other insular fossil artiodactyls, although to a lesser extent than in *M. balearicus*. In *Cervus cretensis* from the Pleistocene in Crete different tarsal bone fusions have been found (Sondaar, 1977). They have also been described in another insular fossil species, *Hoplitomeryx* from the Miocene in *Gargano* (Leinders & Sondaar, 1974; Van der Geer, 1999).

The anatomical changes produced in the calcaneus of *M. balearicus* serve to reduce the muscular tension in this area, thus favouring greater tarsal stability and decreasing the danger of breakages and injuries. Moyà-Solà (1979) observed great roughness in the calcaneus for the strong insertion of ligaments, which provide a greater rigidity to the tarsus (above all in the calcaneus-talus articulation).

The talus has also been the object of a series of functional interpretations, in comparison with the insular deer *Hoplitomeryx* and with continental artiodactyls (Van der Geer, 1999). Its peculiar morphology, with an important lateral distortion (in anterior view, *sensu* DeGusta & Vrba, 2003, the upper part of the talus is laterally displaced), was interpreted as being related to a loss in muscular power and a rise in stability. This author also explains that the peculiar form of the talus could be related to a convergent position of the proximal bones in the hind limbs due to the fact of having a very large abdomen. A relative separation of the limbs was also postulated by Spoor (1988b).

One way of verifying some of the anatomical characteristics of the limbs, and at the same time, one of the indirect ways of inferring locomotor aspects of a fossil species, is the study of footprints and trails left in sediment. Prints, trails and tracks can be important sources of information as far as locomotion and the behaviour of fossil and extant species are concerned (e.g., deer counts, Mayle *et al.*, 2000), and have provided important information in the case of dinosaurs (e.g., Gillette & Lockley, 1991; Lockley & Hunt, 1995). In the Pleistocene-age calcareous eolianite in the south-east coast of Mallorca a series of *Myotragus balearicus* trails were found and attributed to the ichnospecies *Bifipides aeolis* (Fornós *et al.*, 2002). The first findings of footprint remains of this bovid were made in Santanyí (Fornós & Pons-Moyà, 1982), and these studies are not resumed until Fornós *et al.* (2002). These authors gave a detailed description of the *Myotragus* tracks and trackways characteristics, especially from the Upper Pleistocene of Mallorca. In Menorca, ichnites of one of the accompanying species, the rodent *Eliomys sp.*, and also trails of *Myotragus*, were found (Quintana, 1993). Recently, Quintana & Arnau (2004) have analysed and studied a trail and other footprints of the fossil rodent found in a cave in Menorca.

MATERIALS AND METHODS

Although different nomenclatures have been erected to name the carpal bones (e.g., Barone, 1968; May, 1970; Sisson & Grossman, 1982; Schaller, 1992), in this paper will be used those proposed by Yalden (1971). The used names for each bone are:

Magnum for *os carpale II et III, os trapezoideo-capitatum*, fused second and third carpal bones.

Unciform for *os carpale IV, os hamatum*, fourth carpal bone.

Cuneiform for *os carpi ulnare, os triquetrum*, ulnar carpal bone.

Lunar for *os carpi intermedium, os lunatum*, intermediate carpal bone.

Scaphoid for *os carpi radiale, os scaphoideum*, radial carpal bone.

Pisiform for *os carpi accesorium, os pisiforme*, accesory carpal bone.

The *Myotragus* bones studied in this work come mainly from two deposits in which a lot of *Myotragus balearicus* bones have been obtained, the Cova Estreta (Pollença, Mallorca) (Encinas & Alcover, 1997) and the Cova des Moro (Manacor, Mallorca) (Trias, 2000). The number of carpal bones of each deposit is 318 (87 scaphoids, 76 lunars, 38 cuneiforms, 68 magnums, 45 unciforms and 4 pisiforms) and of 72 (17 scaphoids, 15 lunars, 4 cuneiforms, 22 magnums, 12 unciforms and 2 pisiforms), respectively. Additionally, more bones from other deposits have been studied. From these deposits a lesser number of bones has been obtained. For example, the Cova de Son Maiol (Palma, Mallorca) with 38 bones (7 scaphoids, 12 lunars, 4 cuneiforms, 8 magnums, 5 unciforms and 2 pisiforms) and the Cova C-2 (Ciutadella, Menorca) with 5 bones (2 scaphoids, 1 lunar, 1 magnum and 1 unciform). All these bones are curated in the vertebrate collection MNIB and their catalogue numbers are related in Bover (2004).

As a comparison material the carpal bones of several species taxonomically related to *Myotragus* genus have been studied. The acronyms of the studied material are:

AMNH: American Museum of Natural History (New York, USA).

NMNH: National Museum of Natural History-Smithsonian Institution (Washington D.C., USA)

MNCN: Museo Nacional de Ciencias Naturales (Madrid, Spain)

MZB: Museu de Zoologia de Barcelona (Barcelona, Spain)

MNIB: Museu de la Naturalesa de les Illes Balears (Mallorca, Spain)

The extant species studied are: *Ammotragus lervia* (MZB 94-0661 and 97-0680), *Bos taurus* (MNIB 48177 and 48292), *Bison bison* (AMNH 3754 and 98954 and NMNH 839 and 22664), *Budorcas taxicolor* (AMNH 57013, 57014, 57016 and 57017 and NMNH 259079), *Capra hircus* (MNIB 39996, 40000, 48167-48175, 48208-48212, 48222, 48223, 60096, 60148, 60149, 65277 and 73196), *Capra pyrenaica* (MZB 94-0682), *Capricornis crispus* (AMNH 165685 and NMNH 20934), *Capricornis sumatrensis* (NMNH 258670 and 259025), *Nemorhaedus goral* (AMNH 43001, 43004 and 110481), *Oreamnos americanus* (AMNH 35286, 35492, 35786 and 130223), *Ovibos moschatus* (AMNH 35588, 35612, 80095, 100058 and 202866), *Ovis aries* (MNIB 39997-39999, 48176, 48181, 60098, 60147, 60150, 73865 and 73866), *Ovis musimon* (MZB 92-0233), *Rupicapra pyrenaica* (MNCN 2218 and 2271 and MNIB 60091, 60092 and 65276), *Rupicapra rupicapra* (MZB 98-0258 and 98-0259).

Although there is a considerable quantity of *Myotragus* footprints available (sometimes to excess, defined as myoturbation in Fornós *et al.*, 2002), only very few trails can actually be followed and measured which seem, clearly, to be the trail made by an isolated individual. Specifically, the sites in S'Estret des Temps and Ses Piquetes in Santanyí (Fornós & Pons-Moyà, 1982; Fornós *et al.*, 2002) have provided three trails that can be studied in detail. We have also included in this work the measurements obtained by Quintana (1993) of the *Myotragus* trails in Menorca.

The measurements carried out are (Fig. 1):

- Stride Length (SL): distance measured between two homologous points of two footprints belonging to the same foot, that is, the distance covered by one limb.
- Trail Width (TW): distance between two imaginary lines traced between the outside of two footprints on each side. This measurement serves to infer the transversal distance between two limbs.
- Feet Angle (FA): angle made from two lines, one parallel to the direction of the animal's stride and the other parallel to the line of separation of the two toes in each hoof.
- Trail Index (TI): the result of the SL/TW division. This index enables us to compare the trails of different species.

Only in the cases of our own measurements have we obtained values in cm of the SL and TW, due to the fact that in the literature the trail is only drawn or photographed, without any real values. Thus, we have taken values obtained from the photos to calculate the TI.

These measurements can provide information as to the locomotion and body design of this species (Bover, 2004). As material for comparison we used the trails of extant bovids which can be found in Cabrera (1997) and in the literature on the trails of extant species (Bang & Dahlström, 1975). What is more, we carried out measurements on the trails of sheep (*Ovis aries*) in the farm of Son Cotoner d'Avall (Puigpunyent, Mallorca) and goats (*Capra hircus*) in the area of Cala Sant Vicenç (Pollença, Mallorca).

RESULTS

The carpal bones of *M. balearicus* were not described in detail by Andrews (1915). Only Spoor (1988b) mentions that they have normal proportions, although he does observe that the *stop-facets* of the distal area are well developed, a characteristic which gives more stability to the articulation. This author states that the flexion of the proximal and ulnar carpal articulations are less than 90º and 75º, respectively, calculated by Yalden (1971) in different bovids.

Here we present a more detailed description of the carpal bones in *M. balearicus* as there is no complete one available. We have also compared the morphology of these bones with that of different species of bovids.

All the carpal bones have, as happens with other bones in *M. balearicus*, a high degree of robustness. In general, all the carpal bones in *M. balearicus* have a proximal-distal compression, a fact which causes the areas of ligament insertion to be much more important than in other caprines (Fig. 2 and 3). This compression is also present in *Oreamnos americanus* and in *Ovibos moschatus*, albeit to a lesser degree.

The anatomical description of each part of the carpal bones will be done for each margin of each bone and not according to the view from which it is observed.

The description is always carried out using the bones of *Myotragus balearicus* as a reference.

Scaphoid

Proximal margin

The articulation surface with the distal epiphysis of the radius is "S"-shaped in flexor-extensor view [FES, according to Yalden, (1971)], although the articulation surfaces have a more abrupt relief, that is, the different articulation areas are separated by crests which are more or less developed (Fig. 2C).

In the proximal part, the highest prominence on this surface, which articulates with the fossa for this prominence in the distal part of the radius, is not rounded, neither is it surrounded by more articular surface (not in all cases) (Fig. 2a), rather there are basically three morphologies:

- In front of the prominence there is a transversally convex-shaped articular surface, (as happens in *Capra hircus*), but much more acute.
- In some cases, the articular surface can become transformed into a crest which joins the more dorsal margin (extensor margin) of the scaphoid with the prominence (similar to *Oreamnos americanus*) (Fig. 3a1-4). The dorsal prominence is more elevated than or at the same height as the palmar.
- In four of the pieces observed in Cova Estreta (MNIB 44841, 50128, 53352 and 55935) there is no articular surface in front of the prominence, but rather the prominence forms an apical margin, which means a restriction in the extensor movement.

The medial prominence is very well-developed (Fig. 2b), as happens in *Oreamnos americanus* (Fig. 3a1), projecting towards the axis of the limb, fitting with a notch in the proximal-medial margin of the lunar. In *Nemorhaedus goral* this medial prominence is also quite well marked. It is not so well marked in the other caprines studied.

Lateral margin

The distance between the fossas of the dorsal and ventral sides in some cases is proportionally less than in the other caprines. The articular facet is rounder (Fig. 2c) and is more ventrally developed. Its orientation is different; it is not as parasagittal, but rather takes a proximal-dorsal-lateral orientation.

On the distal-palmar side there is a very pointed prominence (absent in *Oreamnos americanus* and rounded in *Capra hircus*), which has an articular facet facing in a proximal-palmar direction. This is absent in practically all the species studied and serves as an articulation with the lunar (Fig. 2d). Only in *Ovibos moschatus* can a ridge be found sticking out of the lateral articular area (Fig. 3c1). In the other extant species this articulation is not there since the dorsal crest of the magnum impedes it. In *Capricornis sumatrensis* this articular surface is quite large, but does not have this articular ridge.

Distal margin

The main difference is that the prominence explained by the lateral margin, means that the distal contact surface with the magnum is larger, which means that there are restrictions to the movement between the scaphoid and the lunar.

The articulation area with the magnum is "S"-shaped (Fig. 2e). The concave part is more rounded and is at times cup-shaped because the lateral edge is closed. The convex part (dorsal) is, proportionally, much smaller

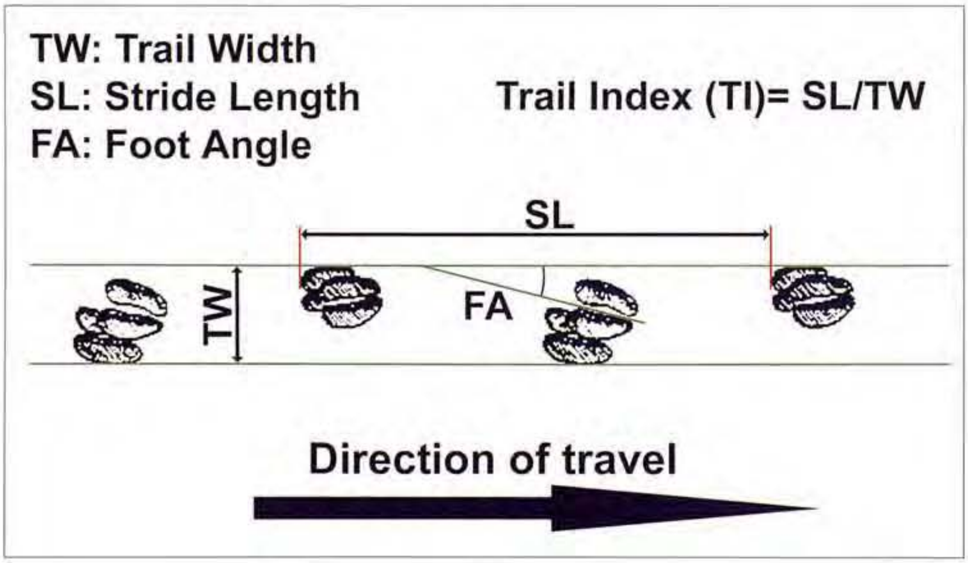

Fig. 1. Measurements on trackways of the different species studied.

Fig. 1. Mesures realitzades sobre les petjades de les diferents espècies estudiades.

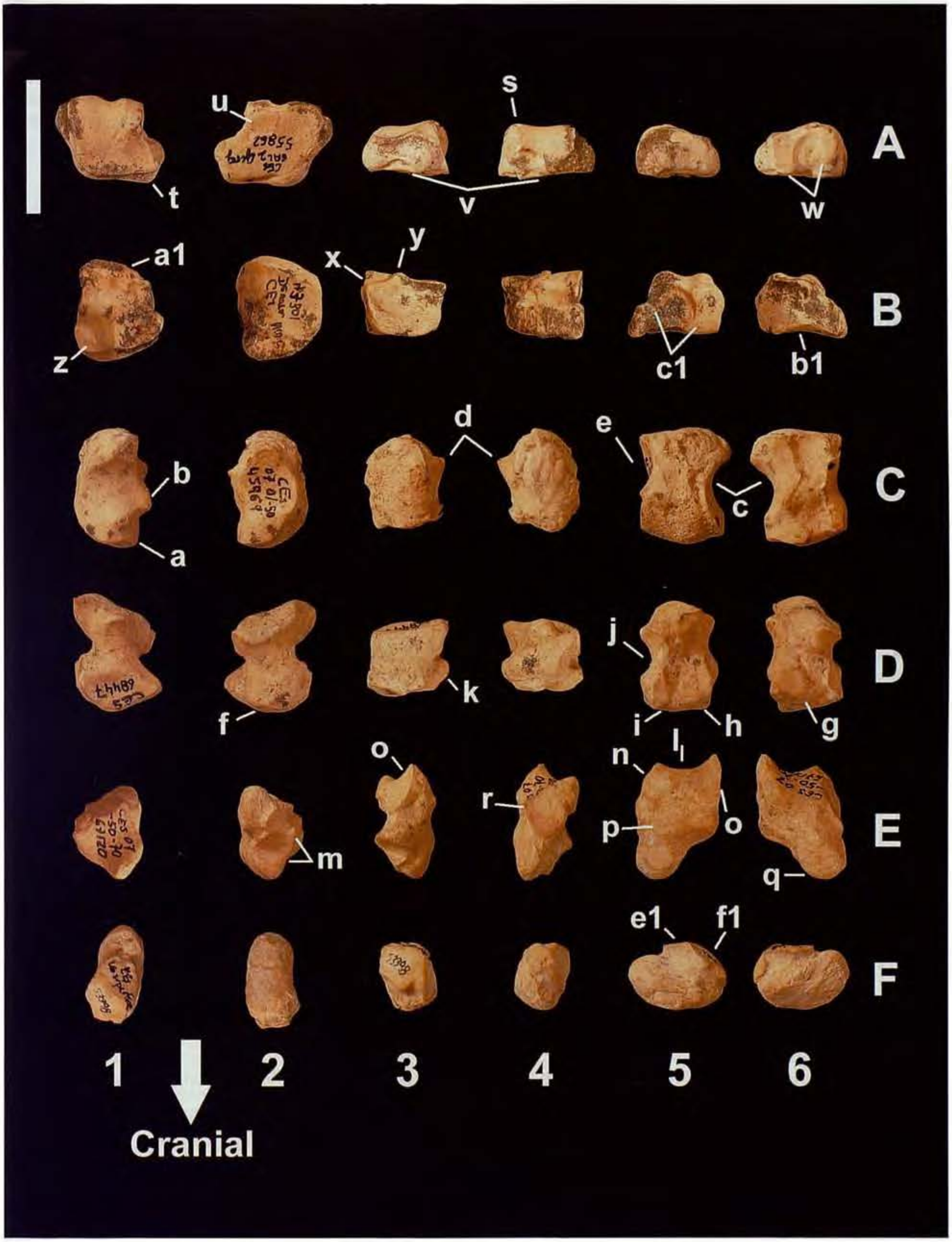

Fig. 2. *M. balearicus* carpal bones. A: left magnum MNIB 55682. B: right unciform (inverted photos) MNIB 43301. C: left scaphoid MNIB 68447. D: left lunar MNIB 45969. E: left cuneiform MNIB 67120. F: left pisiform MNIB 53398. 1: proximal view; 2: distal view; 3: dorsal view; 4: palmar view; 5: medial view; 6: lateral view. Cranial part for 1 and 2 views is indicated. Small letters explained in text. Scale bar 2 cm.

Fig. 2. Ossos del carp de M. balearicus. *A: capitatotrapezoide esquerre MNIB 55682. B: unciforme dret (fotos invertides) MNIB 43301. C: escafoide esquerre MNIB 68447. D: semilunar esquerre MNIB 45969. E: cuneïforme esquerre MNIB 67120. F: pisiforme esquerre MNIB 53398. 1: norma proximal; 2: norma distal; 3: norma dorsal; 4: norma palmar; 5: norma medial; 6: norma lateral. Se situa la part cranial de l'animal per a les normes 1 i 2. Les lletres en minúscules s'expliquen al text. Escala 2 cm.*

than in the other species studied. In *Budorcas taxicolor* this articulation surface is not "S"-shaped, but rather flat in its dorsal region (where it has a crest), and is even slightly concave (Fig. 3b2).

Medial margin

The insertion surfaces of the different ligaments are much more developed than in the rest of the caprines.

Lunar

In general, the aspect of this bone in *M. balearicus* is really robust (as in *Budorcas taxicolor*), and the crests which separate the smooth articulation areas are not very well-marked (Fig. 2D). This is, in general, the aspect also in different species studied (*Capra hircus, Ovis aries, Capricornis crispus* and *C. sumatrensis, Nemorhaedus goral* and *Ovibos moschatus*), but above all in *Budorcas taxicolor*, in which, for instance, the proximal articulation surface is quite flat and the distal ones are hard to distinguish, due to the fact that there is no clear crest to mark them (Fig. 3c). On the other hand, in *Oreamnos americanus* the crests are marked, although not exaggeratedly (Fig. 3a5-7).

Proximal margin

There is no significant differential feature in comparison with the other caprines.

Distal margin

This has a relatively well-developed dorsal prominence (Fig. 2f). This is likely to be related to restrictions in carpus extension movements.

The ventral channel of articulation with the magnum and unciform is more excavated and closed than in the other caprines (Fig. 2j). In some cases the distal dorsal facet (which is more rounded in shape) and the proximal dorsal facet are also joined with an articular bridge.

The distal lateral articular facet is directed and oriented more towards the lateral side than in the rest of the caprines studied (Fig. 2k).

Lateral margin

In *Capra*, the distal articulation surface is separated from the palmar side by a crest which extends transversally to the sagittal plane. In *Oreamnos* and *M. balearicus* this articulation surface is not continuous, as in *Capra hircus* and *Ovis aries*, becoming thinner towards the palmar side but rather it forms a very thick, broad surface on the dorsal side (Fig. 2g), tapering very slowly, disappearing in some cases, and even, at times, there is only a circular or triangular surface left on the palmar side.

There is an articular facet on the distal palmar side which articulates with the cuneiform.

Medial margin

There is a small articular facet for articulation with the scaphoid (Fig. 2h), which corresponds with the aforementioned lateral prominence of the scaphoid. In *Ovibos moschatus* there is also an articular surface on the lunar for this scaphoid prominence (Fig. 3c3-4). The central fossa is deeper.

The notch in the ulnar proximal margin is more marked due to, just as has been explained with the scaphoid, a more intimate articulation with this bone (Fig. 2i). Due to the presence of this notch, the dorsal and palmar articular facets of the proximal area are separated and do not form a continuum, as happens in the species with which it has been compared.

Cuneiform

Proximal margin

No great differences with respect to the other species studied are observed (Fig. 2E).

The articular surface with the ulna is flatter, that is, the articular sulcus is not as deep (Fig. 2l).

Distal margin

In general, the articular surface with the unciform is broader in an ulnar-lateral direction than in the other caprines (Fig. 2m). The articular surface of the distal-palmar spur is reduced, with the facet taking on a more medial orientation (Fig. 2m).

In two cases, (MNIB 56293 and 43304) the articular surfaces of the sulcus and the spur, are of more or less the same breadth, taking, however, a more medial orientation.

Medial margin

The proximal articular surface with the lunar is reduced, above all on the palmar side (Fig. 2n), even disappearing in some cases. The dorsal area is proportionally wider in a proximal-distal direction than in other caprines (Fig. 2o), except in *Capra hircus*, where it is similar, but with a much thinner dorsal area.

The central articular surface is, in general, smaller, circular and oriented in a more palmar way (Fig. 2p). Specimen MNIB 43304 does not have this surface.

Lateral margin

The surface is smoother than in the other caprines. In *Oreamnos americanus* there are several very well-marked crests which are absent in *Myotragus* and *Capra*.

The spur which articulates with the unciform does not end in a sharp point, but is rounded (Fig. 2q). The articular sulcus with the unciform is less deep and has a small articular surface.

Dorsal margin

There are few differences with respect to the other species studied.

In *Oreamnos americanus* the crests for the insertion of ligaments are very well developed. In *Myotragus* there are none, and the surface is not as abrupt.

Palmar margin

In general, the articulation surface for the pisiform is more rounded and broader in medial-lateral direction than in the other caprines (Fig. 2r). It is a concave surface on all sides. In *Oreamnos americanus* it is convex in lateral-medial direction. In *Capra hircus* it is concave dorsal-ventrally and convex in lateral-medial direction, just as happens in *Budorcas, Nemorhaedus goral* and *Capricornis crispus*.

Magnum

The magnum looks like being compressed proximal-distally, with a degree of compression greater than that observed in other caprines (Fig. 2A). Due to this compression the areas for insertion of ligaments are well developed. In this case, the magnum in *Capricornis sumatrensis* and *Nemorhaedus goral* also has a slight dorsal-ventral compression, but it is not as evident as in *Ovibos* or *Oreamnos*.

Proximal margin

As happens in other species studied (*Capricornis sumatrensis, Ovibos*) (Fig. 3c7), the crest and the separation prominence of the articulation surfaces for the scaphoid and the lunar are very low (Fig. 2s), not too well marked, so that in *M. balearicus* this allows a certain caudal contact of the scaphoid and the lunar. In *Oreamnos* (Fig. 3a13), *Budorcas, Capra hircus, Ovis aries* and *Capricornis crispus* (Fig. 3d1) this crest is quite high and is well marked.

Fig. 3. Comparison carpal bones (all bones, left side). a: *Oreamnos americanus* AMNH 130223; b: *Budorcas taxicolor* AMNH 57017; c: *Ovibos moschatus* AMNH 100058; d: *Capricornis crispus* AMNH 165685; e: *Capricornis sumatrensis* NMNH 258670. a1: scaphoid, proximal view; a2: scaphoid, distal view; a3: scaphoid, medial view; a4: scaphoid, lateral view; a5: lunar, distal view; a6: lunar, medial view; a7: lunar, lateral view; a8: cuneiform, lateral view; a9: cuneiform, medial view; a10: magnum, proximal view; a11: magnum, distal view; a12: magnum, dorsal view; a13: magnum, palmar view; a14: unciform, proximal view; a15: unciform, distal view; a16: unciform, lateral view; a17: unciform, medial view; a18: pisiform, lateral view; a19: pisiform, medial view. b1: scaphoid, proximal view; b2: scaphoid, lateral view; b3: lunar, lateral view. c1: scaphoid, proximal view; c2: scaphoid, lateral view; c3: lunar, medial view; c4: lunar, proximal view; c5: cuneiform, dorsal view; c6: magnum, proximal view; c7: magnum, dorsal view; c8: magnum, medial view; c9: unciform, dorsal view; c10: unciform, medial view; c11: unciform, proximal view; c12: pisiform, medial view. d1: magnum, lateral view. e1: magnum, dorsal view. Scale bar 2 cm.

Fig. 3. *Ossos del carp de comparació (tots els ossos dels costat esquerre). a:* Oreamnos americanus *AMNH 130223; b:* Budorcas taxicolor *AMNH 57017; c:* Ovibos moschatus *AMNH 100058; d:* Capricornis crispus *AMNH 165685; e:* Capricornis sumatrensis *NMNH 258670. a1: escafoide, norma proximal; a2: escafoide, norma distal; a3: escafoide, norma medial; a4: escafoide, norma lateral; a5: semilunar, norma distal; a6: semilunar, norma medial; a7: semilunar, norma lateral; a8: cuneïforme, norma lateral; a9: cuneïforme, norma medial; a10: capitatotrapezoide, norma proximal; a11: capitatotrapezoide, norma distal; a12: capitatotrapezoide, norma dorsal; a13: capitatotrapezoide, norma palmar; a14: unciforme, norma proximal; a15: unciforme, norma distal; a16: unciforme, norma lateral; a17: unciforme, norma medial; a18: pisiforme, norma lateral; a19: pisiforme, norma medial. b1: escafoide, norma proximal; b2: escafoide, norma lateral; b3: semilunar, norma lateral. c1: escafoide, norma proximal; c2: escafoide, norma lateral; c3: semilunar, norma medial; c4: semilunar, norma proximal; c5: cuneïforme, norma dorsal; c6: capitatotrapezoide, norma proximal; c7: capitatotrapezoide, norma dorsal; c8: capitatotrapezoide, norma medial; c9: unciforme, norma dorsal; c10: unciforme, norma medial; c11: unciforme, norma proximal; c12: pisiforme, norma medial. d1: capitatotrapezoide, norma lateral. e1: capitatotrapezoide, norma dorsal. Escala 2 cm.*

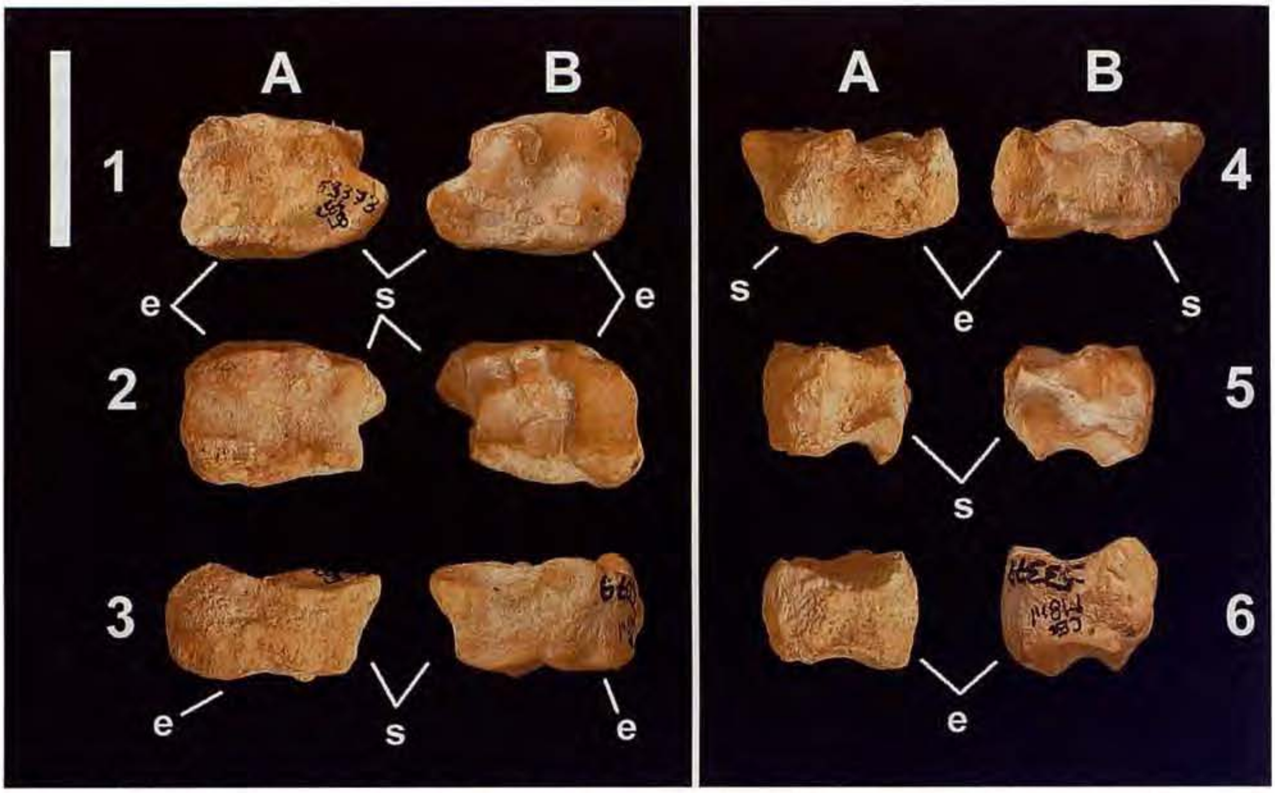

Fig. 4. Fused scaphoids and lunars of *M. balearicus*. A: left scapho-lunar MNIB 53378. B: right scapho-lunar MNIB 53379. 1: proximal view; 2: distal view; 3: dorsal view; 4: palmar view; 5: lateral view; 6: medial view. s: lunar; e: scaphoid. Scale bar 2 cm.

***Fig. 4.** Escafoides i semilunars fusionats de* M. balearicus. *A: escafo-semilunar esquerre MNIB 53378. B: escafo-semilunar dret MNIB 53379. 1: norma proximal; 2: norma distal; 3: norma dorsal; 4: norma palmar; 5: norma lateral; 6: norma medial. s: semilunar; e: escafoide. Escala 2 cm.*

The perimeter of the magnum in *M. balearicus* in proximal view is more square than in the other caprines studied.

Specimen MNIB 53360 has a fossa on the articular surface which can not be observed in the other specimens, and which probably represents a sinovial mark.

The medial dorsal margin is well developed (Fig. 2t) and is ulnarly longer than the palmar.

Distal margin

In general, as happens in extant species, the articulation surface with the metacarpus follows the shape of the bone. It is basically concave in most extant caprines, although the surface edges are more irregular.

The distal non-articular region is larger (Fig. 2u), deeper and more irregular than in the other caprines.

The articulation surface in *M. balearicus* is flat (like in *Capricornis sumatrensis*), and even has a small concavity which would act as a *stop-facet* (Fig. 2v). There is no possibility of magnum/metacarpus flexion, contrary to what happens in extant species, which have a convex surface which allows a certain degree of flexion [20° according to Yalden (1971)]. In *Capricornis crispus* there is an articular facet in this area which penetrates within the region of the non-articular shallow fossa of the metacarpus, whereas in *Ovibos* there is a small concavity on the lateral-palmar tip which gives it an S-shape.

Lateral margin

There are, in all the species studied (Fig. 3), basically two articular facets: a more or less developed, square dorsal facet and another palmar one which follows the curvature of the crest (Fig. 2w). In *M. balearicus* the dorsal surface is smaller and is oriented in medial-proximal direction (obliquely) and not medially, which allows the unciform to slightly overlap with the magnum. The palmar articular facet is generally smaller and is limited to the proximal-palmar tip. In some cases it sticks out in a distal-palmar direction thus acquiring a semi-lunar shape. In this posterior articular region, in *Ovibos*, there is a small prominence. In *Oreamnos* there is no type of ridge or prominence.

In *Budorcas*, the dorsal articular surface is sloped, offering a sort of support to the unciform (just as can be seen in *M. balearicus*).

Unciform

The unciform is robust and is proximal-distally compressed, just as happened with the magnum (Fig. 2B). The ligament insertion areas are well marked.

Proximal margin

The proximal articular surface for the cuneiform, on its more palmar side, does not have such a lateral orientation as the other caprines (Fig. 3C11), but rather it takes a more palmar orientation (Fig. 2x). The crest limiting this articulation surface is also laterally deviated.

The separation crest between the two articulation surfaces for the unciform and the lunar, in general, is not very well developed (like in *Capricornis sumatrensis, Ovibos, Budorcas*), except in its more palmar position (Fig. 2y), in which it is well marked (but not as much as in *Oreamnos americanus, Capricornis crispus, Capra hircus, Ovis aries*, in which it is a protuberant crest).

The articulation surface for the lunar is proportionally broader transversally than in other species (Fig. 2z).

The groove under the lateral-medial crest is very deep, above all on the medial side (Fig. 2a1). The palmar ridge where this groove can be found is only slightly developed (as in *Oreamnos, Capra hircus* and *Ovis aries*), contrary to what happens in *Ovibos* and, to a lesser extent, in *Budorcas* (Fig. 3c10) and *Nemorhaedus goral* (in the latter case, the ridge gives off a distal projection).

Distal margin

The surface is concave in dorsal-palmar direction, as happens in *Oreamnos americanus, Budorcas*, but in *M. balearicus* it is even more so (Fig. 2b1). In *Capra hircus* it is flat or slightly convex.

Medial margin

There are generally two articular bands with the magnum, which coincide with the articular areas of the latter.

In *M. balearicus* there is a dorsal articular area, which is square and obliquely oriented, in distal-medial direction, coinciding with the morphology of this surface corresponding to the magnum (Fig. 2c1).

This dorsal articulation surface of the unciform connects, in most bones, with the proximal-palmar articulation surface of the same bone, which is semi-lunar (Fig. 2d1). At times it has a ridge following the palmar margin of the bone (Fig. 2c1).

Pisiform

In general it has a more globular shape than in other caprines (Fig. 2F). The size of the articular surface with the cuneiform is smaller (Fig. 2e1), whereas the articulation surface with the distal tip of the ulna is greater (Fig. 2f1). At times the two articular surfaces are the same size (e.g., MNIB 43297). In *M. balearicus* a clear separation can be seen between these two articular surfaces, whereas in *Oreamnos* this separation is not as clear (Fig. 3a19). In *Capricornis crispus* and *Nemorhaedus goral* the articulation with the ulna is practically inappreciable, whereas in *Budorcas* this articulation surface is very small and is situated on a dorsally projecting spur (Fig. 312). In the

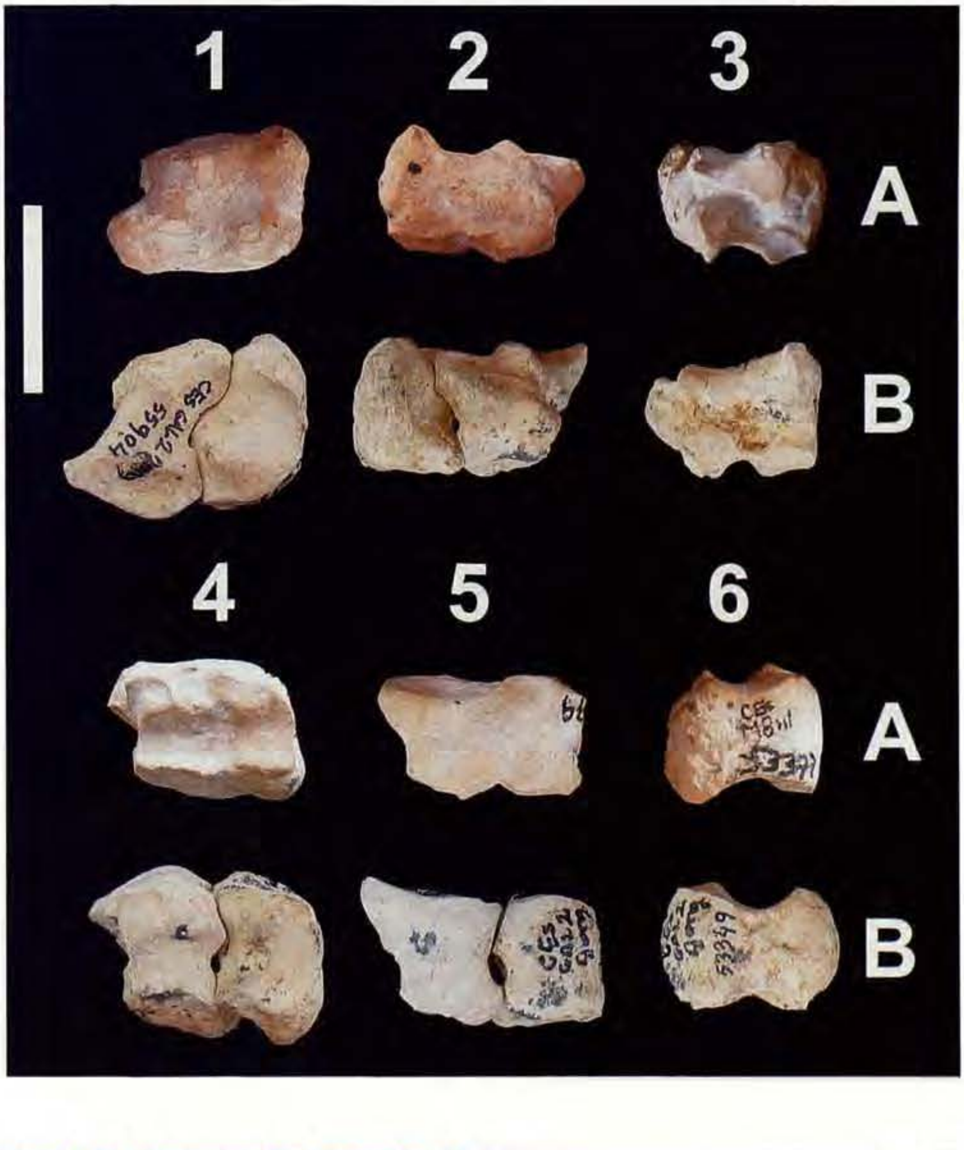

Fig. 5. Comparison between (A) right scapho-lunar MNIB 53379 and (B) articulated right scaphoid MNIB 53349 and right lunar MNIB 55904 of *M. balearicus*. 1: proximal view; 2: palmar view; 3: lateral view; 4: distal view; 5: dorsal view; 6: medial view. Scale bar 2 cm.

Fig. 5. Comparació entre (A) escafo-semilunar dret MNIB 53379 i (B) escafoide dret MNIB 53349 i semilunar dret MNIB 55904 articulats de M. balearicus. *1: norma proximal; 2: norma palmar; 3: norma lateral; 4: norma distal; 5: norma dorsal; 6: norma medial. Escala 2 cm.*

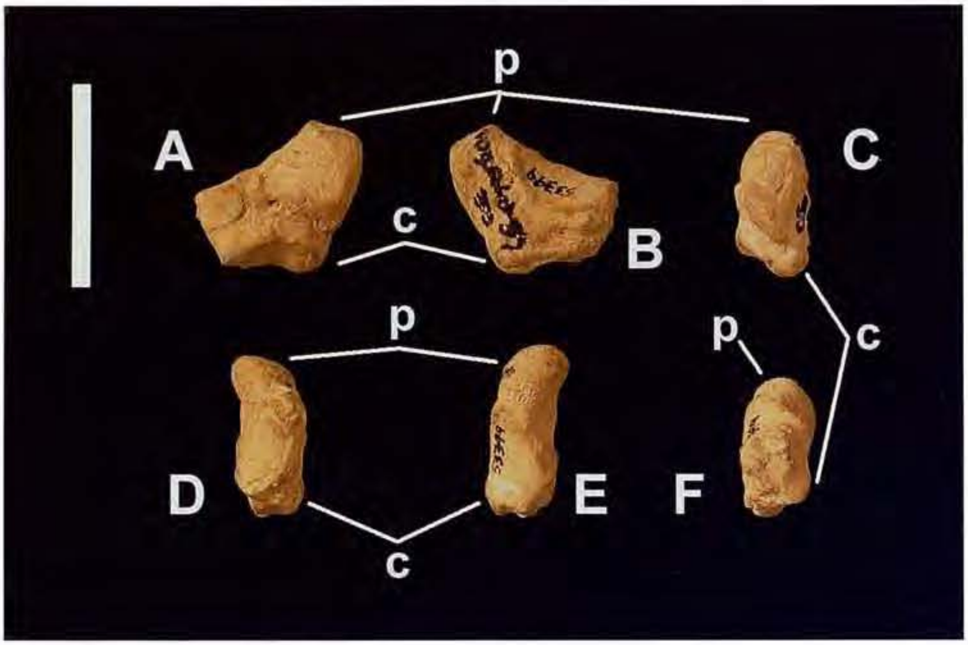

Fig. 6. Fused right cuneiform and pisiform of *M. balearicus* MNIB 53399. A: medial view; B: lateral view; C: palmar view; D: distal view; E: proximal view; F: dorsal view. Lower part of photo is the cranial side for D and E. p: pisiform; c: cuneiform. Scale bar 2 cm.

Fig. 6. *Cuneïforme i pisiforme drets fusionats de* M. balearicus *MNIB 53399. A: norma medial; B: norma lateral; C: norma palmar; D: norma distal; E: norma proximal; F: norma dorsal. La part inferior de la foto seria la part cranial per a D i E. p: pisiforme; c: cuneïforme. Escala 2 cm.*

extant caprines studied there are differences between the morphology of the articulation surface with the cuneiform: in *Capricornis crispus* it is convex, in *Capricornis sumatrensis* it is flat and in *Budorcas* it is wavy.

Carpal fussions

In Cova Estreta (Pollença, Mallorca) two *M. balearicus* bones have been obtained which were not identified until a short time ago. They are two small, robust, prism-shaped bones (MNIB 53378 and 53378, Fig. 4) measuring 19.82 x 11.66 x 14.46 mm and 21.06 x 11.06 x 14.76 mm, respectively. An in-depth study, comparing their morphology with the different *M. balearicus* bones of this size, has enabled their identification as a bone resulting from the fusion of a scaphoid and a lunar by their anatomical region of contact (see Fig. 5). Specifically, MNIB 53378 is the fusion of a left scaphoid and lunar and MNIB 53379 is the fusion of a right scaphoid and lunar. On their dorsal side, the fusion is produced even as regards the scapholunar ligament insertion area. On the palmar edge, the radius-lunar and scapholunar-magnum ligament insertion areas are very marked and rough. Their union area does not have any type of bone re-growth or any type of arthritic osteologic pathology. For this reason, it would seem that this fusion is natural and does not present any type of pathological situation.

Another bone obtained which has a very highly modified morphology is specimen MNIB 53399 (Cova Estreta, Pollença). This is a right cuneiform which has a bony prominence in the pisiform articulation area (Fig. 6). Once studied in detail, it was possible to identify that, actually, this bony prominence is the pisiform itself, which is fused in its natural articular region with the cuneiform. In this case neither does there appear to be any type of bone re-growth. The articular area for the ulna is continuous from the cuneiform to the pisiform, and the ligament insertion areas also form a continuous structure.

Among the carpal bones obtained from the excavation of this same cave there is another bone with a previously unobserved morphology. This is specimen MNIB 56300. Even though we have identified it as a carpal bone, we have been unable to diagnose with precision which bone it is (Fig. 7). It is a bone which has some articular areas which look like the three bones in the proximal row of the carpus (scaphoid, lunar and cuneiform), basically due to the morphology of the different articular facets and crests. On one of its lateral sides there are no articular areas, so we can discount it being a lunar. If it were a cuneiform it would have a totally modified articular facet for the ulna, divided into two very clear facets. What is more, the articular facet for the unciform would be situated in an medial and not distal position like in normal specimens. In the case of it being a scaphoid we would find a similar situation. The articular facet with the radius would have more than one surface, and the articulation surface with the magnum would also be ulnarly oriented. As a result, it has not been possible to diagnose which bone we are dealing with (scaphoid or cuneiform). Neither has another altered bone been found that could be associated with it.

Tracks and trackways

The measurements obtained for the different trails studied, defined in the section on materials and methods, are related in Table 1.

The foot angle (radial rotation of the foot) of *M. balearicus* is considerably greater than the angles of the other species studied, like the cervids and domestic caprines in Mallorca (*Ovis aries* and *Capra hircus*).

Another of the parameters measured of the trails made by extant bovids which differ significantly with respect to *Myotragus* is the width of the trail (a characteristic already observed by Quintana, 1993). The distinction between the footprints made by the fore and hind limbs are difficult to distinguish in the case of the trails of *Myo-*

tragus, since the sediment in which the animal walked was soft (sand) and many of the footprints are made up of only one mark. However, in some cases, as Fornós *et al.* (2002) also explain, it is possible to distinguish the mark of the footprint of the hind limb situated on the mark (but slightly behind) the footprint of the fore limb. Contrary to what happens with the trails of the extant comparison species, the width of the trails of *Myotragus* is proportionally greater (see Table 1, Fig. 8, Index TI). Whereas the TI index in *M. balearicus* acquires values between 2.1 and 2.9, in *Sus* it is slightly above 3 and in the extant bovids and cervids studied the TI value is greater than 4, with the greatest value calculated for *Odocoileus hemionus* (5.9). In proportion, the width of the trail with respect to the length of the stride is greater in *M. balearicus*. This measurement, together with the anatomic arrangement of the limbs established from the study of the femur, suggests that the limbs of this species were not as near the sagittal plane during gait as in the species they have been compared with. Spoor (1988b) already mentions this particularity for the species.

Fig. 7. Non identified modified carpal bone of *M. balearicus* MNIB 56300. Could be a scaphoid or a cuneiform. Scale bar 2 cm.

Fig. 7. Os modificat del carp no identificat de M. balearicus *MNIB 56300. Pot tractar-se d'un escafoide o d'un cuneïforme. Escala 2 cm.*

DISCUSSION

The observations made about the different anatomical particularities of the carpal bones of *M. balearicus* corroborate, in a general way, what had already been observed by other authors (e.g., Alcover *et al.*, 1981; Spoor, 1988b; Köhler, 1993; Köhler & Moyà-Solà, 2001). The fact that in *M. balearicus* there are prominent, rough regions of muscular and ligament insertions in the different bones both in the fore and hind limb, indicate that the collateral ligaments were of an important length, and must have contributed in an important way to stabilising the articulations. This fact can be observed clearly in the carpal bones, which have a proximal-distally compressed aspect. The thickening of the edges where the ligaments were inserted between the different carpal bones, and between the carpal bones and adjacent bones, must be understood as the important relevance of these ligaments in providing stability in an area prone to suffering injuries, like the different carpal articulations. In fact, a certain reduction in the flexion capacity in this articulation is also observed (Spoor, 1988b).

The other observations made in the carpus are also in agreement with this, as is the case of the synostosis observed in this area. Synostoses are bony unions between bones which usually have mobile or semi mobile articulations. They could be of congenital, traumatic or other type of origin. Carpal synostoses are extraordinarily rare, and we are unaware of cases previously described in bovids. The registered cases of fusion between the scaphoid and the lunar and between the cuneiform and

SPECIES	TI	FA	SOURCE
BOVIDAE			
Ovis aries	4,58	8	Unpublished
Capra hircus	4,49	7,5	Unpublished
M. balearicus (S'Estret des Temps)	2,78	14	Unpublished
M. balearicus (S'Estret des Temps)	2,84	-	Unpublished
M. balearicus (Ses Piquetes)	2,13	15	Unpublished
M. balearicus (Penyes d'Alparico)	2,46	-	Quintana (1993)
SUIDAE			
Sus scrofa	3,21	-	Bang i Dahlström (1975)
CERVIDAE			
Odocoileus hemionus	5,9	7	Cabrera (1997)
Cervus elaphus	4,5	9	Bang i Dahlström (1975)
Cervus elaphus	5,4	-	Cabrera (1997)

Table 1. Values for Trail Index (TI) and Feet Angle (FA) of the different species studied. Source of the tracks pictures or photos measured is indicated.

Taula 1. Valors de l'Index de Rastre (TI) i de l'Angle del Peu (FA) de les diferents espècies estudiades. S'indica la font de les fotos o dibuixos dels rastres mesurats.

Fig. 8. Example of *M. balearicus* trackways from s'Estret des Temps (Mallorca).

Fig. 8. Exemple de rastres de M. balearicus *de s'Estret des Temps (Mallorca).*

pisiform are few and far between, and do not allow us to talk about an evolutionary tendency towards the appearance of these synostoses, however neither can the beginning of these tendencies be excluded (even more so if we take into account the existence of tarsal fusion precedence). What it does seem to be able to exclude is that these fusions could be of traumatic origin. According to Yalden (1970, 1971), ungulates have a separate scaphoid and lunar in order to allow a certain ulnar deviation of the fore limb so as to facilitate the passage of leg behind leg during the protraction movement without them coming into contact. The fusion of the scaphoid and lunar, and the fusion of the cuneiform and the pisiform, observed in *M. balearicus* seem to limit this movement. If we observe an associated carpus in *M. balearicus*, the mobility of the lunar and the scaphoid separately is different. Whereas the scaphoid-magnum articulation permits a flexion of around 55º, the lunar-unciform articulation only allows a flexion of 40º, caused, apart from by a lesser articular surface of the unciform, by a caudal ridge which limits the flexor movement of the lunar. If the lunar fuses with the scaphoid, the angle of flexion between the distal carpal row and proximal row is reduced to 40º, much smaller than the 75º which can be observed in extant ruminants (Yalden, 1971). Spoor (1988b) previously observed that there was an important reduction in the articulation angle of the two carpal articulations, but he did not quantify it.

The fusion of the pisiform and the cuneiform is more difficult to interpret clearly. The pisiform basically acts as sesamoid bone for the flexors *carpi ulnaris* and *carpi radialis* (Sisson & Grossman, 1982). The restriction in the movement of the pisiform-cuneiform articulation, not only in the specimen that had these fused bones, but also in the ones that have non-fused bones, due to the reduction in the articular areas registered in *M. balearicus* in a general way, seems to produce a similar effect to the fusion between the lunar and the scaphoid. The rigidness that could be produced by having a cuneiform with limited movement, with respect to the distal epiphysis of the ulna, has a smaller ulna articular movement, and therefore, a smaller ulnar deviation.

The articular facets of the different carpal bones, some flat, some without an articular movement and some with eminences which act as *stop-facets*, indicate the reduction in mobility and lack of general flexion capacity in the area.

The lack of capacity for ulnar deviation, to avoid the two limbs hitting each other when one moves in front of the other when walking, agrees with the lateral separation of the radius with respect to the humerus (Bover, 2004). Spoor (1988b) also previously detected a separation of the front limbs with respect to the sagittal plane of the body based on the inclination of the articular trochlea of the humerus with the radius. This separation can now be confirmed, both as far as the fore limb and the hind limb are concerned (based on the morphology, amongst others, of the radius-humerus articulation and the distal and proximal regions of the femur, respectively; Bover, 2004). It is not possible to know whether the fusion of these carpal bones would have become a generalised evolutionary tendency in all the populations of *M. balearicus*, basically since there are only two conserved examples of scapholunar fusion (out of tens of specimens obtained for each of these bones) and one example of pisiform-cuneiform fusion. Either way, the rigidness caused from the morphology of ligament insertion and of the different carpal articular regions, indicates that this gave an important stability to this limb. What is more, as has already been said, other evolutionary patterns of the species have also led to fusions which restrict locomotor movements (e.g., distal tarsal fusions).

Therefore, in summary, some articular anatomical characteristics of the fore limb indicate that they were not positioned just under the body, as happens in nearly all the other extant bovids, but rather they were situated more laterally (Spoor, 1988b; Bover, 2004). Thus, it seems that these fusions (together with the robustness of the carpal bones) are related to greater stability in the articulations, with greater muscular power, and with slow, but powerful movements, all in all, with "low gear" locomotion (Sondaar, 1977). The acquisition of this type of locomotion could have been evolutionarily favoured for different reasons. Firstly, the lack of predators in the Gimnesics would have allowed the loss of anti-predatory anatomical and ethological characteristics (Leinders & Sondaar, 1974; Sondaar, 1977; Leinders, 1979; Moyà-Solà, 1979; Alcover *et al.*, 1981; Spoor 1988a and b; Köhler, 1993; Köhler & Moyà-Solà, 2001; Bover, 2004; Bover & Tolosa, 2005). Secondly, there could have been some sort of relationship with the acquisition of locomotion adapted to a more mountainous habitat (Andrews, 1915; Leinders, 1979). Thirdly, slow locomotion could be important in energy saving processes, as has been observed in certain parameters studied in the species (e.g., Köhler & Moyà-Solà, 2004). And finally, the anatomical characteristics observed could be related to the acquisition of a relatively high weight of the species with respect to its size (Alcover *et al.*, 1999; Bover, 2004).

We have been able to corroborate the separation of both limbs in *M. balearicus* with respect to the sagittal plane of the body of the animal with the study of the footprints and trails left by individuals of this species in different sediments in *Mallorca* and *Menorca*. The TI index in *M. balearicus* is nearly half that of the species of cervids and bovids studied, and is inferior to the suids studied. This indicates that, proportionally, the trails left by *M. balearicus*, are transversally broader than in the species with which they were compared. Quintana (1993) previously stated that the trails that an individual of *M. balearicus* left in the sediments of the Penyes d'Alparico in Menorca are more similar to those of *Sus* than other artiodactyls, such as *Cervus*.

As far as the trails of *M. balearicus* are concerned, the significance of the FA values, foot angle with respect to the axis of the animal's gait, is not clear. The greatest values in this species with respect to the other species studied indicate that the feet were rotated laterally. Either way, the measurement of this angle entails a series of problems due to the fact that there is no clear separation between the two hooves in the trails studied.

There are other sites near fossilised dunes that have provided other types of trails attributed to *Myotragus*. These are the cases of the sites in Cala Figuera (Calvià, Mallorca) and Son Mulet (Llucmajor, Mallorca) where considerable quantities of coprolites can be observed in the eolianite. These coprolites, together with the footprints, show that *Myotragus* has some sort of attraction and/or preference to these areas. The presence of possible "fossil" sources of water resources very near these areas or the presence of fresh vegetation could express the attraction of the species for these areas.

Although the considerable amount of *Myotragus* tracks and trackways in Pleistocene dunes, the findings of *Myotragus* bones in these kind of deposits are not abundant (Muntaner & Cuerda, 1956; Muntaner, 1957).

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08

REQUIEM FOR *MYOTRAGUS BALEARICUS* DOMESTICATION

Pere BOVER & Damià RAMIS

BOVER, P. & RAMIS, D. 2005. Requiem for *Myotragus balearicus* domestication. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 73-84.

Resum

La proposta de la domesticació de *Myotragus balearicus* pels primers pobladors humans de Mallorca, una hipòtesi clàssica de la prehistòria balear durant les darreres dècades del segle passat, ha estat recentment qüestionada. Les alteracions en forma de "V" observades a banyes de *Myotragus*, obtingudes a jaciments que contenien restes humanes i de fauna prehumana, varen ser inicialment considerades com a una prova de manipulació humana. Les banyes s'haurien seccionat per tal d'evitar que animals presumptament estabulats dins corrals es fessin mal entre ells. Ramis & Bover (2001) rebutjaren aquesta aproximació, i identificaren les alteracions en "V" observades a les banyes de *Myotragus balearicus* com resultat d'un comportament osteofàgic, una conducta coneguda a diversos bòvids i cèrvids, però no registrada fins a les hores a *Myotragus balearicus*. El comportament osteofàgic no ha estat acceptat per alguns autors en articles recents, que encara proclamen l'autoria humana de les alteracions a les banyes, en base a dades de $\delta^{13}C$. En aquest article, es presenten noves evidències que recolzen inequívocament que la conducta osteofàgica de *Myotragus* és la causa exclusiva del patró d'alteració registrat a les banyes. Recentment s'han recol·lectat nous materials de banyes de *Myotragus* que presenten alteracions en "V" provinents d'un jaciment subaquàtic a 10 m de profunditat en una cavitat submergida (un lloc sense possibilitat de relació entre *Myotragus* i humans) i materials provinents d'un jaciment del Pleistocè Mitjà.

Paraules clau: *Myotragus balearicus*, domesticació, osteofàgia, Mallorca.

Abstract

The proposal of the domestication of *Myotragus balearicus* by the first settlers on Mallorca, a topic in the Balearic prehistory during the last part of the previous century, has been recently disqualified. The "V"-trimmed *Myotragus* horn cores obtained from deposits containing human remains and pre-human fauna were initially considered as a proof of human manipulation in order to avoid damage in animals assumedly gathered in corrals. After Ramis & Bover (2001) this approach has been refused and the "V"-trimmed horn cores of *Myotragus balearicus* were identified as the result of an osteophagic behaviour, a kind of behaviour previously known in some extant bovids and cervids, but as so far unrecorded on *Myotragus balearicus*. Although the osteophagic behaviour has been unaccepted by some recent authors, still claiming for a human-caused trimming of horn cores, new evidence supports our approach. Claims of Davis (2002) are based in $\delta^{13}C$, a methodology recently used to study the diet of fossil and recent mammals. In our presentation we argue again on the osteophagic behavior of *Myotragus* as a exclusive cause for the recorded trimmed horn cores. New materials displaying the same "V"-trimmed horn cores pattern come from recently exhumed materials discovered in a subaquatic deposit at 10 m underwater in a flooded cave (a place with no possibility of relation between *Myotragus* and humans) and from Middle Pleistocene deposits.

Key words: *Myotragus balearicus*, domestication, osteophagy, Mallorca.

INTRODUCTION

The hypothesis of the existence of a domestication process for *M. balearicus* by the first settlers in Mallorca, which was considered a classical approach in Balearic prehistory during the end of the last century, has recently been brought into doubt (Ramis & Bover, 2001). The model under question was based on a set of evidence. In different sites, containing human remains and prehuman fauna, *M. balearicus* skulls with a peculiar horn typology were obtained and were interpreted to be the result of human action. Alterations in different long bones of the species were also documented, supposedly also caused as a result of human manipulations (see Fig. 1, Waldren, 1982). The horns would have been cut to avoid any possible harm that assumedly stabled animals could do among them in reduced spaces during fights. On the other hand, the manipulations of the species' bones were attributed to manipulations to prepare them for eating. The theory of animal retention in stables was supported by the presence of coprolite accumulations in the Balma de Son Matge (Waldren, 1982).

The finding of new skulls with a similar horn typology as that documented in Balma de Son Matge (Fig. 2) made it possible to present an alternative interpretation as to their origin. The importance of these skulls lay in the fact that they all came from exclusively paleontologi-

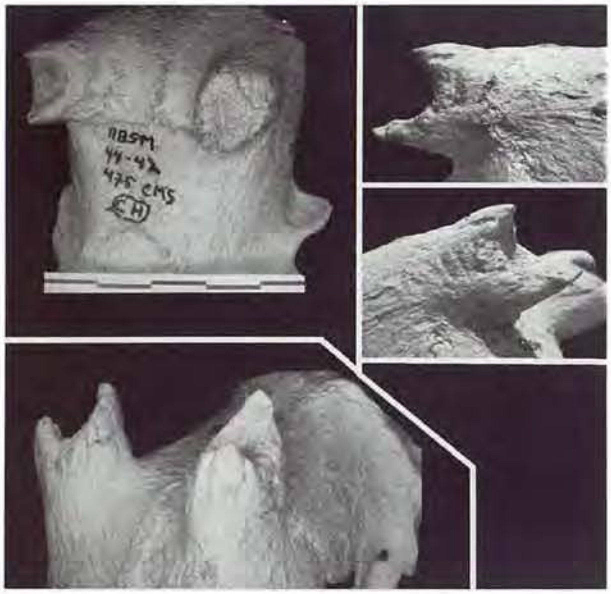

Fig. 1. Photo of one of the *M. balearicus* skulls with "V"-trimmed horn cores from Balma de Son Matge. Left upper side, caudal view. Left lower side, dorso-lateral view. Right upper side, detail of "V"-trimmed horn cores. Photos obtained from Waldren (1982).

Fig. 1. Fotografia d'uns dels exemplars de crani de M. balearicus *amb les banyes alterades trobat al jaciment de la balma de son Matge. Adalt a l'esquerra en norma caudal. Abaix a l'esquerra en norma dorsolateral. Adalt a la dreta, detall de les alteracions de les banyes. Imatges obtingudes de Waldren (1982).*

cal sites (e.g., Bufador de Son Berenguer, Cova de Son Maiol, Fig. 3) or from levels in archaeological-paleontological sites considered to be prehuman (inferior levels in Cova des Moro). What is more, in some of these sites, bones belonging to the postcranial skeleton were identified with the same alteration pattern as the horns of *M. balearicus* in Balma de Son Matge (Fig. 4).

A review of these materials (e.g., Ramis, 2000; Pérez-Ripoll & Nadal, 2000; Ramis & Bover, 2001) made it possible to reach the conclusion that the "V"-shaped horns of *M. balearicus* were the result of osteophagic behaviour, a type of behaviour previously known in a series of living artiodactyls, but not identified to date in *M. balearicus* (Ramis & Bover, 2001), and also that there was no evidence of species domestication. This osteophagic behaviour is supposedly produced in order to make up for the lack of phosphates in the diet in terrains that are poor in phosphates (e.g., Wika, 1982). On the other hand, the accumulation of coprolites in Balma de Son Matge was interpreted as the result of behaviour natural to the species, both due to the finding of coprolite deposits in a cavern without any type of human remains inside, Cova Estreta (Pollença) (Encinas & Alcover, 1997), and because of what can currently be observed in caves or caverns where goats (*Capra hircus*) normally spend a certain amount of time. Furthermore, modifications registered in different *Myotragus* bones were identified to be the result of osteophagic effects (Ramis & Bover, 2001), while some supposed bone needles found in Cova de Moleta were reinterpreted as non-modified *M. balearicus* fibulas (Ramis & Alcover, 2001a). It was also documented that some supposed traces of flesh removal from a *Myotragus* radius (Waldren, 1974) were actually made on the radius of an introduced caprine (Alcover *et al.*, 2001).

Davis (2002) and Waldren *et al.* (2002) have rejected osteophagic behaviour as a cause of the alterations found in the bones of *M. balearicus*, and continue arguing that the typology observed in the horns of the species found in Balma de Son Matge is the result of human activities. Davis' arguments (2002) are based on the $\delta^{13}C$ and $\delta^{15}N$ study of bones from different species (among them, *M. balearicus*), a methodology used to study the diet of fossil and living mammalian species. This author contends that a habitual consumption of bones by *M. balearicus* which would have represented between 5% and 20% of their diet would be reflected in a rise in the $\delta^{13}C$ values, due to the fact that the value of this parameter is increased over the trophic chain (e.g., Palmqvist *et al.*, 2003). Another of the arguments proposed by Waldren *et al.* (2002) is that the symmetry of the alterations in the two horns could only be possible if they had been made by humans. These authors, also, argue that only domestication could explain the great accumulation of coprolites in Balma de Son Matge. In their opinion, a long coexistence of *M. balearicus* and humans could be demonstrated due to the fact that the isotopic analysis of some very fragmented bones (not taxonomically diagnosable from their morphology) from a relatively modern site, Son Ferrandell-Olesa (Early Bronze Age), supposedly fall within the isotopic profile of *M. balearicus*. These authors also use the basis of the $\delta^{13}C$ and $\delta^{15}N$ comparison of *M. balearicus* bones and the goat currently living in Mallorca (*Capra hircus*). Davis (2002), once the values of these two isotopic parameters were analysed for these two species, reaches the conclusion that they are similar, and therefore, since actually there has been no observed osteophagic behaviour in goats, it would have to be deduced that neither did *M. balearicus* have this behaviour.

The aim of this article consists of assessing the validity of the conclusions we expounded at the time about the supposed domestication process of this species (Ramis & Bover, 2001), by analysing the reliability of the arguments proposed in a sense contrary to Davis (2002) and Waldren *et al.* (2002).

MATERIALS AND METHODS

The new materials studied are two *Myotragus* skulls from two locations in Mallorca:

1- Avenc Socarrat (Calvià, Mallorca)

2- Cova Genovesa (Manacor, Mallorca)

From the first location (Fig. 5) a fragmented *Myotragus* skull with altered horns was obtained (MNIB 68749, Fig. 6) (Crespí *et al.*, 2001). The only part of the skull left is the top of the neurocranium. It still has the horns, which have the same morphology as that recorded in the examples from Balma de Son Matge described by Waldren (1982). From the same place in the site, a mandible corresponding to *M.* cf. *batei*, a species from Lower Pleistocene, was obtained (Crespí *et al.*, 2001). These materials come from a breccia situated between blocks of one of the halls in the cavern.

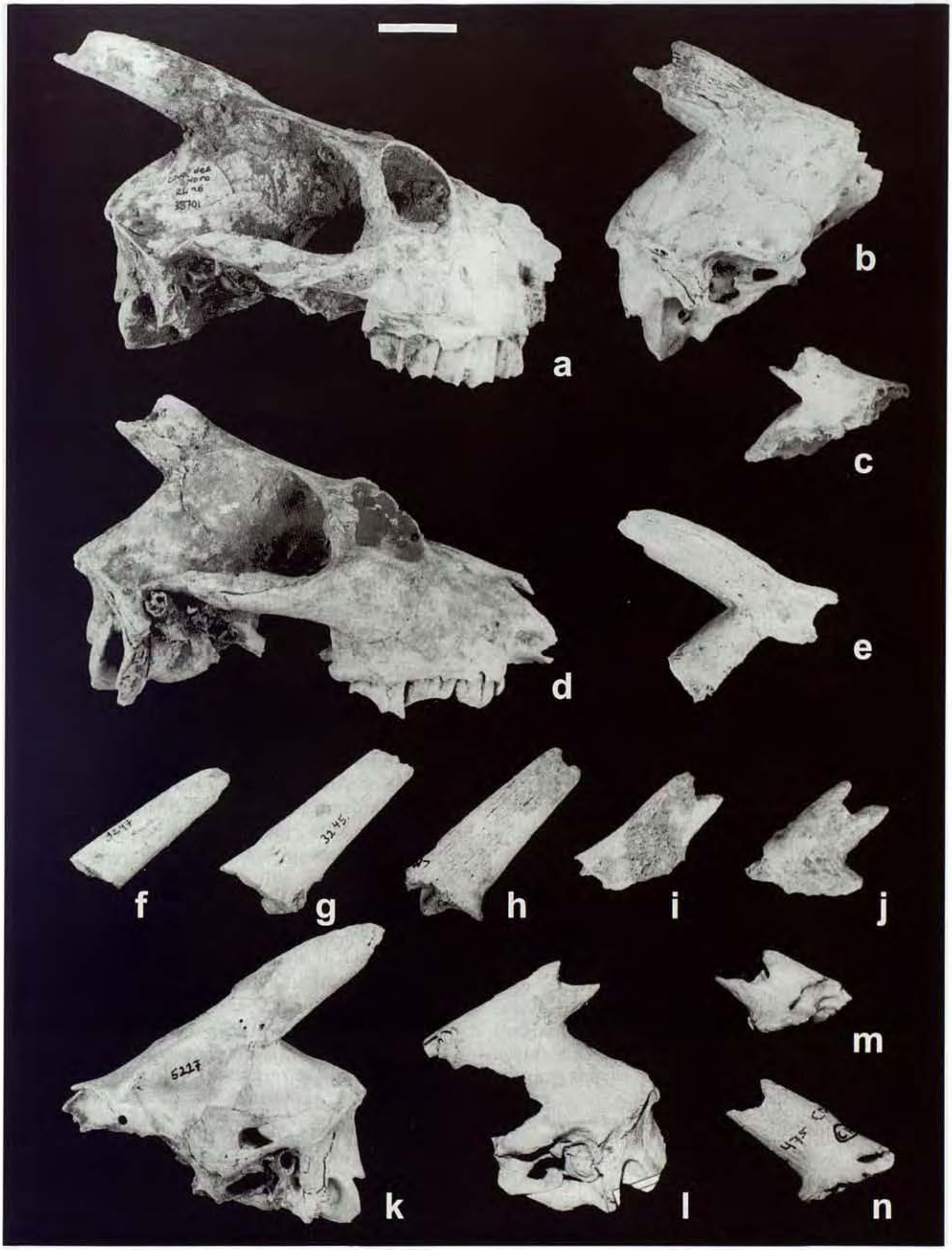

Fig. 2. Holocene skulls of *M. balearicus* with "V"-trimmed horn cores from different deposits. a-k : Cova des Moro and l-n, Balma de Son Matge. a: MNIB 38701; b: MNIB 5226; c: MNIB 3180; d: MNIB 60750; e: MNIB 3181; f: MNIB 3247; g: MNIB 3245; h: MNIB 3249; i: MNIB 8165; j: MNIB 60751; k: MNIB 5227; l: without number (Museu de Mallorca); m: without number (Museu de Mallorca); n: without number (Museu de Mallorca). Bar scale 2 cm. Photo obtained from Ramis & Bover (2001).

Fig. 2. Cranis holocènics de M. balearicus *amb banyes alterades procedents de diversos jaciments. a-k : cova des Moro i l-n, balma de son Matge. a: MNIB 38701; b: MNIB 5226; c: MNIB 3180; d: MNIB 60750; e: MNIB 3181; f: MNIB 3247; g: MNIB 3245; h: MNIB 3249; i: MNIB 8165; j: MNIB 60751; k: MNIB 5227; l: sense número (Museu de Mallorca); m: sense número (Museu de Mallorca); n: sense número (Museu de Mallorca). Escala 2 cm. Imatge obtinguda de Ramis & Bover (2001).*

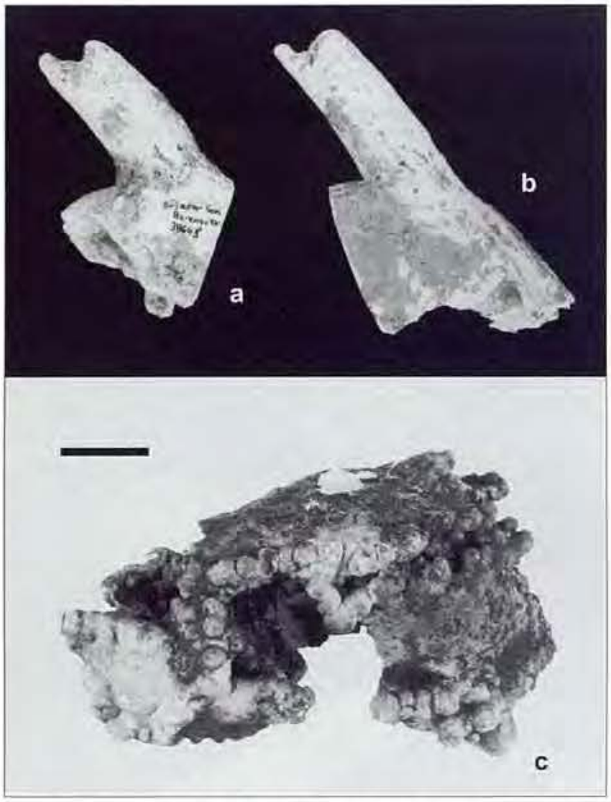

Fig. 3. Pleistocene skulls of *M. balearicus* with "V"-trimmed horn cores. A and B, skulls from Bufador de Son Berenguer; C, skull from Cova de Son Maiol. A: MNIB 38643; B: MNIB 38644; C: MNIB 60805. Bar scale 2 cm. Photo obtained from Ramis & Bover (2001).

Fig. 3. Cranis de M. balearicus *del Pleistocè amb banyes alterades. A i B, cranis del bufador de son Berenguer; C, crani de la cova de Son Maiol. A: MNIB 38643; B: MNIB 38644; C: MNIB 60805. Escala 2 cm. Imatge obtinguda de Ramis & Bover (2001).*

Cova Genovesa is a cavern which is under water for most of its length (Fig. 7) (Gràcia *et al.*, 2003a). In one part of its flooded galleries, an important number of *M. balearicus* bones were found on the floor surface, at a depth of 10 metres (Fig. 8) (Gràcia *et al.*, 2003b). Among them it is worth noting, for the present study, a series of skulls with the same type of aforementioned horn alteration. The bad state of conservation in which the bones were found (Crespí & Bover, en prep.) did not recommend the extraction from the site of all the skulls. The original layout of the *M. balearicus* skulls was recorded on film, with the aim of documenting it for later studies. From the skulls with this type of alteration, which can be seen in the video film recorded in the cavern study project (Consell de Mallorca and Grup Nord de Mallorca) (Fig.9), only one has been extracted, so as to carry out a detailed study.

This skull from Cova Genovesa (MNIB 85105) is a piece made up of the top of the neurocranium, with well conserved frontal bones (Fig. 10) and with alterations in the horns, also "V"-shaped, just like the ones recorded in Balma de Son Matge. On its surface a series of ridges produced by too quick drying during its conservation process can be observed (Crespí & Bover, in prep.).

Additionally, a series of carbon fractioning values have been obtained from the radiocarbon dating carried out on material from archaeological and paleontological excavations which the IMEDEA palaeontology team has carried out or collaborated in. The values available for *Myotragus* and domestic caprine samples have been compared, so as to assess whether it is actually possible to distinguish between the two from the results. Unfortunately there is no particular numerical value for Nitrogen fractioning available for any of the bovid species (fossils or present day) in the Balearics (Bover, 2004) therefore the results obtained from the literature have been analysed (basically Davis, 2002 and van Strydonck *et al.*, 2002). These authors do not present in their works any table with the specific results obtained. Hence, the values of these parameters have been estimated from their graphs. These authors' data come from an analysis of the bones in Cova de Moleta (Sóller) and Balma de Son Matge (Valldemossa) sites for *M. balearicus*, and from three Bronze Age archaeological sites in the municipality of Valldemossa (Mallorca), Son Mas, Son Ferrandell/Son Oleza and Naveta Baduia, for the introduced bovids. All these sites are situated very nearby, in the Serra de Tramuntana.

RESULTS

Direct observation of the horns on the *M.* cf. *batei* skull from Avenc Socarrat (MNIB 68749, Fig. 6) and from the different *M. balearicus* skulls from Cova Genovesa (MNIB 85105, Fig. 9 and 10), indicates that the alteration patterns are identical to those observed in the horns of skulls interpreted to be the result of human manipulation by Waldren (1982), and in the skulls studied by Ramis & Bover (2001) which were interpreted to be the result of natural osteophagic conduct in the species.

In the case of the skull from Avenc Socarrat (MNIB 68749), the chewing effect in *Myotragus* reached the *collum processus cornualis*, leaving the *sinus frontalis caudalis* of the skull uncovered. Ramis & Bover (2001) present a figure in which the wear gradually produced in *M. balearicus* horns can be seen as they are worn down. The case of Avenc Socarrat would be the most extreme case in which the wear has surpassed the spongy tissue of the horn, nearly reaching the external surface of the frontal bone.

The skull from Cova Genovesa (MNIB 85105) also has the typical marks on the horns produced by the osteophagic conduct of *M. balearicus*. It has a different wear on the horns. One of the horns (the left one) is more worn down than the right one. The form of wear, or to put it another way, the orientation of the "V"-shaped cleft in the horns, is really, broadly speaking, symmetrical.

In Tables 1 and 2 the Carbon fractioning data obtained for *M. balearicus* and domestic caprines are related respectively, from the datings carried out by the IMEDEA paleontological team. The $\delta^{13}C$ data for the *M. balearicus* bones studied are between 19.7 and 22.1 ‰ (mean value 20.67 ‰). The values for introduced caprine species for different archaeological sites are 20.4 and 21.3 ‰, which is clearly within the $\delta^{13}C$ interval for *M. balearicus*. The data for *M. balearicus* and introduced caprines in the same site (Cova des Moro, Mallorca) also overlap, as well as the data of these two species in the same geographical zone, Serra de Tramuntana in Mallorca (Cova Estreta, Coveta des Gorgs and Coval Simó).

The data obtained from the graphs for *M. balearicus* and the domesticated bovids of Davis (2002) and van Strydonck *et al.* (2002) are shown in Table 3.

The $\delta^{15}N$ values obtained from the literature seem to be quite scattered for *M. balearicus* (Bover, 2004). The lowest $\delta^{15}N$ values are found in *M. balearicus* (+1.57 ‰, whereas the highest values are observed in introduced caprines (*Ovis aries*/ *Capra hircus* group, +7.23 ‰) and in *Bos taurus* (+6.85 ‰). Apart from these two extreme values, the rest of the intervals calculated for introduced bovids totally overlap with the intervals obtained for *M. balearicus*.

As can be appreciated in Table 3, the $\delta^{13}C$ data obtained by other authors for *M. balearicus* and for introduced caprines are basically in line with the data obtained by the IMEDEA paleontology team. There are no important differences that can allow us to define a clear differential pattern between *M. balearicus* and the introduced bovids. In some cases (*Capra hircus*), the values appear to be slightly higher than in *M. balearicus*. It can also be observed that another of the higher $\delta^{13}C$ values corresponds to *Bos taurus*. As extreme values, it can be appreciated that the lowest $\delta^{13}C$ values are found in *M. balearicus* (-22.1 ‰).

DISCUSSION

Osteophagic osteologic evidence

The main difference between the two aforementioned skulls and those studied by other authors lies in their inaccessibility, both timewise and spacewise, to human hands. In the first case, the skull from Avenc Socarrat was attributed, with certain reservations, to *M. batei* (Crespí *et al.*, 2001), a species from the lower Pleistocene (Crusafont & Angel, 1966; Alcover *et al.*, 1981). If the alterations observed in the skull were of human origin, the finding in

DEPOSIT	LAB NUMBER	2σ (years calBC)	$\delta^{13}C$ (‰)
Cova Estreta (MA)	UtC-5171	4720-4400	-21,0 (1)
Coveta des Gorgs (MA)	Beta-177239	6010-5830	-20,2
Coveta des Gorgs (MA)	Beta- 143117	7790-7580	-20,1
Cova des Moro (MA)	UtC-6671	9150-8450	-20,8
Cova des Moro (MA)	Beta-155644	11180-10700	-22,1
Pas den Revull (ME)	Beta-177237	3970-3760	-20,9
Cova des Myotragus (ME)	Beta-177238	22000-20400	-20,6
Cova des Penyal Blanc (CAB)	UtC-6517	3650-3380	-19,7

Table 1. $\delta^{13}C$ values from *M. balearicus* bones from different Gymnesic deposits. MA) Mallorca; ME) Menorca; CAB) Cabrera. (1) Estimated value due to small size of sample.

Taula 1. *Valors de $\delta^{13}C$ obtinguts a partir d'ossos de* M. balearicus *de diferents jaciments de les Gimnèsies. MA) Mallorca; ME) Menorca; CAB) Cabrera. (1) Valor estimat degut a que la mostra era molt petita.*

DEPOSIT	LAB NUMBER	2σ (years calBC)	$\delta^{13}C$ (‰)
Coval Simó (MA)	Beta-154196	2300-2030	-21,3
Cova des Moro (MA)	Beta-155645	2290-2030	-20,6
Coval Simó (MA)	Beta-177240	770-400	-20,4

Table 2. $\delta^{13}C$ values from bones of introduced caprine (*Ovis aries* or *Capra hircus*) from two deposits of Mallorca. MA) Mallorca.

Taula 2. *Valors de $\delta^{13}C$ obtinguts a partir d'ossos de caprí introduït (*Ovis aries *o* Capra hircus*) a dos jaciments de Mallorca. MA) Mallorca.*

TAXA	n	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
		Min	Max	Min	Max
Myotragus pre 10000BC	3	-21,7	-19,65	+4	+5,42
Myotragus post 10000 BC	9	-21,85	-19,74	+1,64	+4,64
Myotragus 14000-6000 BC	6	-21.26	-19,98	+1,57	+6,43
Bos taurus	*13*	*-21,12*	*-19,31*	*+4*	*+6,85*
Ovis aries	5	-21	-19,81	+4,85	+5,84
Capra hircus	2	-19,47	-19,30	+4,15	+4,84
Ovis aries/Capra hircus	22	-21,34	-21,18	+2,84	+7,23

Table 3. $\delta^{13}C$ and $\delta^{15}N$ values obtained from Davis (2002) and van Strydonck et al. (2002) for different bovid species.

Taula 3. *Valors de $\delta^{13}C$ i $\delta^{15}N$ obtinguts a partir dels treballs de Davis (2002) i van Strydonck et al. (2002) per a diferents espècies de bòvids.*

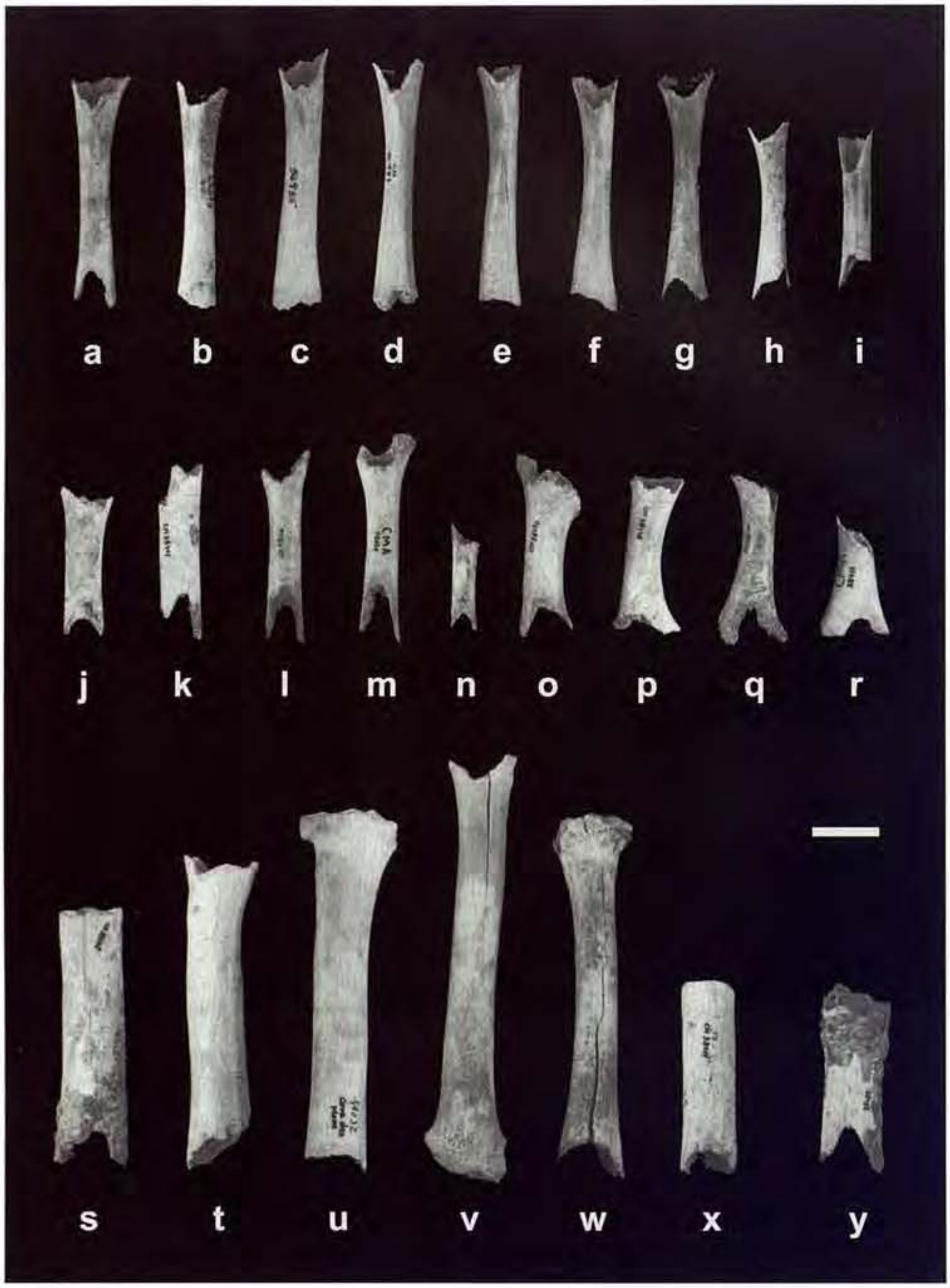

Fig. 4. V-trimmed leg bones of *M. balearicus* from Cova des Moro. All bones from MNIB collection. a: 38463; b: 56983; c: 56935; d: 56984; e: 38468; f: 38465; g: 38466; h: 38464; i: 38469; j: 38442; k: 38441; l: 38444; m: 38446; n: 39440; o: 38470; p: 38448; q: 38450; r: 38451; s: 38443; t: 38439; u: 49032; v: 49088; w: 49096; x: 38447; y: 38453. Bar scale 2 cm. Photo obtained from Ramis & Bover (2001). See this paper for further details of illustrated bones.

Fig. 4. *Ossos alterats de les extremitats de* M. balearicus *provinents de la cova des Moro. Tots els ossos de la col·lecció MNIB. a: 38463; b: 56983; c: 56935; d: 56984; e: 38468; f: 38465; g: 38466; h: 38464; i: 38469; j: 38442; k: 38441; l: 38444; m: 38446; n: 39440; o: 38470; p: 38448; q: 38450; r: 38451; s: 38443; t: 38439; u: 49032; v: 49088; w: 49096; x: 38447; y: 38453. Escala 2 cm. Imatge obtinguda de Ramis & Bover (2001). Veure aquest treball per a més informació detallada sobre els ossos il·lustrats.*

Avenc Socarrat would indicate that the first human presence in the Balearics would be much earlier than that determined to date by different authors, and that this would even be before the appearance of *Homo sapiens*. The lack of any type of human presence in the Balearics in the paleontological records of this time (lower Pleistocene) and the fact that the archaeological record of the Balearics only dates at the uppermost part of the III millennium cal BC (Alcover *et al.*, 2001; Ramis & Alcover, 2001b; Ramis *et al.*, 2002) allows us to conclusively refute the possibility that the alterations found in the skull in Avenc Socarrat - identical to the skulls from Balma de Son Matge - could be attributed to human activities.

In the second case, that of Cova Genovesa, the remains of different skulls are submerged at an average depth of 10 metres, and in some galleries at least 125 metres from the cave's actual entrance (Gràcia *et al.*, 2003a and b). In fact, there is a great accumulation of *M. balearicus* skeletal remains in a small lateral hall only 50 cm in height, near to where the animals possibly died (see Fig. 11). The layout of the bones and the topography of the cave suggest that the animals entered the cavern at a time when the sea level was at least 10m below the current level (before the Holocene; with a chronology attributable to an undetermined moment in the last glaciation). A step of about 1.5 metres, which can be found at the beginning of the galleries where the bovid remains were found (Francesc Gràcia, pers. comm.), could have impeded the exit of the animals once they had fallen inside the so-called Galeria dels Myotragus. In fact *Myotragus* remains have been found approximately 400 metres from the actual cave's entrance (Fig. 7). The fact that the Cova Genovesa galleries - where remains of the *M. balearicus* species (from the upper Pleistocene – Holocene) can be found - were dry at

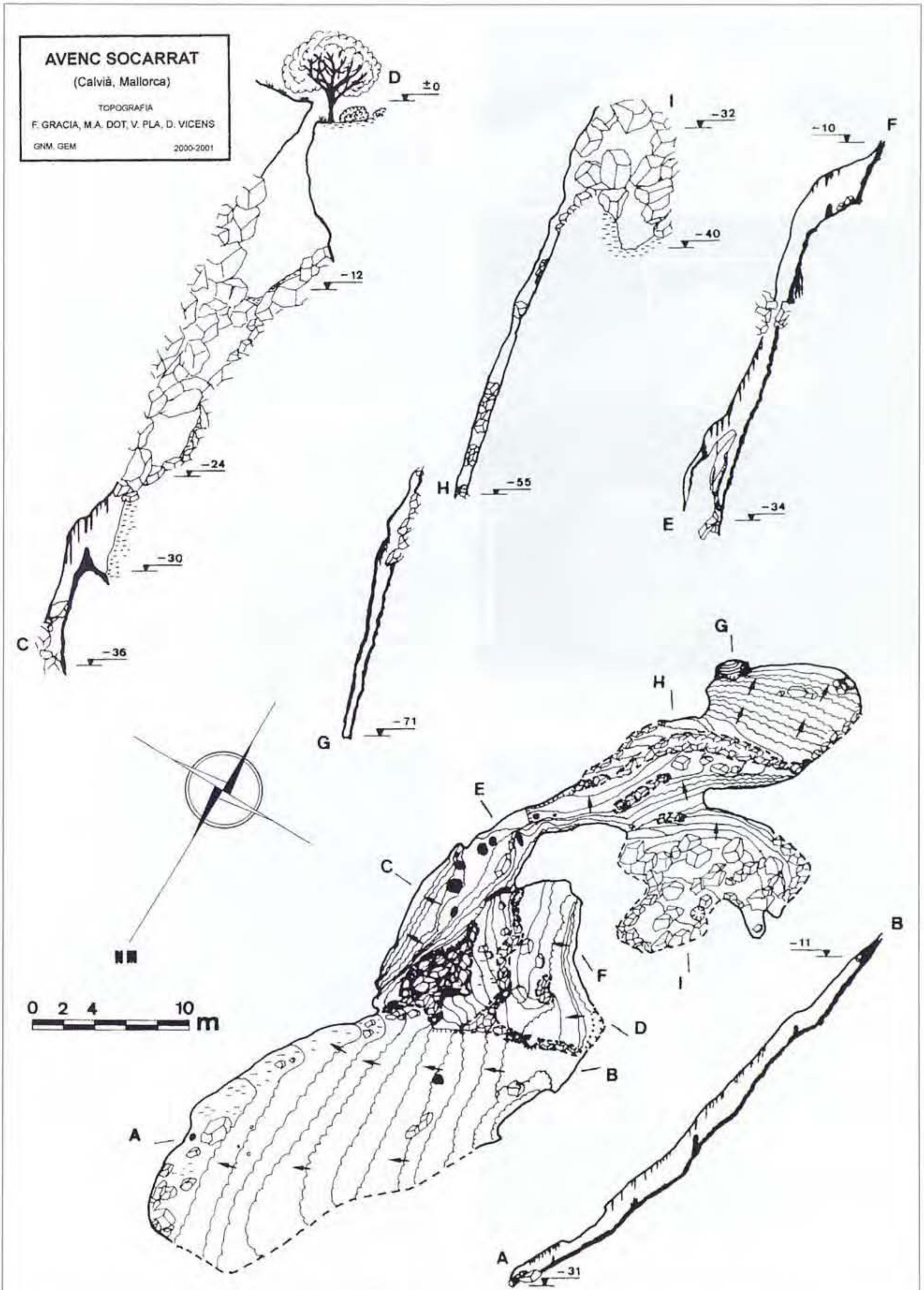

Fig. 5. Topographic survey of Avenc Socarrat (Calvià, Mallorca). Obtained from Crespí *et al.* (2001).

Fig. 5. *Topografia de l'avenc Socarrat (Calvià, Mallorca). Obtinguda de Crespí* et al. *(2001).*

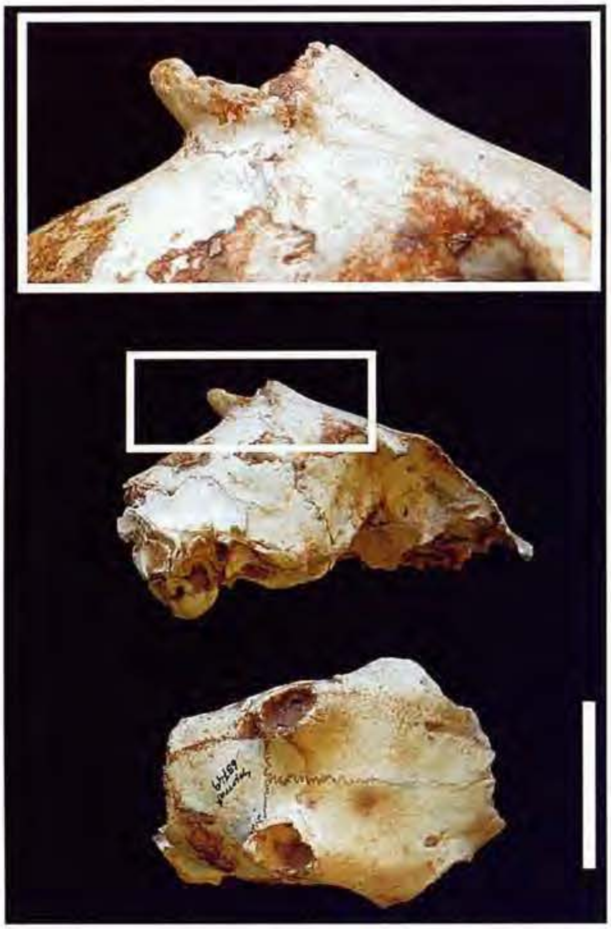

Fig. 6. *Myotragus* cf. *batei* skull MNIB 68749 from Avenc Socarrat. Lower side, dorsal view; Centre side, lateral view; Upper side, detail of trimmed horn core. Bar scale 4 cm.

***Fig. 6.** Crani de* Myotragus *cf.* batei *MNIB 68749 de l'avenc Socarrat. Abaix, en norma dorsal; enmig, en norma lateral; adalt, detall de la banya alterada. Escala 4 cm.*

the time the bones were deposited, and that these were not very displaced by dragging by mud or water, allows us to assume that the bones were deposited at the time of a glaciation, very possibly the Würm, in any case over 10000 years ago. To date there are no radiocarbon datings available for this site. The fact that all this material has been under water since the end of the Würm allows us to conclusively refute that the alterations found in the skulls from Cova Genovesa could be attributed to human activities. The attribution to human activities would imply a human presence in *Mallorca* at least during the Würm, a fact which can undeniably be excluded.

Apart from the geographical situation, it is worth repeating that the alterations in the horns observed in these skulls have a pattern which is morphologically compatible with the osteophagic patterns observed in other species of present day bovids (Anderson, 1974; Brothwell, 1976; Warrick & Krausman, 1986; Bover *et al.*, in prep), cervids (Sutcliffe, 1973; 1977; Gordon, 1976; Hasegawa, 1977; Krausman & Bisonette, 1977; Wika, 1982; Bowyer, 1983; Kahlke, 1990; Kierdorf, 1993), giraffids, camelids (Johnson & Haynes, 1985) and suids (Greenfield, 1988).

Stable isotopes

The $\delta^{13}C$ and $\delta^{15}N$ data from different *M. balearicus* and present-day bovids have been compared. As can be seen in Tables 1, 2 and 3, there is no important difference between these parameters for *M. balearicus* and for the introduced bovids which have been studied in Mallorca based on prehistoric materials (datings basically made on *Capra hircus* bones). It must be said, firstly, that osteophagic behaviour is a conduct that has irrelevant trophic implications, and that it is not expected to reach an appreciable nutritional value, As a consequence, it is not expected to be reflected in the analysis of the stable isotopes of carbon and nitrogen.

Osteophagic behaviour emerges as the most feasible hypothesis of the origin of the alterations in the horns of *Myotragus*. The great quantity of bones which have actually been extracted from paleontological excavations leads us to believe that this behaviour was of limited extension. It has only been recorded inside the caverns where animals could enter normally and comfortably, and the proportion of chewed bones is always very small. By way of example, this is the case of Cova des Moro (Manacor), Cova de Son Maiol (Palma), Bufador de Son Berenguer (Santa Maria) and Cova Genovesa (Manacor), all of which are caves with an important development in volume, or Balma de Son Matge (Valldemossa), an open cavern. On the other hand, in caves such as Cova Estreta (Pollença*)*, a narrow cavern, where it may not have been comfortable to move about and chew bones, the incidence of osteophagic behaviour in the remains of *Myotragus* is much lower. From Cova des Moro, where nearly 9000 bones have been found, fewer than a hundred have osteophagic marks (this represents close to 1% of the total bones extracted). Logically, not all of the bones are susceptible to being chewed, since small bones (phalanges, sesamoid, tarsal and carpal bones) are difficult to chew.

Recently, a goat (*Capra hircus*) was photographed in the Serra de Tramuntana in Mallorca, chewing the mandible of an individual belonging to its own species (Bover *et al.*, in prep.; Fig. 12). What is more, numerous bones of present day *Capra hircus*, *Ovis aries* and *Bos taurus* have been collected with the same morphology as that observed in the *M. balearicus* bones. Some specimens of skull chewed in symmetrical "V"-shapes have even been found (Bover *et al.*, in prep.), and actually no type of cut is made in the horns of wild goats in *Mallorca*, neither is it the habitual practice in goats enclosed in stables. In the analyses carried out on individuals of the same species (see Table 2) no type of evidence of osteophagic behaviour has been found using $\delta^{13}C$. Since it is to be expected that in the past in Mallorca *Capra hircus* had a similar behaviour to nowadays, it would seem that osteophagic behaviour is not registered by this parameter. This must be valid both for introduced bovids and for *M. balearicus*.

Davis (2002) considers that different non-morphologically identifiable bone fragments from the Bronze Age site of Son Ferrandell-Oleza (Valldemossa) could be attributed to *Myotragus* due to their isotopic similarity to those belonging to this species. Nevertheless, in the preliminary faunistic study of this site carried out by Clutton-Brock (1984), the presence of *Myotragus* was not identified and this species was considered to have already

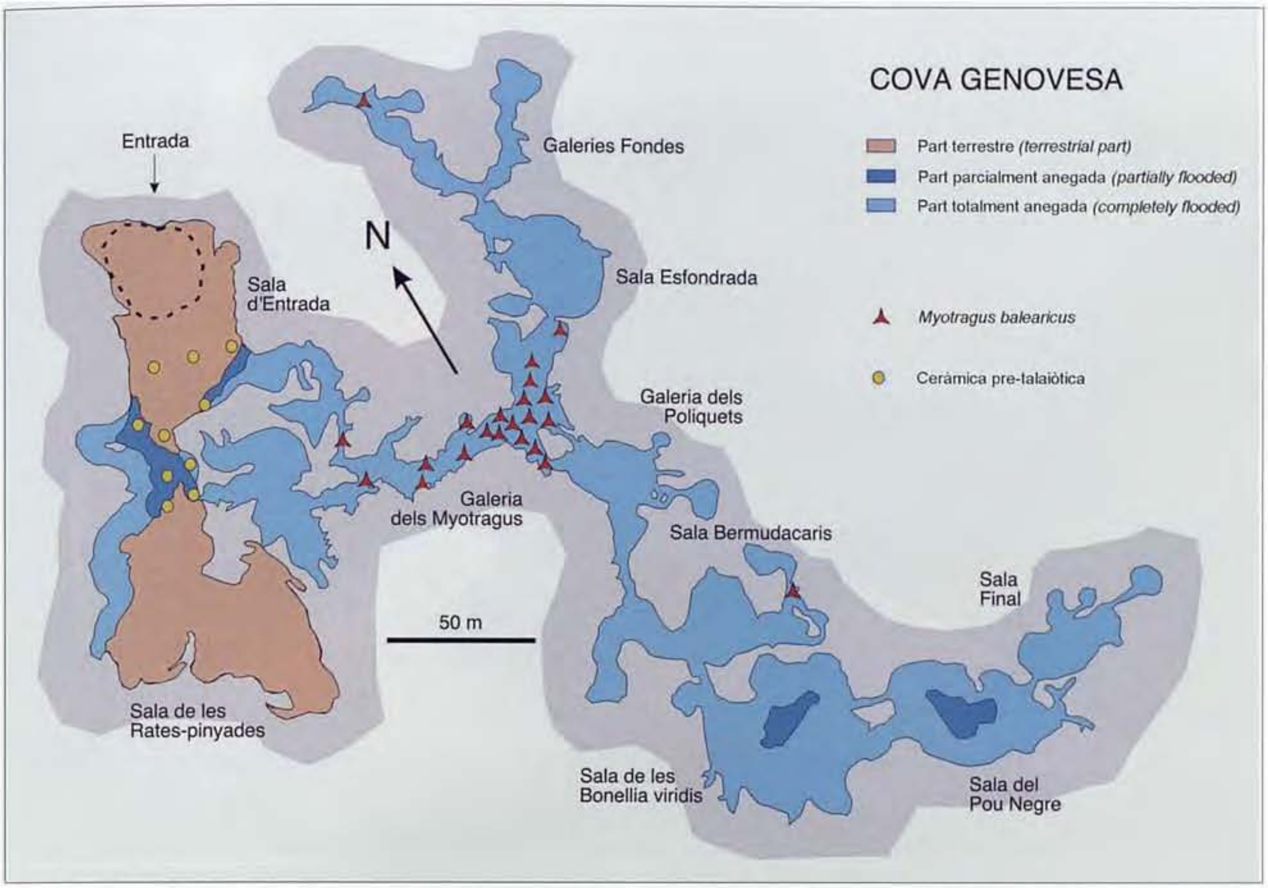

Fig. 7. Sketch of the topographic survey of Cova Genovesa (Manacor, Mallorca) where the *M. balearicus* bones distribution can be observed. Drawing obtained from Gràcia *et al.* (2003b).

Fig. 7. *Croquis de la topografia de la cova Genovesa (Manacor, Mallorca) on s'observa la distribució de les restes osteològiques de* M. balearicus. *Imatge obtinguda de Gràcia* et al. *(2003b).*

Fig. 8. Bones of *M. balearicus* from Cova Genovesa. These bones are located in a place 10 m underwater. Photo courtesy of F. Gràcia

Fig. 8. *Vista de diversos ossos de* M. balearicus *de la cova Genovesa. Aquests ossos es troben a 10 m de profunditat. Imatge cortesia de F. Gràcia*

disappeared by the time of human occupation of Son Ferrandell-Oleza. Isotopic analyses can be affected by different factors (Bowman, 1990).

In our opinion, there should be no difference due to bone chewing - as far as nitrogen and carbon fractioning is concerned - between living bovids and *Myotragus*. Just as can be observed in Tables 1, 2 and 3, the small differences existing between *M. balearicus* and introduced

Fig. 9. Detail of *M. balearicus* bones submerged in Cova Genovesa. Arrows show "V"- trimmed horn cores of both skulls. Photo obtained from Gràcia *et al.* (2003b).

Fig. 9. *Detall d'ossos de* M. balearicus *submergits a la cova Genovesa. Les fletxes indiquen les banyes alterades de dos cranis. Imatge obtinguda de Gràcia* et al. *(2003b).*

Fig. 10. *M. balearicus* skull MNIB 85105 from Cova Genovesa. From upper to lower side and from left to right: dorsal view, caudal view, lateral views. Down, detail of trimmed horn cores. Bar scale 2 cm.

Fig. 10. *Crani de* M. balearicus *MNIB 85105 de la cova Genovesa. D'adalt abaix i d'esquerra a dreta : norma dorsal, norma caudal, normes laterals. Abaix, detall de les banyes alterades. Escala 2 cm.*

bovids can be explained as the result of differences in the diet. The slightly lower values in *M. balearicus* for $\delta^{13}C$ respond to a type of *browser* diet (Bover, 2004) mainly based on shoots from bushes and trees (C3 plants), whereas in the introduced bovids, the presence of herbaceous plants (C4) in their diets would produce not as low $\delta^{13}C$ values.

Very possibly, one of the most important effects of human arrival in the Balearics was in opening up clearings in woods in order to settle, grow crops and move around. The creation of open habitats favours the presence of herbaceous plants (C4 plants) which the different introduced bovids would have fed on. What is more, two of the species studied (*Ovis aries* and *Bos taurus*) have *grazer* types of diet based on herbaceous plants (giving higher $\delta^{13}C$ values).

The interpretation of the small differences as far as $\delta^{15}N$ is concerned is more complicated. This parameter is affected by a factor which is intrinsic to each species, that is, its nitrogen metabolism. We do not know whether *M. balearicus* had a different metabolism for this element to present day bovids. Herbivores living in more arid areas have higher $\delta^{15}N$ values, while those living in more closed habitats have lower $\delta^{15}N$ values (Palmqvist *et al.*, 2003). In

Mallorca and Menorca, a vegetational change has been recorded, mainly expressed by the replacement of *Buxus* by *Olea*, as well as the appearance of plants that are more common in more open, drier environments (Yll *et al.*, 1999; Pérez-Obiol *et al.*, 2000, 2001). Based on palynological data, the accurate chronology of this vegetational change in Mallorca is uncertain (it can only be stated that it was later than 5380 calBC) however in Menorca it has been shown to be later than 2880 cal BC (Bover & Alcover, 2003). The fact of having a more arid climate in the Bronze Age (the time of origin of the introduced bovid bones from which the $\delta^{15}N$ data were obtained) than at much earlier times (times of origin of the *M. balearicus* bones to obtain the $\delta^{15}N$), could contribute to explaining the higher values of this marker for the introduced bovids.

The specific diagnosis of small caprine bone fragments based on the fractioning values of stable isotopes seems, for the time being, not to be very reliable. In the Balearics, these types of studies have only been used to differentiate between human bones and introduced artiodactyl bones (van Strydonck *et al.*, 2002).

Final remarks

Even though the most recent dating in Mallorca (Balma de Son Matge site) made on *Myotragus balearicus* bones, is not reliable (van Strydonck *et al.*, this volume), so far the most recent solid evidence available places the presence of *Myotragus* in the Balearics later than 3650 cal BC, although it is not known how much later (Bover & Alcover, 2003). Current available data allow us to establish that humans and *Myotragus* could have lived together at most for around 960 years in Mallorca and 1070 years in Menorca (Bover & Alcover, 2003; Quintana *et al.*, 2003). However, the most important fact is that this coexistence could have been considerably shorter. The supposed coexistence between humans and *Myotragus* of over 3000 years is not supported by the evidence available (Waldren *et al.*, 2002). The postulated domestication can not be explained either by the presence of coprolite accumulations (already commented on above) or by the supposed long coexistence of *M. balearicus* and humans.

In the sight of the documentation presented it must be concluded that the alteration patterns described by Waldren (1982) and by Ramis & Bover (2001) observed in different *M. balearicus* bones (and an ancient form of the species, *M.* cf. *batei*) are unmistakeably the consequence of osteophagic conduct of the species itself, natural behaviour which has nothing to do with the domestication of the species by the first colonisers of the island, and it must be definitely excluded that there may be proof of the domestication of *M. balearicus* by humans.

Fig. 11. View of Saleta gallery of Cova Genovesa. This small hall is near 50 cm tall. In the deep side of the hall an important number of *M. balearicus* bones can be observed. Photo courtesy of F. Gràcia.

Fig. 11. *Vista de la Saleta de la cova Genovesa. L'alçada d'aquesta sala és d'uns 50 cm. Al fons s'observa un nombre important de restes de* M. balearicus. *Foto cortesia de F. Gràcia.*

Fig. 12. Individual of feral goat (*Capra hircus*) from Serra de Tramuntana (Mallorca) chewing a jaw of its own species. In this zone of Mallorca the osteophagic behaviour of this species has been widely recorded. Photo courtesy of Josep Solivelles.

Fig. 12. *Exemplar de cabra orada* (Capra hircus) *de la serra de Tramuntana (Mallorca) rosegant una mandíbula de la seva espècie. A aquesta zona de Mallorca s'ha pogut constatar la conducta osteofàgica d'aquesta espècie. Foto cortesia de Josep Solivelles.*

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09

THE OLFACTORY ABILITY OF *MYOTRAGUS BALEARICUS*: PRELIMINARY NOTES

Pere Bover & Ferran Tolosa

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Resum

Als mamífers insulars fòssils s'ha observat una reducció relativa de la mida del cervell. *Myotragus balearicus*, el bòvid nan de les Balears, no va ser una excepció, i la petita mida del cervell podria haver afectat a la capacitat d'algun dels seus sentits. Aquest és el cas de la capacitat olfactòria. S'han estudiat les làmines criboses de diferents espècies de bòvids i d'altres grups taxonòmics. La làmina cribosa és un envà prim i petit que està travessat pels nervis que connecten l'epiteli olfactori (a la cavitat nasal) i el bulb olfactori del cervell. Cada una de les ramificacions del nervi que travessen aquest envà produeixen un orifici en ell, de forma que les espècies amb una gran capacitat olfactiva tenen una làmina cribosa altament perforada (e.g., *Canis familiaris*), mentre que les espècies amb una capacitat olfactiva relativament minvada tenen un nombre d'orificis reduït (e.g., *Phoca vitulina*).

Si se compara la làmina cribosa de *Myotragus balearicus* amb la d'altres bòvids actuals, es pot observar que la densitat d'orificis és considerablement menor que el de les altres espècies de bòvids estudiades. Per tant, es pot inferir que l'espècie tenia una pèrdua de capacitat olfactiva. El nombre i densitat d'orificis de la làmina cribosa de *Myotragus* és inclús menor que el de les espècies amb cervells petits (com *Madoqua kirkii*). Aquesta característica podria estar relacionada amb la manca de depredadors terrestres a les illes on va viure aquest animal (absència de carnívors). A les illes Gimnèsies no era necessària una gran capacitat olfactiva per a detectar un atac per part de depredadors, i l'orientació frontalitzada de les òrbites oculars de *Myotragus* ha estat també relacionada a aquesta manca de depredadors. No s'ha trobat cap efecte de la inclinació de la làmina cribosa sobre la capacitat olfactòria. Aquesta capacitat olfactòria minvada derivada de l'estudi de la làmina cribosa s'adiu amb la mida reduïda dels bulbs olfactoris en els motlles endocranials estudiats.

Només a *Ovibos moschatus* el nombre d'orificis de la làmina cribosa és semblant al registrat a *Myotragus*. Aquest fet podria estar relacionat amb el comportament defensiu peculiar d'aquesta espècie davant d'atacs de depredadors. Quan un grup es atacat per un depredador (bàsicament llops), se situen tots junts, en forma de cercle o semicercle, amb les cries a l'interior. Per tant, per a aquesta espècie, sembla ser més important un comportament defensiu que no un comportament de fugida.

Paraules clau: *Myotragus balearicus*, capacitat olfactiva, organs dels sentits, bòvids, Illes Gimnèsies.

Abstract

In insular fossil mammals a relative reduction of the brain size has been quoted. *Myotragus balearicus*, the dwarf fossil bovid from Balearic Islands, was not an exception, and the small size of its brain could affect the capacity of some of its senses. This is the case of the olfactory capacity. We studied the criba nasalis of different bovid species' and of other taxonomic groups. The criba nasalis is an small and thin septum crossed by the nerves that connect the olfactory epitelium (in the nasal cavity) and the olfactory bulb of the brain. Everyone of the nerves that cross the septum produces an orifice on it, so that the species with a great olfactory ability have a criba nasalis highly perforated (e.g., *Canis familiaris*), while in the species with a scarce olfactory ability the number of orifices is reduced (e.g., *Phoca vitulina*).

If we compare the criba nasalis of *Myotragus balearicus* and extant bovids we observe that the orifices density in the fossil species is considerably lesser than in the other studied bovids. A lost of olfactory ability can be consequently inferred. The number and density of orifices in the criba nasalis of *Myotragus* is even smaller than in some small-brained species (as *Madoqua kirkii*). This feature could be related to the terrestrial predator free environment where this animal lived (carnivores absence). In Gymnesic Islands there was not necessary a good olfactory ability to detect predators before they attacked, and the frontal orientation of the eye sockets in *Myotragus* has been also related to this lack of predators. We have not found any effect of the inclination of the criba nasalis on the olfactory ability. The small olfactory ability derived from the study of the criba nasalis is consistent with the small-sized olfactory bulbs in the studied brain casts.

Only in *Ovibos moschatus* the number of orifices in the criba nasalis is close to that recorded in *Myotragus*. This could be related to the peculiar defensive behaviour of this species against predators. When a herd is approached by a putative predator (mainly wolves), they bunch together, in the form of a circle or semicircle with the calves inside. Then, for this species is seems more important the defensive behaviour than the escape.

Key words: *Myotragus balearicus*, olfactory ability, sense organs, bovids, Gymnesic Islands.

INTRODUCTION

Evolution in isolated conditions entailed a series of extraordinary morphological changes in fossil vertebrate species (e.g., Caloi *et al.*, 1988; Caloi & Palombo, 1990; Alcover *et al.*, 1999; Alcover, 2004). Among these morphological changes we find those affecting the nervous system. Evidently, in fossils, as a general rule, there are no conserved remains of the soft structures of the nervous system, however, the prints and foramina left by the brain and nerves in the bones can be evaluated. There are many scientific works which study the brain of fossil species by the elaboration of endocranial moulds with different techniques (e.g., Holloway, 1978). Apart from the studies on endocranial volume, which is so important in the evolution of primates, and more specifically in Hominids (e.g., Holloway, 1968; Tobias, 1975), there is a series of studies evaluating the circumvolutions of the skull caused by the shape of the brain (e.g., Dechaseaux, 1961; Accordi & Palombo, 1971).

In insular fossil mammals a relative reduction in brain size has been detected (e.g., Fleagle, 1988 in *Oreopithecus*; Quintana, 2002, in the giant leporid of Menorca). *Myotragus balearicus*, the Balearic fossil dwarf bovid, is no exception (Köhler & Moyà-Solà, 2004). In *M. balearicus* the ocular orbits are relatively frontalised, making stereoscopic vision possible (Alcover *et al.*, 1981). The frontalisation of the ocular orbits observed for the genus *Myotragus* has been associated with the lack of terrestrial predators in the islands where it lived, making lateral orbits unnecessary (as can be seen in present day bovid species). Furthermore, it has been recently observed that the size of the ocular orbits is relatively small in *M. balearicus* (Köhler & Moyà-Solà, 2004).

The reduction in brain size could have affected the capacity of some of its senses. In this work we evaluate the olfactory capacity. The relationship between the olfactory bulb of the brain and the olfactory capacity has been known for a long time (see review of current literature on the subject made by Xu *et al.*, 2000).

To such an effect, we have studied the lamina cribrosa (or cribriform plate) of *M. balearicus* and have compared it with the different species of bovids and other taxonomic groups. The lamina cribrosa is a small, thin plate located in the ethmoid bone in the skull (see Fig. 1), separating the cranial cavity from the nasal cavity. This plate is divided (seen from the inside of the skull) into two surfaces by the *crista galli*. This plate is perforated by ramifications of the olfactory nerve which connect the olfactory epithelium (in the nasal cavity) to the olfactory bulb of the brain (located in the front part of the neurocranium). Each of the nervous ramifications which perforate the plate do so through a foramen. Embryologically, the ossification of this area is posterior to the innervation, therefore, these nervous ramifications are the ones that are already present in the foetus (Tolosa, 1980), without there being any posterior variations due to environmental motives. It seems that species with a great olfactory capacity have a highly perforated lamina cribrosa (e.g., *Canis familiaris*), whereas in species with a lesser olfactory capacity, the number of perforations is reduced (e.g., *Phoca vitulina*). What is more, in species with a highly developed olfactory capacity (such as *Canis*), the position of the lamina cribrosa is oblique with respect to the saggital plane, a fact which leads to increasing its surface, thus allowing the passage of a larger number of nervous ramifications, whereas in *Phoca*, the shape of the lamina cribrosa is practically perpendicular to the saggital plane of the skull.

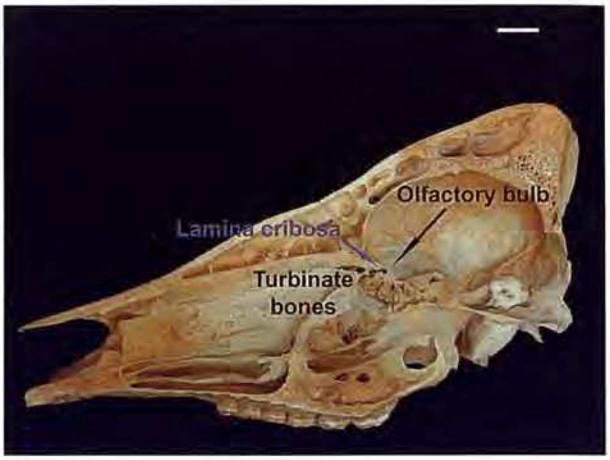

Fig. 1. *Tayassu pecari* skull (NMNH 269185) in which the anatomical position of lamina cribrosa is showed. This lamina is an small septum that separates olfactory bulb and the olfactory epithelium located in the nasal cavity. Scale bar. 2 cm.

Fig. 1. Crani de Tayassu pecari *(NMNH 269185) on s'ha situat anatòmicament la posició de la làmina cribosa. Aquesta làmina és un envà prim que separa el bulb olfactori de l'epiteli olfactori situat a la cavitat nasal. Escala, 2 cm.*

MATERIALS AND METHODS

The materials from present day species used in this study are deposited in the vertebrate collection of the Mammal Division of the National Museum of Natural History-Smithsonian Institution in Washington, D.C. (USA), acronym (NMNH). In this collection there is an important quantity of skulls from different species, in which the top of the neurocranium has been removed, leaving the area of the lamina cribrosa clearly visible. This fact has been taken advantage of to take the photographs and measurements used in this study. Table 1 gives a relation of the materials from the living species studied. So as to compare the lamina cribrosa of the different species, we selected, out of the ones in which it was possible to directly observe this part of the inside of the skull, (1) those bearing some sort of relation to *Myotragus* (*Oreamnos, Ovibos, Nemorhaedus, Ovis*, Lalueza *et al.*, 2000, 2002), (2) those of a similar size (*Madoqua*), (3) those which, due to their large size, did not depend strictly on their sense of smell as an anti-predatory strategy (*Syncerus, Taurotragus*) and (4) the supposed extreme cases (according to the development of the olfactory capacity) of lamina cribrosa morphology (*Canis, Phoca, Monachus*).

From the collection of vertebrates MNIB (Museu de la Naturalesa de les Illes Balears, Palma de Mallorca) we studied the skull of a sheep (*Ovis aries*, MNIB 85104) and a dog (*Canis familiaris*, MNIB 85103) in which a transversal cut was made just behind the ocular orbits in order to be able to observe the lamina cribrosa. Furthermore, a skull of *Ovis aries* (MNIB 85107) and one of *Canis familiaris* (MNIB 85106) were cut in a horizontal section so as to observe the position of the lamina cribrosa in dorsal view.

SPECIES	COL	NUM
ARTIODACTYLA		
Cephalophus leucocephalus	NMNH	220389
Hemitragus jemlahicus	NMNH	49884
Litocranius walleri	NMNH	164034
Madoqua kirkii	NMNH	396306
Madoqua kirkii	NMNH	538106
Nemorhaedus goral	NMNH	259411
Neotragus pygmaeus	NMNH	467679
Neotragus pygmaeus	NMNH	467686
Oreamnos americanus	NMNH	218758
Oreamnos americanus	NMNH	218789
Oreamnos americanus	NMNH	201003
Oreamnos americanus	NMNH	201002
Oreamnos americanus	NMNH	287532
Oreamnos americanus	NMNH	287553
Oreamnos americanus	NMNH	287552
Ovibos moschatus	NMNH	6251
Ovibos moschatus	NMNH	120921
Ovis aries	MNIB	85104
Ovis aries	MNIB	85107
Ovis canadensis	NMNH	3668
Ovis canadensis	NMNH	244189
Ovis canadensis	NMNH	218006
Saiga tatarica	NMNH	336265
Syncerus caffer	NMNH	220129
Taurotragus oryx	NMNH	199548
Tayassu pecari	NMNH	269185
Tayassu tajacu	NMNH	499758
CARNIVORA		
Canis familiaris	MNIB	85103
Canis familiaris	MNIB	85106
Canis familiaris	NMNH	20851
Monachus tropicalis	NMNH	100357
Phoca vitulina	NMNH	504110
Phoca vitulina	NMNH	550060
MARSUPIALIA		
Vombatus ursinus	NMNH	19566

Table 1. List of extant species in which lamina cribrosa has been studied.

Taula 1. Llistat d'espècies actuals a les que s'ha estudiat la làmina cribosa.

As regards the materials of *M. balearicus* studied, 4 skulls were used in which the lamina cribrosa was visible (MNIB 5222, 85108 and 85109 and an unnumbered example from Cova des Moro), and observations were carried out using laparoscopic techniques (with a rigid Storz optic of Ø 4 mm) in three others (MNIB 5213, 48139 and 51345). Only in two cases, MNIB 5222 and 85109, was an incision with a small saw made so as to observe the area under study. The quantity of skulls and skull fragments of *M. balearicus* deposited in the MNIB collection is important, but for different reasons it was not possible to study all of them: the most common motive being the fragmentation of the lamina cribrosa due to the fact that it is such a thin, delicate lamina. One of the other habitual motives is the fact that the plate is covered by a layer of concretioned sediment, and could be destroyed by an attempt at cleaning (both via mechanical and chemical means). In some cases the concrecions are placed in such a way that they obstruct the foramina in the lamina cribrosa, a fact which makes its evaluation difficult. Neither was it possible to study the lamina cribrosa of the oldest species of the *Myotragus* genus. As well as the scarcity of skulls, the few that there are, are either so fragmented, or are surrounded by an extraordinarily hard matrix, which makes it very difficult to clean them.

An attempt was made to correlate the measurements of the lamina cribrosa and the skulls of the different species studied. The *M. balearicus* skulls used to study the lamina cribrosa are incomplete and it was not possible to measure condylobasal length in any of them. Therefore, in the case of *M. balearicus* only the parameters related to the nasal area and the lamina cribrosa can be assessed. The measurements carried out are the following (Fig. 2):

AmCR: Width of the Lamina Cribrosa. Maximum width measured in the area of union between the olfactory bulb and the rest of the brain. It is measured from the *crista galli* to the side of the concavity of the olfactory bulb.

- AlCR: Height of the Lamina Cribrosa. Maximum height measured in the area of union between the olfactory bulb and the rest of the brain. It is measured from the ventral end to the dorsal end of the concavity of the olfactory bulb.
- CBL: Condylobasal Length. Length measured between the front of the premaxillary bones and the caudal part of the occipital condyles (Von Den Driesch, 1976).
- AmN: Nasal Width. Width of the maxillary bones measured at the height of the base of the first upper premolar present (P^2 in present day bovids and P^3 in *M. ba-learicus*).
- Angle of the Lamina Cribrosa: angle made by the side of the *crista galli* with the roof of the palate, in lateral view.

The total measurement of the lamina cribrosa is complicated to carry out without destroying the skulls studied. In fact, the AmCR and AlCR measurements were carried out in the area of union between the olfactory bulb of the brain and the rest of the brain hence it is an indirect measurement of the transversal size of the olfactory bulb.

The angle of the lamina cribrosa was calculated in the skulls which were sectioned in such a way that it was possible to stick a small rod on the *crista galli* and another on the palate. After taking digital photos in the lateral view, the angle between the two sticks was calculated using the Photoshop 6.0 programme. The length measurements were carried out with a Kern callibre (precision, 0.02 mm).

The task of measuring the number of foramina perforating the lamina cribrosa, or calculating the surface they occupy with respect to the total surface of the lamina cribrosa has, so far, turned out to be very complicated, without it being possible to establish methodology which can give us very precise results. The main complication of measuring the number of foramina, is that each foramen which can be seen with the naked eye in the first layer of the plate is subdivided into others (a variable number) as we look on the inside using a stereomicroscope. This fact, together with the irregular surface of the plate also complicates very much the measurement of the surface occupied by these foramina. Hence, in this work we make only an anatomical description of the plate, trying to give an accurate illustration of the features observed, but without presenting the measurements pertaining to the foramina observed. The differences between species are clear enough to be defined using categories based on the number and distribution of the perforations in the lamina cribrosa by direct visual estimation. The quantification of these features will have to be made after finding an adequate method to carry out the measurements so as not to introduce significant errors.

RESULTS

The region of the lamina cribrosa shows different distributions of foramina for the passage of the ramifications of the olfactory nerve. Using a sheep's skull (*Ovis aries*, MNIB 85104, Fig. 3) as a model to describe this distribution in bovids, it can be observed, in caudal view (see Fig. 3), that the lamina cribrosa is made up of two highly perforated regions, separated, as mentioned above, by quite a highly developed saggital crest, the *crista galli* (in *Canis familiaris* this crest is a very thin, very slightly developed lamina). These two perforated areas are slightly concave in the bovids studied. In each of these areas a row of parallel perforations can be found, just by the *crista galli*. These perforations are the largest ones observed in the lamina cribrosa. On the lateral side of this row a more or less oval region can be found with a low number of perforations with a very small diameter. In the rest of the lamina cribrosa a multitude of uniformly distributed perforations with varying diameters can be seen, although at the lower margin, upper margin and in the centre of the lamina cribrosa small accumulations of perforations with a wider diameter can be observed (similar to the row of perforations by the *crista galli*). The lamina cribrosa has a perpendicular saggital orientation if the skull is observed in dorsal view (Fig 5).

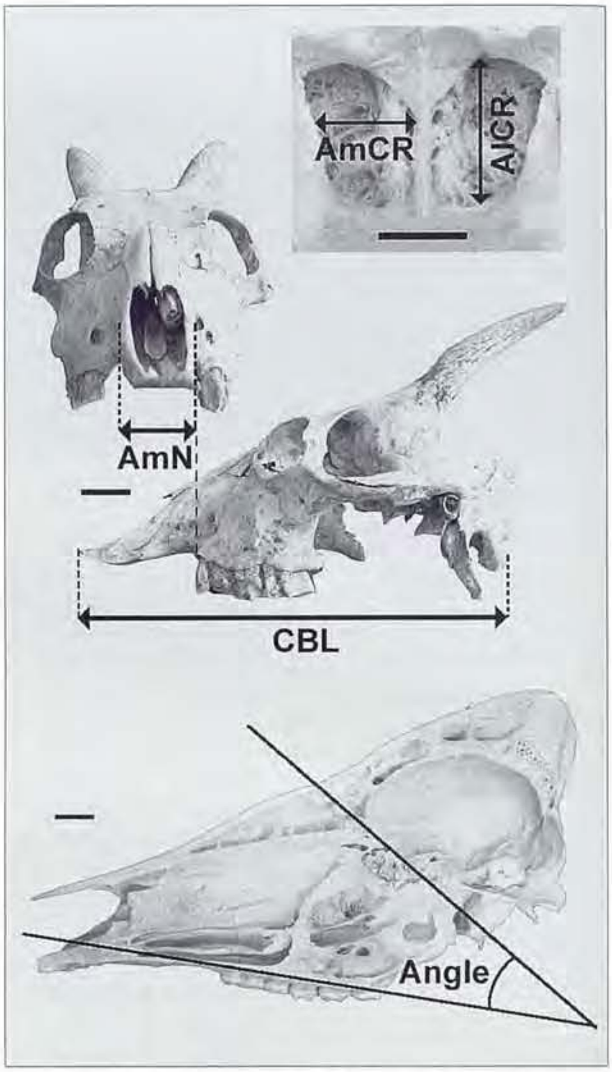

Fig. 2. Measurements made on nasal region. AlCR: Lamina cribrosa Height; AmCR: Lamina cribrosa Breadth (measurements shown on an *Oreamnos americanus* skull, NMNH 201002). AmN: Nasal Breadth; CBL: Condilobasal Length (measurements shown on a *M. balearicus* skull (sn, Cova des Tancats). Angle: Angle of Lamina cribrosa (measurement shown on a *Tayassu pecari* skull, NMNH 269185). Scale bar, 2 cm.

Fig. 2. *Mesures realitzades a la regió nasal. AlCR: Alçada de la Làmina Cribosa; AmCR: Amplada de la Làmina Cribosa (mesures il·lustrades sobre un crani d'*Oreamnos americanus*, NMNH 201002). AmN: Amplada Nasal; CBL: Longitud Còndilo-Basal (mesures il·lustrades sobre un crani de* M. balearicus *(sn, Cova des Tancats). Angle: Angle de la Làmina Cribosa (mesures il·lustrades sobre un crani de* Tayassu pecari, *NMNH 269185). Escala, 2 cm.*

To serve as an example of the lamina cribrosa of a species with a high olfactory capacity, we used *Canis familiaris* (MNIB 85103, Fig. 4). The lamina cribrosa, if a horizontal cut is made in the skull in dorsal view, is "V"-shaped, with the vertex facing towards the area of the nasal cavity (Fig. 5). In this vertex we find a very thin *crista galli*, flanked by a row of large perforations (as happens in the bovids). The slightly perforated area is not as centrally placed as in the bovids, but is found in the upper margin of each perforated area. The rest of the lamina cribrosa is very highly perforated (more than in *Ovis*). The perforations are of a large diameter, in general, but without reaching the dimension of the perforations of the rows adjacent to the *crista galli*.

Among the species in which the olfactory capacity does not seem to be as important (if compared, for instance, with the fissipedes) it is worth noting the pinnipeds in which the sense of smell seems to be related to short-distance recognition between mothers and young and to territorial behaviour and reproduction (Ryg *et al.*, 1992; Insley *et al.*, 2003), and not to the search for food or to anti-predatory conduct. As an example of a species with a reduced olfactory capacity, we used *Phoca vitulina* (NMNH 504110, Fig. 6). The lamina cribrosa of *Phoca* is very flat and practically perpendicular to the saggital plane of the skull, in dorsal view. The number of perforations is extraordinarily low. Just as happens in the other groups, the lamina cribrosa is separated by a *crista galli*, which in this case is very highly developed. There are no rows of foramina adjacent to the crest, rather only one single elongated foramen can be seen (at times reduced in size) on each side, parallel to the *crista galli*. Along the peripheral line of the lamina cribrosa different groups comprising a small number of foramina can be found, surrounding areas without perforations.

If the lamina cribrosa of *M. balearicus* and present day bovids are compared it can be seen that the density of foramina in this fossil species is considerably lower than in the other bovids studied. In *M. balearicus*, the number of perforations parallel to the *crista galli* seems to be lower in all the cases studied (Fig. 7). The central part of each lobule of the plate either has no perforations or, if it has, they are very few and very small. This central part, in some of the skulls, is made up of a protuberance (e.g., MNIB 5213, Fig. 7.A), however, in other cases this surface is more or less flat (e.g., MNIB 5222, Fig. 7.C). In the peripheral area on each side of the plate there is an abundant number of perforations which are distributed more or less uniformly (Fig. 7). Another of the relevant characteristics with respect to the other bovids studied is that in *Myotragus* there are no perforations in the lateral peripheral walls of the concavity where the olfactory bulb is situated, so this part of the brain can only have received nervous endings from the frontal part of the plate (see Fig. 7).

Apart from studying the morphology of this area in the bovids related to *Myotragus*, so as to evaluate the possible effect of size on this region, we observed the lamina cribrosa from two small-sized bovids, *Madoqua kirkii* and *Neotragus pygmaeus*. In these two species we can see a similar pattern of foramina, broadly speaking, to that described for *Ovis*. As a result, the number and density of foramina in the lamina cribrosa of *Myotragus* is also lower than in species with a small brain (such as *Madoqua kirkii*).

Regarding the nearest relatives of *Myotragus* (*Oreamnos, Capricornis, Nemorhaedus, Budorcas, Ovibos*), it is worth pointing out that the morphology of the lamina cribrosa follows the pattern observed in *Ovis*, with only one exception. In *Ovibos moschatus* the pattern of the number of foramina in the lamina cribrosa is comparable to that documented in *Myotragus*. Just as happens in the fossil bovid species, the two *Ovibos moschatus* skulls studied (NMNH 6251 and 120921) have a central area in each part of the lamina cribrosa which is only very slightly perforated. They have a row parallel to the *crista galli*, whereas the rest of the perforations are situated in the peripheral areas of the plate.

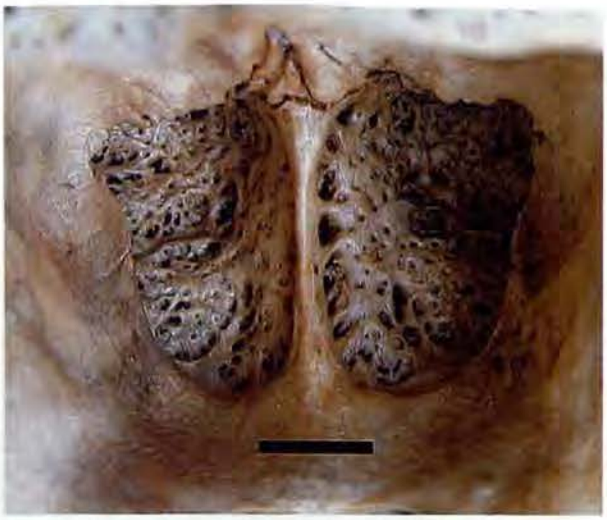

Fig. 3. Detail of the lamina cribrosa of *Ovis aries* MNIB 85104. The median ridge that divides the lamina cribrosa is the *crista galli*. Scale bar, 1 cm.

Fig. 3. *Detall de la làmina cribosa d'*Ovis aries *MNIB 85104. La cresta sagital que separa les dues làmines perforades és la* crista galli. *Escala, 1 cm.*

Fig. 4. Detail of the lamina cribrosa of *Canis familiaris* MNIB 85103. The *crista galli* is not much developed in this species. Scale bar, 1 cm.

Fig. 4. *Detall de la làmina cribosa de* Canis familiaris *MNIB 85103. La* crista galli *està molt poc desenvolupada en aquesta espècie. Escala, 1 cm.*

In order to classify the different morphologies of the perforations in the lamina cribrosa observed we defined four categories based on the analysis of the number and distribution of the perforations produced by the passage of the nerves. These are:

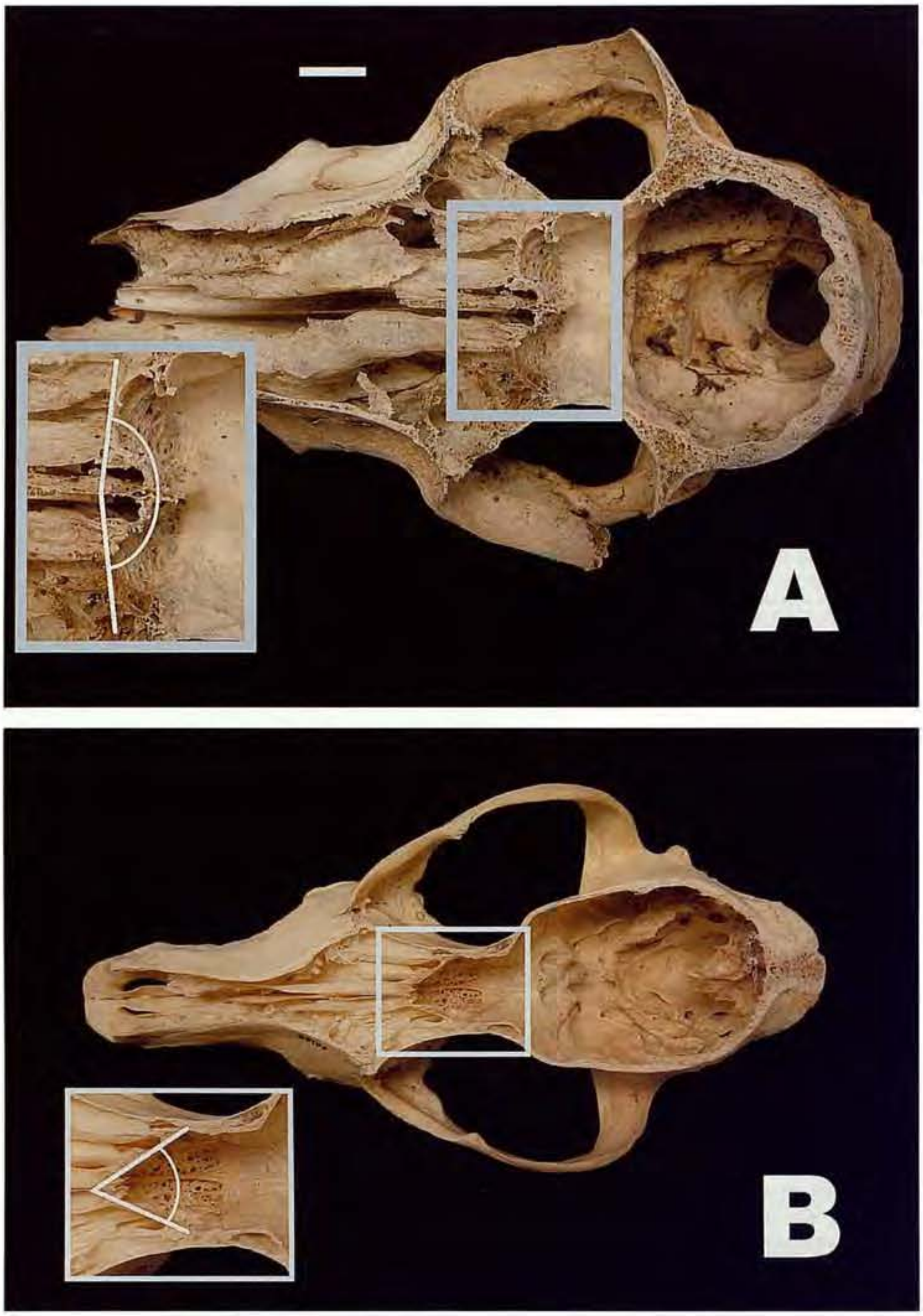

Fig. 5. Skulls wih removed dorsal region of neurocranium. A: *Ovis aries* MNIB 85107. B: *Canis familiaris* MNIB 85106. Detail, lower left part of each skull, position of lamina cribrosa in each species. While in *Canis* the position of the lamina is oblique in relation to sagittal plane, in *Ovis*, the lamina is positioned in a transverse plane. Scale bar, 2 cm.

***Fig. 5.** Cranis amb la regió dorsal del neurocrani seccionada. A:* Ovis aries *MNIB 85107. B:* Canis familiaris *MNIB 85106. En detall, a la part inferior esquerra de cada crani, l'orientació de la làmina cribosa a cada espècie. Mentre que a* Canis *la posició de la làmina és obliqua respecte al pla sagital, a* Ovis, *la làmina està situada en un pla transversal. Escala, 2 cm.*

- Category 1: numerous perforations distributed uniformly on the whole surface of the lamina cribrosa (except for the row of larger foramina on each side of the *crista galli*, see above). This is the case of *Nemorhaedus goral* (see Fig. 8).
- Category 2: numerous perforations distributed nearly uniformly on the whole surface of the lamina cribrosa (except for the row of larger foramina on each side of the *crista galli*), with a small region which is very slightly or not at all perforated in the central area of each side of the plate. For instance *Ovis aries* (see Fig. 3).
- Category 3: reduced number of perforations, distributed in peripheral areas of the lamina cribrosa (except for the row of larger holes on each side of the *crista galli*). The non-perforated central area occupies an important surface area on each side of the plate. By way of example, *Ovibos moschatus* (see Fig. 9).
- Category 4: extraordinarily reduced number of perforations distributed in the peripheral area of the lamina cribrosa. The most representative case studied is that of the pinnipeds, for instance *Phoca vitulina* (see Fig. 6).

Table 2 relates the species of present day mammals studied according to their morphology and distribution of the perforations in the lamina cribrosa.

The measurements carried out in bovids are presented in Table 3. Only in the case of the AmCR/AlCR index (lamina cribrosa width/lamina cribrosa height) does there seem to be any differences in *M. balearicus*, which basically respond to the more rounded morphology of the area of the olfactory bulb, like in *Nemorhaedus goral*, *Syncerus caffer*, *Taurotragus oryx* and *Ovis aries*. The greatest values of the AmCR/AmN index (lamina cribrosa height/nasal width) are produced in *M. balearicus*, basically due to the reduced nasal width in this species. Moreover, we observe considerable variability in practically all the indexes calculated in which there are more than one individual per species.

The angles calculated for the different species studied do not indicate any type of outstanding anatomical particularity. In fact, the angle formed by the lamina cribrosa seems to be more related to the anatomical posture of the animal, always so as to make the plate perpendicular to the nasal cavity. In humans for instance, with a bipedal posture, the lamina cribrosa is situated horizontally (Tolosa, 1980).

Morphologically the lamina cribrosa of *M. balearicus* is included in category 3, in agreement with the morphology and distribution of the foramina in the lamina cribrosa.

DISCUSSION

The morphology of the lamina cribrosa of *M. balearicus* clearly indicates a reduction in the olfactory capacity of the species in relation to other caprines or other similar-sized bovids. The only species of artiodactyl studied which has a similar morphology is *Ovibos moschatus*. This reduction in the olfactive capacity could be related to the terrestrial predator free environment where *Myotragus* lived (absence of carnivorous mammals). In the Gymnesics Islands a great olfactory capacity was not necessary in order to detect terrestrial predators. The reduced olfactory capacity of the species inferred by our study is in agreement with the small size of the olfactory bulb of the *Myotragus* brain revealed by the study of many skulls (e.g., Dechaseaux, 1961).

Category	Species
1	***Madoqua kirkii, Nemorhaedus goral,*** *Canis familiaris*
2	***Hemitragus jemlahicus, Litocranius walleri, Neotragus pygmaeus, Oreamnos americanus, Ovis aries, Ovis canadensis, Syncerus caffer, Taurotragus oryx***
3	***Ovibos moschatus,*** *Vombatus ursinus*
4	*Monachus tropicalis, Phoca vitulina*

Table 2. List of mammal species studied, ordered by category of morphology and distribution of lamina cribrosa foramina. Bold, Bovidae species.

Taula 2. Relació de les espècies de mamífers estudiats segons la seva categoria de la morfologia i distribució de les perforacions de la làmina cribosa. En negreta es posen les espècies pertanyents a la família Bovidae.

Fig. 6. Detail of the lamina cribrosa of *Phoca vitulina* NMNH 504110. Number of foramina is reduced. Scale bar, 1 cm.

Fig. 6. *Detall de la làmina cribosa de* Phoca vitulina *NMNH 504110. El nombre de perforacions està molt reduït. Escala, 1 cm.*

It would seem logical to believe that the absence of predators living in the Balearic Islands could be related to the supposed reduction in the olfactory capacity of *M. balearicus*. Among the species of living bovids, the antipredatory strategy before attack is basically guided by the location of possible predators by sight and hearing, above all in species in open habitats and savannahs (Carl & Robbins, 1988). Small species of bovids living in closed habitats of dense woods use their sense of smell in an important way to locate predators (Macho & Williamson, 2002).

As far as the sense of smell is concerned as a response to food stimuli, it must be said that it has not yet been studied as regards skull morphology and even less regarding the lamina cribrosa in bovids. What is known is the importance of the use of smell for reproductive times and to follow the herd (Nowak & Paradiso, 1984).

What is more, it is worth bearing in mind how the relative reduction of brain size observed in *M. balearicus* (Köhler & Moyà-Solà, 2004) could have affected the morphology observed for the lamina cribrosa. Kaas (2000) states that an evolutionary increase in brain size produces both an increase in the number of neurons and in their size (which is reflected in a change in nerve size). The same author states that a reduction in the number of neurons due to a reduction in brain size could, basically, produce an important problem. A certain number of neurons is necessary so that a function can be executed correctly. A loss in neurons could cause certain circuits not to be func-

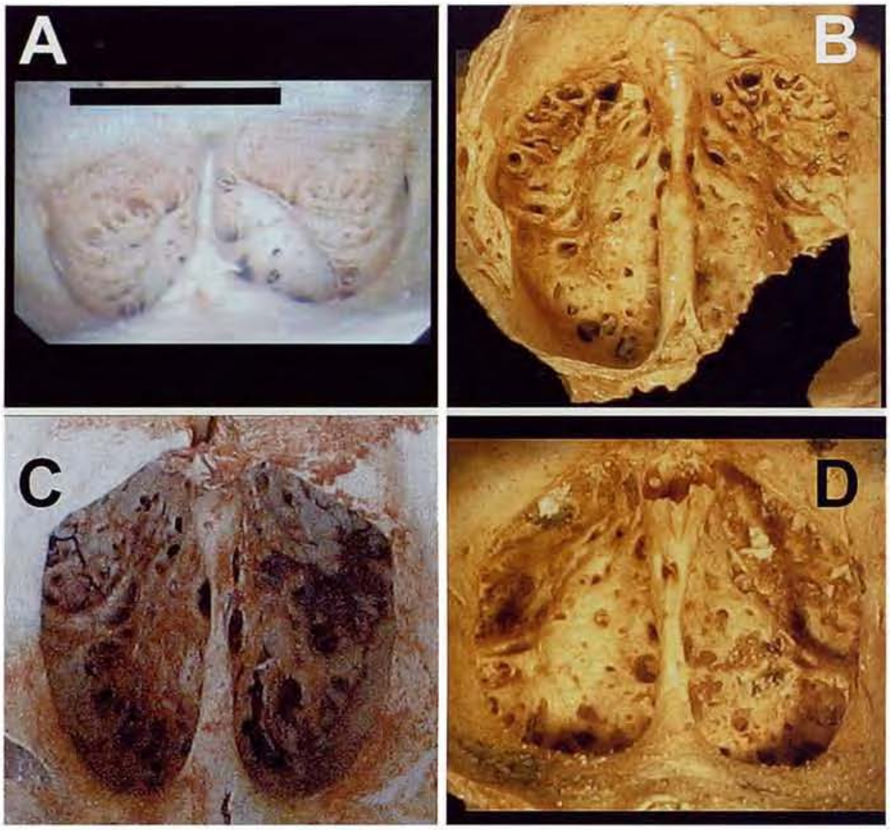

Fig. 7. Detail of the lamina cribrosa of some *M. balearicus* skulls. A: MNIB 5213; B: without number; C: MNIB 5222; D: MNIB 85109. On the MNIB 5213 skull (A) the bulk near *crista galli* can be seen. The lower number of foramina is also noted. Scale bar, 1 cm.

***Fig. 7.** Detall de la làmina cribosa de diversos cranis de* M. balearicus. *A: MNIB 5213; B: sense numerar; C: MNIB 5222; D: MNIB 85109. Al crani MNIB 5213 (A) es pot observar l'abultament que presenta devora la* crista galli. *També es poden apreciar el nombre reduït de perforacions. Escala, 1 cm.*

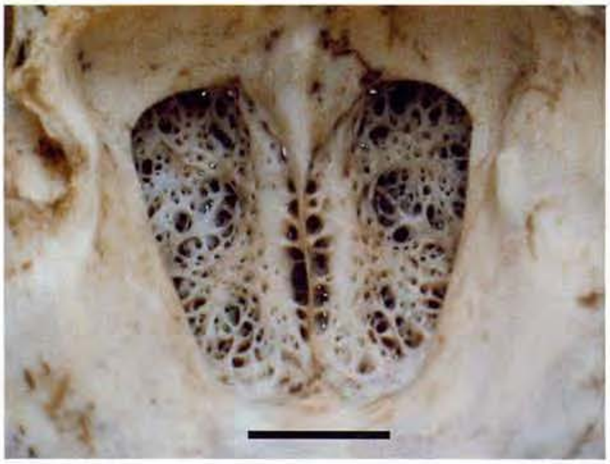

Fig. 8. Detail of the lamina cribrosa of *Nemorhaedus goral* NMNH 259411. Foramina are uniformely distributed in the lamina cribrosa. Scale bar, 1 cm.

***Fig. 8.** Detall de la làmina cribosa de* Nemorhaedus goral *NMNH 259411. Les perforacions estan repartides de forma uniforme per la làmina. Escala, 1 cm.*

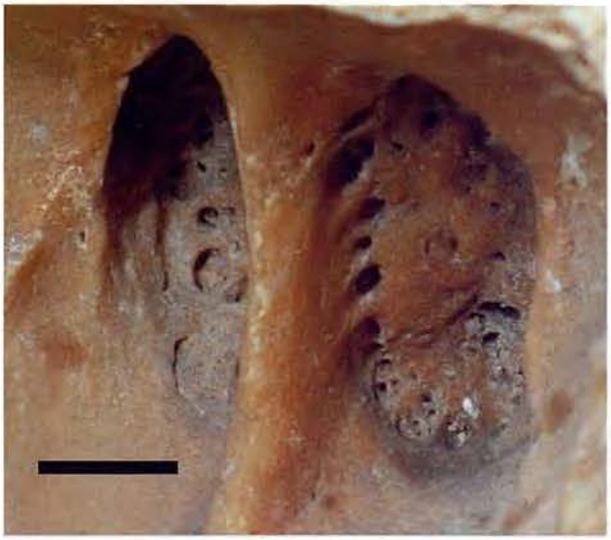

Fig. 9. Detail of the lamina cribrosa of *Ovibos moschatus* NMNH 6251. This species shows a similar morphology of lamina cribrosa than that of *M. balearicus*. Scale bar, 1 cm.

***Fig. 9.** Detall de la làmina cribosa d'*Ovibos moschatus *NMNH 6251. Aquesta espècie presenta una morfologia de la làmina similar a la de* M. balearicus. *Escala, 1 cm.*

tional, with all the negative consequences that this would produce. Once this point has been reached, one solution is to completely abandon some circuits in order to keep others functional (Kaas, 2000). The intrinsic effect of the reduction in brain size in *M. balearicus* does not seem to have been the main cause of the reduction in nervous connections with the olfactory epithelium. Other species, with proportionally larger brains than *M. balearicus*, such as pinnipeds and the bovid *Ovibos moschatus* have either a lower or similar number of ramifications of the olfactory nerves as the Balearic fossil caprine. On the other hand, small-brained species (*Madoqua kirkii, Neotragus pygmaeus*) have a very highly perforated lamina cribrosa (categories 1 and 2 respectively).

Seeing the information provided, it can be concluded that the olfactory capacity of *M. balearicus* was lessened, a fact which is quite possibly linked to the lack of predatory mammals in the Balearics. *Aquila chrysaetos* has been identified as a possible predator of *M. balearicus* young (Arnau *et al.*, 2000; Alcover *et al.*, 2004). The pressure of bird predation on a medium-sized mammal is not as hard as the pressure of predation from a mammal (e.g., Worthy & Holdaway, 2002). The detection of a flying predator is not made by smell, but rather by sight or by hearing.

M. balearicus was very possibly capable of eating any type of plant (Bover, 2004). As the current state of knowledge stands, the reduction in olfactory capacity cannot be related to feeding, even though it cannot be excluded that it may have had some sort of effect on the selection of the most nutritional parts of plants.

Ovibos moschatus also has a certain reduction in olfactory capacity. Interpreting this fact proves to be complicated. The fact that in *Ovibos moschatus* the number of foramina in the lamina cribrosa is similar to *M. balearicus* could be related to the peculiar defensive behaviour of the species in the presence of predators. When a group of *O. moschatus* is attacked by a predator (basically wolves), the individuals in the group have singular defensive behaviour: they all group together, forming a circle or semicircle with the young on the inside of the group (Nowak & Paradiso, 1984). In this species a collective defensive strategy seems to be more important than fleeing behaviour in the presence of terrestrial predators.

ACKNOWLEDGEMENTS

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SPECIES	COL	NUM	AmCR	AlCR	CBL	AmN	AmN/CBL	AmCR/AlCR	AmCR/AmN	AlCR/AmN	ANGLE	CAT.
Oreamnos americanus	NMNH	218758	14,18	20,00	274,84	47,92	0,174	0,709	0,296	0,417	60,4	2
Oreamnos americanus	NMNH	218789	10,13	15,34	306,64	47,28	0,154	0,660	0,214	0,324	52,0	2
Oreamnos americanus	NMNH	201003	12,40	15,84	249,84	35,28	0,141	0,783	0,351	0,449	54,9	2
Oreamnos americanus	NMNH	201002	12,70	17,92	245,80	38,48	0,156	0,708	0,330	0,466	68,6	2
Oreamnos americanus	NMNH	287532	13,14	20,14	270,00	44,38	0,164	0,652	0,296	0,454	52,7	2
Oreamnos americanus	NMNH	287553	14,22	19,70	271,14	44,24	0,163	0,722	0,321	0,445	60,3	2
Oreamnos americanus	NMNH	287552	11,54	18,54	271,90	45,96	0,169	0,622	0,251	0,403	64,6	2
Nemorhaedus goral	NMNH	259411	11,90	21,68	192,92	32,12	0,166	0,549	0,370	0,675	80,3	1
Ovibos moschatus	NMNH	6251	14,02	21,94	457,70	86,04	0,188	0,639	0,163	0,255	63,0	3
Ovibos moschatus	NMNH	120921	17,02	26,56	469,12	98,34	0,209	0,941	0,173	0,270	43,8	3
Syncerus caffer	NMNH	220129	16,56	28,30	400,60	73,80	0,184	0,585	0,224	0,383	72,4	2
Taurotragus oryx	NMNH	199548	16,66	30,72	422,36	71,88	0,170	0,542	0,232	0,427	63,4	2
Madoqua kirkii	NMNH	396306	-	-	112,28	14,80	0,132	-	-	-	67,3	1
Madoqua kirkii	NMNH	538106	-	-	104,80	12,40	0,118	-	-	-	58,0	1
Saiga tatarica	NMNH	336265	14,68	19,16	210,30	28,66	0,136	0,766	0,512	0,669	76,7	2
Tayassu tajacu	NMNH	499758	10,82	16,66	195,90	35,88	0,183	0,649	0,302	0,464	38,0	2
Ovis aries	MNIB	85104	11,04	21,06		31,8	-	0,524	0,347	0,662	74,5	2
Ovis canadensis	NMNH	244189	13,90	19,54	257,96	44,94	0,174	0,711	0,309	0,435	70,1	2
Ovis canadensis	NMNH	218006	15,86	23,20	311,12	60,36	0,194	0,684	0,263	0,384	76,3	2
Myotragus balearicus	MNIB	5222	6,18	12	-	17,18	-	0,515	0,360	0,698	54,7	3
Myotragus balearicus	MNIB	SN	7,53	13,78	-	20,94	-	0,546	0,359	0,658	60,5	3
Myotragus balearicus	MNIB	SN	6,14	10,30	-	-	-	0.596	-	-	-	3

Table 3. Result of the masurements (in mm) proposed in this paper for the different species studied. AmCR: Lamina cribrosa Breadth, AlCR: Lamina cribrosa Height; CBL: Condilobasal Length; AmN: Nasal Breadth. In this table indexs and categories according to lamina cribrosa morphology (CAT) are also shown. NMNH: National Museum of Natural History (Washington, D.C.); MNIB: Museu de la Naturalesa de les Illes Balears (Palma).

Taula 3. *Valors obtinguts de les mesures (en mm) considerades per a les diferents espècies estudiades. AmCR: Amplada de la Làmina Cribosa, AlCR: Alçada de la Làmina Cribosa; CBL: Longitud Còndilo Basal; AmN: Amplada Nasal. Es presenten els valors del índexos estudiats, així com les categories que s'han establert en base a la morfologia de la làmina cribosa (CAT). NMNH: National Museum of Natural History (Washington, D.C.); MNIB: Museu de la Naturalesa de les Illes Balears (Palma).*

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10

REVISIÓN TAXONÓMICA DEL GÉNERO *NESOPHONTES* (INSECTIVORA: NESOPHONTIDAE) EN CUBA. ANÁLISIS DE LOS CARACTERES DIAGNÓSTICOS

Marjorie Mahe CONDIS FERNÁNDEZ, Osvaldo JIMÉNEZ VÁZQUEZ & Carlos ARREDONDO

CONDIS FERNÁNDEZ, M.M., JIMÉNEZ VÁZQUEZ, O. & ARREDONDO, C. 2005. Revisión taxonómica del género *Nesophontes* (Insectivora: Nesophontidae) en Cuba. Análisis de los caracteres diagnósticos. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 95-100.

Resum

S'han emprat 24 mesures i 27 caràcters morfològics de l'esquelet cranià registrats anteriorment a la bibliografia per a fer la revisió de les espècies cubanes del gènere *Nesophontes*. També foren emprats a anàlisis previs per determinar quins són els que caracteritzen millor les espècies estudiades i són més útils per diagnosticar-les. En base a l'anàlisi de la diagnosi d'aquestes espècies es proposa un canvi a la taxonomia del gènere, segons el qual el nombre d'espècies es redueix de cinc a dues: *Nesophontes micrus* Allen, 1917 i *Nesophontes major* Arredondo, 1970 es mantenen com a bones espècies, mentre que *Nesophontes longirostris* Anthony 1919, *Nesophontes submicrus* Arredondo 1970 i *Nesophontes superstes* Fischer 1977, es consideren sinònims de *N. micrus*.

Paraules clau: Musaranyes cubanes, sistemàtica, *Nesophontes*, crani, mandíbula.

Resumen

Para la revisión de las especies cubanas del género *Nesophontes* se utilizaron 24 mediciones y 27 caracteres morfológicos registrados con anterioridad en la literatura, de piezas del esqueleto craneal. Los mismos fueron utilizados en diferentes análisis estadísticos realizados en trabajos previos para determinar cuales caracterizan mejor las especies estudiadas y son por tanto más útiles para diagnosticarlas. En base al análisis de la diagnosis de estas especies se propone un arreglo en la taxonomía del género *Nesophontes*, en el que el número de especies se reduce de cinco a dos: *Nesophontes micrus* Allen, 1917 y *Nesophontes major* Arredondo, 1970 se mantienen como buenas especies; y *Nesophontes longirostris* Anthony 1919, *Nesophontes submicrus* Arredondo 1970 y *Nesophontes superstes* Fischer 1977, son consideradas sinónimos de *N. micrus*.

Palabras clave: Musarañas cubanas, sistemática, *Nesophontes*, cráneo, mandíbula.

Abstract

In this paper the study of Cuban species of genus *Nesophontes* is based upon 24 measurements and 27 morphological cranial characters taken from previous works. They were previously employed in different statistic analysis to determinate the most utile ones as species-level diagnostic traits. A new arrangement in Cuban *Nesophontes* taxonomy is proposed, where the number of species is reduced from five to two: *Nesophontes micrus* Allen, 1917 and *Nesophontes major* Arredondo, 1970, keep their status of recognised species; while N. *longirostris* Anthony 1919, *Nesophontes submicrus* Arredondo, 1970 y *Nesophontes superstes* Fischer 1977 are considered as synonyms of *N. micrus*.

Keywords: Cuban shrews, Systematics, *Nesophontes*. skull, jaw.

INTRODUCCIÓN

La paleofauna de mamíferos del Cuaternario descrita para el Archipiélago Cubano se caracteriza por su gran diversidad y alto índice de endemismo. Sin embargo, los conocimientos actuales sobre la biogeografía del arco de Las Antillas sugieren que esta abundancia de taxones endémicos pudiera no corresponder con la realidad ya que algunas de las especies conocidas tal vez no sean más que variaciones de otras (White y MacPhee, 2001).

Dentro de los mamíferos antillanos la familia Nesophontidae, endémica de Las Antillas fue descrita por Anthony 1916 para ubicar a su único género, *Nesophontes* que cuenta con 11 especies, de las cuales *Nesophontes edithae* Anthony 1916 es la especie tipo. La validez de esta familia ha sido discutida por autores que ubican al género en la familia Solenodontidae (Morgan, 1977; MacFadden, 1980). Las primeras especies descritas de Cuba fueron *Nesophontes micrus* Allen 1917 y *N. longirostris* Anthony 1919. Posteriormente se añadieron *Nesophontes major* Arredondo, 1970, *Nesophontes submicrus* Arredondo, 1970 y *Nesophontes superstes* Fischer 1977, todas del Pleistoceno. Esta última, es conocida hasta hoy solo por el holótipo, al igual que *N. longirostris*, que consiste en piezas mandibulares y craneales, respectivamente. Tampoco se conoce el cráneo de *N. submicrus*. En el resto de Las

Antillas la distribución es la siguiente: tres especies en La Española, una en Puerto Rico y se conoce la presencia del género en Islas Caimán, con dos formas, *Nesophontes* sp. 1 y *Nesophontes* sp 2 (Morgan, 1977).

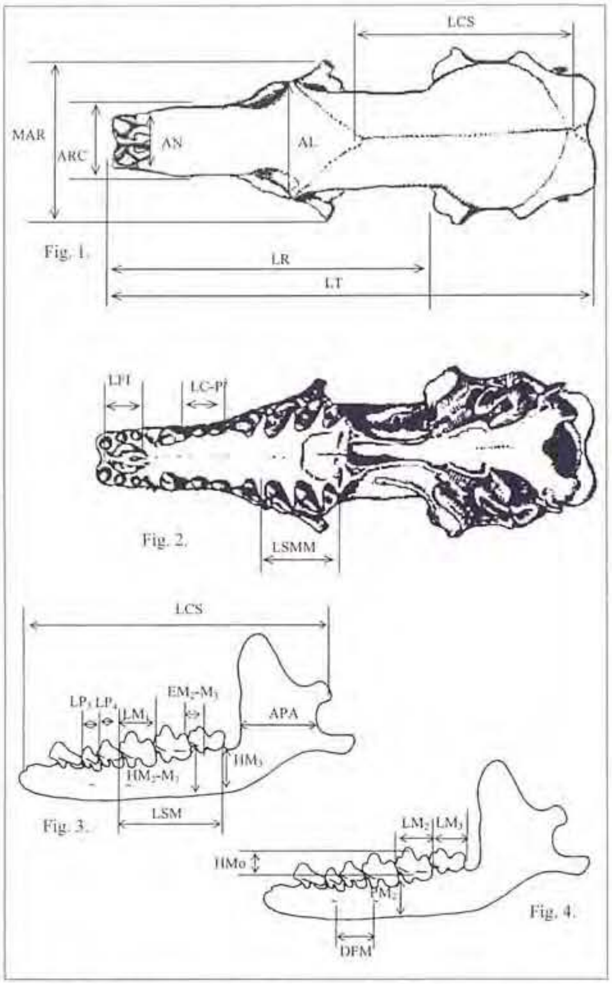
La mayoría de los autores, en base principalmente a análisis filogenéticos, consideran que el grupo pudo originarse en Norteamérica (McDowell, 1958; MacFadden, 1980; Whidden y Asher, 2001), aunque las evidencias geológicas pueden no sustentar esta idea (Iturralde-Vinent y MacPhee, 1999). Sin embargo, la descripción de un rinocerótido para finales del Eoceno Temprano o principios del Eoceno Medio de Jamaica, propone una nueva vía de acceso desde Norteamérica para estos dos grupos de mamíferos, como sugieren las relaciones obtenidas en los análisis filogéneticos (Portell *et al.*, 2001).

En el estudio de los insectívoros antillanos, el material usado en las descripciones de las especies corresponde a la mandíbula o al cráneo, utilizándose muchas veces un único ejemplar. Algunos autores han planteado la variabilidad de los caracteres diagnósticos en las especies cubanas del género (Morgan, 1977). Por esto, se hace necesaria una revisión más minuciosa de las especies cubanas y su comparación con el resto de las antillanas. El presente trabajo pretende discutir la validez sistemática de las especies cubanas del género *Nesophontes* a través del análisis de la variabilidad de los caracteres diagnósticos de las mismas, proponer nuevas diagnosis que posibiliten una mejor identificación de estas especies y aclarar el estatus taxonómico de algunas de ellas.

MATERIALES Y MÉTODOS

Se analizaron 84 restos óseos, pertenecientes a tres especies cubanas del género *Nesophontes*: *N. micrus* (29), *N. major* (48) y *N. submicrus* (7): 25 correspondientes a cráneos y 59 a mandíbulas. Las muestras proceden de la Colección Mastozoológica del Instituto de Ecología y Sistemática, Colección del Museo Nacional de Historia Natural, y de la Colección Personal de Carlos Arredondo. El material fue seleccionado acorde con su estado de conservación, de manera que fuera posible extraer la mayor cantidad de información. De *Nesophontes longirostris* y *N. superstes* sólo se conocen sus respectivos holótipos, cuya consulta no fue posible. Pío Domingo, localidad tipo de *N. superstes*, ha sido transformada y no se pudo colectar nuevamente material de la misma. La pieza craneal solo se conoce para *N. major*, *N. micrus* y *N. longirostris*.

Se utilizaron 24 medidas de piezas del esqueleto craneal registradas con anterioridad en la literatura (Allen, 1917, 1918; Anthony, 1916, 1919; Arredondo, 1970; Miller, 1929; Morgan, 1977; Fischer, 1977; Abreu, 1992; Condis *et al*, en prensa) (Figs. 1-4); así como 27 caracteres morfológicos empleados por otros autores (Allen, 1917, 1918; Anthony, 1919; Arredondo, 1970; Fischer, 1977; Condis *et al*, en prensa) (Figs. 5-22). Entre los caracteres analizados para el cráneo y la mandíbula están los considerados diagnósticos en la descripción de cada una de las especies cubanas del género, a fin de evaluar su consistencia. Tanto las medidas como los caracteres morfológicos que se discuten en este trabajo fueron utilizados previamente en diferentes análisis estadísticos que determinaron cuales caracterizan mejor las especies estudiadas y son por tanto más útiles para diagnosticarlas (Condis *et al.*, en prensa).



Figs. 1-4. Medidas tomadas en la muestra craneal y mandibular de *N. micrus* y *N. major*. (Dibujos de *N. edithae*, modificados de McDowell, 1958).

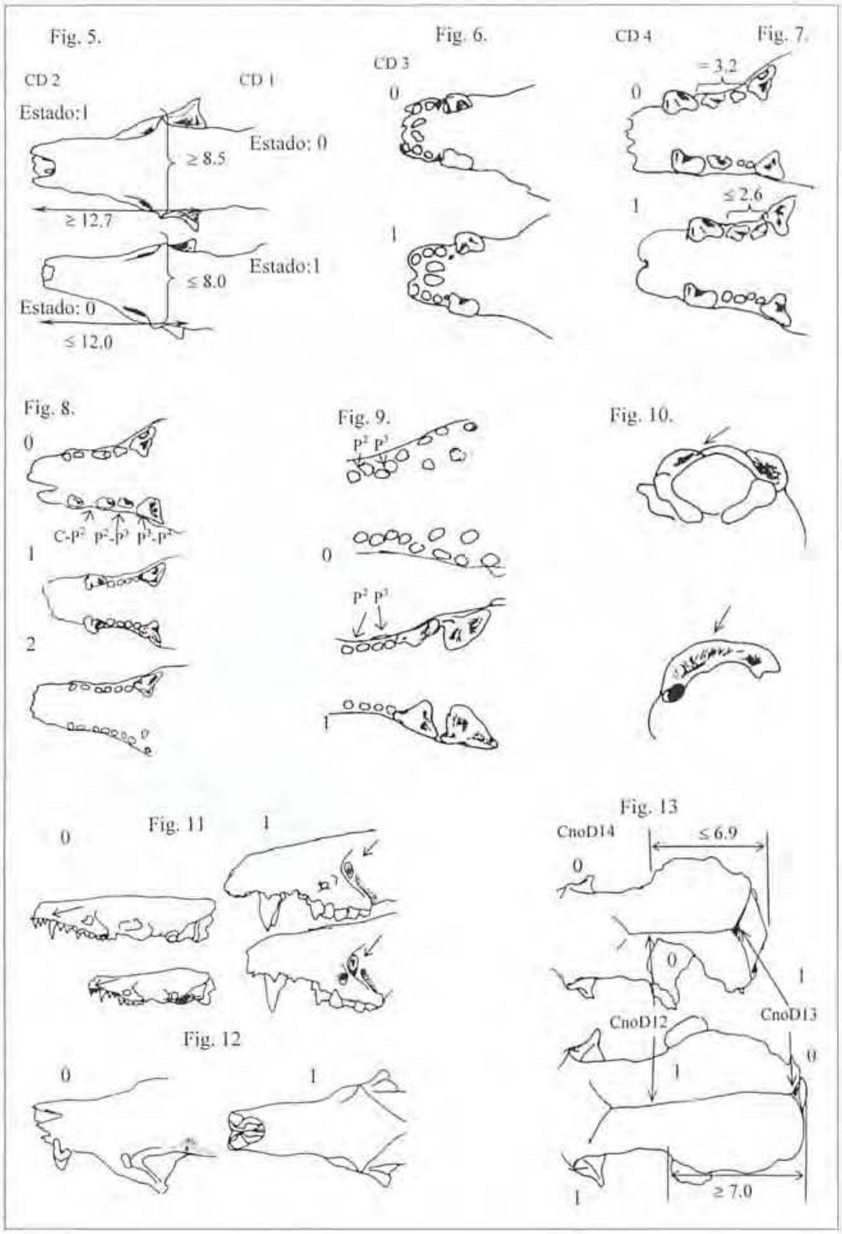
Figs. 1-4. Measurements analyzed in the cranial and mandibular sample of N. micrus *and* N. major. *(Dibujos de* N. edithae, *modificados de McDowell, 1958).*

En los caracteres morfológicos cualitativos las categorías fueron asignadas según el siguiente criterio, utilizado con anterioridad por Condis *et al.* (en prensa):

***Cráneo. Caracteres diagnósticos*:** **1**-ensanchamiento del rostro (Fig. 5; 10,1X): 0=ensanchado, 1=delgado, **2**-longitud del rostro (Fig. 5; 10,1X): 0=menor, 1=mayor, **3**-longitud de los forámenes incisivos (Fig. 6; 10,1X): 0=menor, 1=mayor, **4**-espacio entre canino superior y último premolar (Fig. 7; 10,1X): 0=mayor, 1=menor, **5**-presencia de diastemas entre canino (C) y primer premolar del maxilar (P^2), entre P^2 y segundo premolar del maxilar (P^3) y entre P^3 y tercer premolar del maxilar (P^4) (Fig. 8; 10,1X): 0=presentes, 1=ausentes, 2=forma intermedia, **6**-tamaño relativo de los primeros premolares (P^2 y P^3) (Fig. 9; 12,8X): 0=iguales, 1=diferentes, **7**-desarrollo de la cresta nucal (Fig. 10; 10,1X): 0=menor, 1=mayor, **8**-oblicuidad del P^3 o segundo premolar respecto al borde externo del maxilar (Fig. 7; 12,8X): 0=recto, 1=oblicuo,

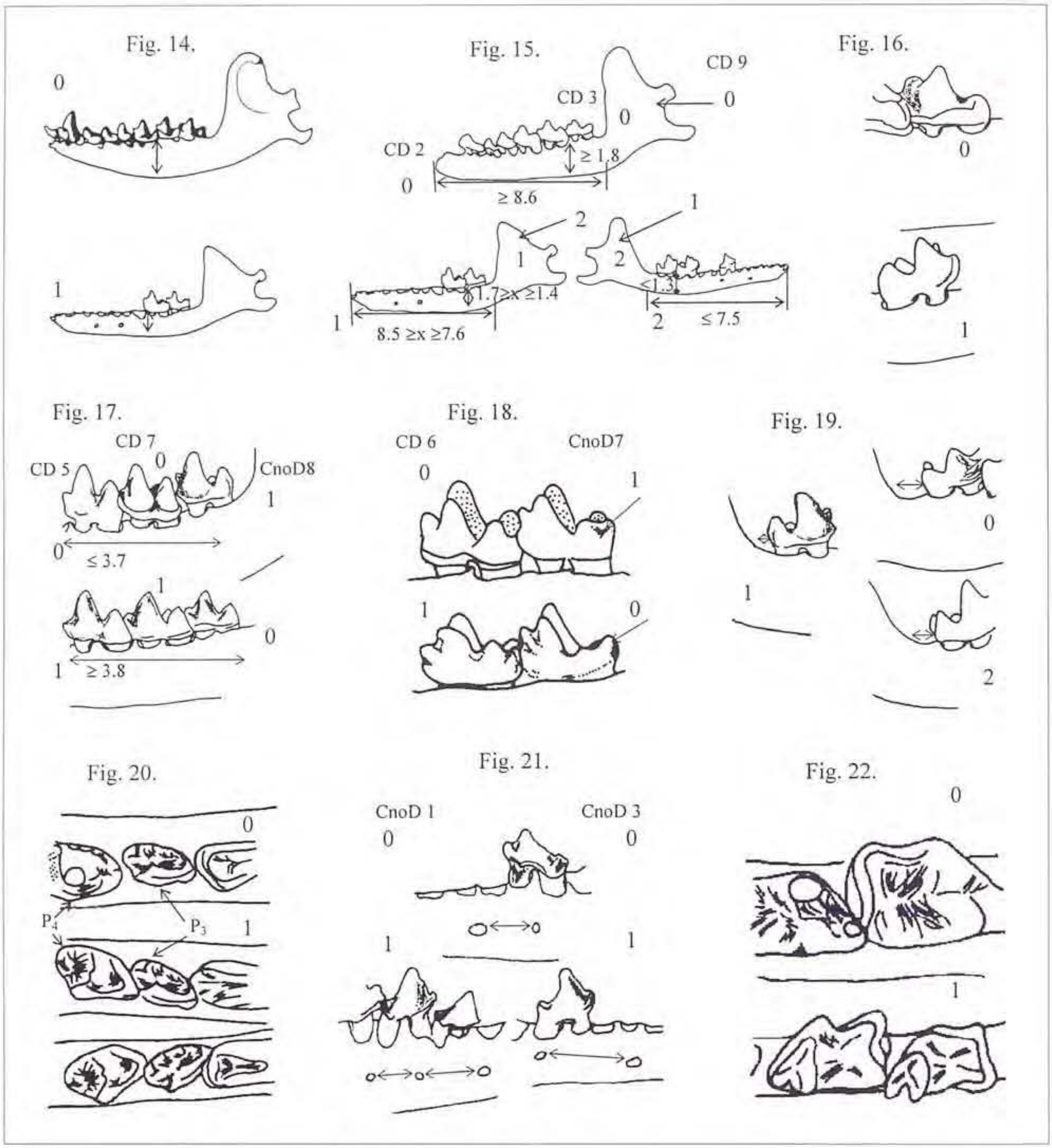
Figs. 5-13. Caracteres morfológicos analizados en el Cráneo: 5. Carácter Diagnóstico 1 (CD1): ensanchamiento del rostro y Carácter Diagnóstico 2 (CD2): longitud del rostro. 6. Carácter Diagnóstico 3 (CD3), longitud de los forámenes incisivos. 7. Carácter Diagnóstico 4 (CD4), espacio entre canino superior y último premolar y Carácter Diagnóstico 8 (CD8), oblicuidad de P^3 respecto al borde externo del maxilar. 8. Carácter Diagnóstico 5 (CD5), presencia de diastemas entre canino (C) y primer premolar del maxilar (P^2), entre P^2 y segundo premolar del maxilar (P^3) y entre P^3 y tercer premolar del maxilar (P^4). 9. Carácter Diagnóstico 6 (CD6), tamaño relativo de los primeros premolares (P^2 y P^3). 10. Carácter Diagnóstico 7 (CD7), desarrollo de la cresta nucal. 11. Carácter no Diagnóstico 9 (CnD9), tamaño del lacrimal, según el tamaño del cráneo. 12. Carácter no Diagnóstico 10 (CnD10), expansión del maxilar en el borde orbital. 13. Carácter no Diagnóstico 12 (CnD12), longitud de la cresta sagital, Carácter no Diagnóstico 13 (CnD13), abultamiento del supraoccipital, Carácter no Diagnóstico 14 (CnD14), longitud de la caja cerebral. (Tomados de Condis et al., en prensa).

Figs. 5-13. Morphological characters analyzed in the skull: 5. Diagnostic Character 1 (CD1): widening of rostrum and Diagnostic Character 2 (CD2): length of rostrum. 6. Diagnostic Character 3: length of incisive foramina. 7. Diagnostic Character 4 (CD4): space between upper canine and last premolar and Diagnostic Character 8 (CD8): obliquity of P^3 or second premolar regarding the external border of the maxilla. 8. Diagnostic Character 5 (CD5): presence of diastemas between C and P^1, between P^1 and P^2 and between P^2 and P^3. 9. Diagnostic Character 6 (CD6): re-lative size of first premolars (P^2 and P^3). 10. Diagnostic Character 7 (CD7): development of the Nukal Crest. 11. No Diagnostic Character 9 (CnoD9): lacrimal size, in correspondence with skull size. 12. No Diagnostic Character 10 (CnoD10): maxillary expansion over orbital border. 13. No Diagnostic Character 12 (CnoD12): length of Saggital Crest, no Diagnostic Character 13 (CnoD13): Supraoccipital bulky and no Diagnostic Character 14 (CnoD14): cerebral box length (sensu *Condis et al., in press).*



hacia el interior del paladar. *Caracteres no diagnósticos*: **9**-tamaño del lacrimal, según el tamaño del cráneo (Fig. 11; 10,1X): 0=se reduce con la reducción del cráneo, 1=longitud, independientemente del tamaño del cráneo y expandido hasta una apertura atrompetada, **10**-expansión del maxilar en el borde orbital (Fig. 12; 10,1X): 0=ausente, borde redondeado, 1=presente, como un saliente, **12**-longitud de la cresta sagital (Fig. 13; 10,1X): 0, menor, 1, mayor, **13**-abultamiento del supraoccipital (Fig. 13; 10,1X): 0, menor, 1, mayor, **14**-longitud de la caja cerebral (Fig. 13; 10,1X): 0, menor, 1, mayor.

Mandíbula: Caracteres diagnósticos: **1**-forma del cuerpo mandibular (Fig. 14; 10,1X): 0=ancho, con una curva profunda bajo los molares, 1=proporcionalmente más delgado, sin la curva profunda bajo los molares, **2**-longitud del cuerpo mandibular (Fig. 15; 10,1X): 0=grande, 1=medio, 2=pequeño, **3**-anchura del cuerpo mandibular (Fig. 15; 10,1X): 0=ancho, 1=estrecho, 2=más estrecho (aproximadamente la mitad del anterior), **4**-altura del M_2, con respecto al cuerpo mandibular (Fig. 16; 40,0X): 0=menos altos, 1=tan altos como el cuerpo mandibular, **5**-longitud de los molares (Fig. 17; 40,0X): 0=menor, 1=mayor, **6**-tamaño relativo de los molares (Fig. 18; 40,0X): 0=robustos, 1=poco robustos, **7**-forma de los molares (Fig. 17; 40,0X): 0=subiguales, 1=decrecientes del primer molar de la mandíbula (M_1) al tercer molar de la mandíbula (M_3), **8**-espacio entre el borde posterior del M_3 y la rama mandibular (Fig. 19; 40,0X): 0=presente, 1=ausente, 2=M_3 más separado que en las demás especies del género, **9**-forma y anchura de la apófisis coronoides (Fig. 15; 10,1X): 0=ancha, alta, mayor que en las demás especies, 1=triangular, estrecha y oprimida, 2=tamaño medio. **10**-orientación de los premolares en el cuerpo mandibular (Fig.20; 40,0X): 0= tercer premolar de la mandíbula (P_4) y segundo premolar de la mandíbula (P_3) situados longitudinalmente a lo largo del cuerpo, 1=P_4, pero particularmente P_3 oblicuamente con respecto al cuerpo mandibular. *Caracteres no diagnósticos*: **1**-



Figs. 14-22. Caracteres morfológicos analizados en la Mandíbula: 14. Carácter Diagnóstico 1 (CD1): forma del cuerpo mandibular. 15. Carácter Diagnóstico 2 (CD2): longitud del cuerpo mandibular, Carácter Diagnóstico 3 (CD3): anchura del cuerpo mandibular y Carácter Diagnóstico 9 (CD9): forma y anchura de la apófisis coronoides. 16. Carácter Diagnóstico 4 (CD4): altura del M_2, con respecto al cuerpo mandibular. 17. Carácter Diagnóstico 5 (CD5): longitud de los molares, Carácter Diagnóstico 7 (CD7): forma de los molares y Carácter no Diagnóstico 8 (CnoD8): agudeza de las cúspides. 18. Carácter Diagnóstico 6 (CD6): tamaño relativo de los molares, Carácter no Diagnóstico 7 (ConD7): presencia de hipoconúlido en M_1 y M_2. 19. Carácter Diagnóstico 8 (CD8): espacio entre el borde posterior del M_3 y la rama mandibular. 20. Carácter Diagnóstico 10 (CD10): orientación de los premolares en el cuerpo mandibular. 21. Carácter no Diagnóstico 3 (CnoD 3): distancia entre los forámenes mentonianos, Carácter no Diagnóstico 1 (CnoD 1): desarrollo de los premolares. 22. Carácter no Diagnóstico 4 (CnoD4): anchura de los molares, con respecto a la anchura del cuerpo mandibular. (Tomados de Condis *et al.*, en prensa).

***Figs. 14-22.** Morphological characters analyzed in the Mandible: 14. Diagnostic Character 1 (CD1): form of mandibular body. 15. Diagnostic Character 2 (CD2): length of mandibular body, Diagnostic Character 3 (CD3): width of mandibular body and Diagnostic Character 9 (CD9): form and width of coronoid apophisis. 16. Diagnostic Character 4 (CD4): height of* M_2*, with respect to the mandibular body. 17. Diagnostic Character 5 (CD5): length of molars, Diagnostic Character 7 (CD7): molars form and no Diagnostic Character 8 (CnoD8): sharpness of cusp. 18. Diagnostic Character 6 (CD6): relative size of molars, no Diagnostic Character 7 (CnoD7): hipoconulid present in* M_1 *and* M_2*. 19. Diagnostic Character 8 (CD8): space between posterior border of* M_3 *and mandibular branch. 20. Diagnostic Character 10 (CD10): orientation of premolars of mandibular body. 21. No Diagnostic Character 3 (CnoD 3): distance between chin foramens, no Diagnostic Character 1 (CnoD 1): develops of premolars. 22. No Diagnostic Character 4 (CnoD4): molars width, with respect of mandibular body width.* (sensu *Condis* et al., *in press*).

desarrollo de los premolares (Fig. 21; 40,0X): 0=pequeños, 1=largos y altos, con una punta elevada, **3**-distancia entre los forámenes mentonianos (Fig. 21; 40,0X): 0=menor, 1=mayor, **4**-anchura de los molares, con respecto a la anchura del cuerpo mandibular (Fig. 22; 40,0X): 0=iguales o menos anchos, 1= más anchos, **7**-presencia de hipoconúlido en M1 y segundo molar de la mandíbula (M2) (Fig. 18; 40,0X): 0=presente, 1=ausente, en su lugar hay un borde agudo posterior elevado, separado del entocónido a través de un surco claro, **8**-agudeza de las cúspides (Fig. 17; 40,0X): 0=más puntiagudas, 1=menos puntiagudas.

Las medidas y caracteres morfológicos fueron tomadas en un Micrómetro ocular acoplado a un Microscopio Zeiss Modelo STEMI 100 (error ± 0,01).

RESULTADOS Y DISCUSIÓN

Análisis de la diagnosis de las especies cubanas del género *Nesophontes*

Cráneo

Entre los caracteres diagnósticos de *N. longirostris* se encuentra la presencia de diastema, de mayor o menor longitud entre el canino (C) y los premolares (Ps) del maxilar (Carácter Diagnóstico 5), que se expresa también como el comportamiento de la distancia entre el C y el tercer premolar (P^4) (Carácter Diagnóstico 4). Como resultado del análisis de los caracteres continuos realizado por Condis *et al.* (en prensa) se obtuvo que la distancia entre C y P^4 del maxilar presenta una alta variabilidad en individuos de *N. micrus* y *N. major*, al igual que lo obtenido en el análisis de los caracteres discontinuos, donde la presencia de diastema mandibular entre C y Ps presenta iguales niveles de correspondencia con individuos de *N. major* que de *N. micrus*. A pesar de que estos caracteres se analizan independientemente ambos reflejan un mismo fenómeno (Anthony, 1919). Otros caracteres discontinuos de la diagnosis de *N. longirostris*, como la delgadez del rostro (Carácter Diagnóstico 1) y el tamaño relativo de los dos primeros premolares (Carácter Diagnóstico 6) (Figs. 5-9), presentan también una alta variabilidad, según lo obtenido por Condis *et al.* (en prensa). Por esta razón, consideramos que *N. longirostris* es un sinónimo de *N. micrus*, a la cual se asemeja en dimensiones generales. Esto coincide con lo considerado por Morgan (1977) tras el examen minucioso del holótipo de *N. longirostris*. Dicho autor apreció una amplia gama de variaciones para los caracteres diagnósticos de la especie en cuestión, en cerca de 10 cráneos de *N. micrus*.

En el caso de *N. major* fue posible examinar el holótipo y pudimos apreciar como caracteres como el P^3 colocado oblicuamente (Carácter Diagnóstico 8) y un buen desarrollo de la cresta nucal (Carácter Diagnóstico 7), varían indistintamente, tanto en individuos de *N. micrus* como en individuos de *N. major*. En el análisis de correspondencia simple (ACS) de Condis et al. (en prensa) se observa que el P^3 colocado oblicuamente no se corresponde con ninguna de las dos especies analizadas (*N. micrus* y *N. major*). Por su parte, la longitud de los forámenes incisivos (Carácter Diagnóstico 3) se mantiene constante en la muestra correspondiente a *N. major* pero varía en los individuos de *N. micrus*. Se mantienen constantes también, en ambas especies la mayor longitud del rostro (Carácter Diagnóstico 2) y el tamaño de la caja craneal (Carácter no Diagnóstico 14). Pero, estos caracteres resultan redundantes en el análisis de componentes principales (ACP) realizado por Condis et al. (en prensa). No obstante, en el ACS obtenido en este mismo artículo, el menor abultamiento del supraoccipital (Carácter no Diagnóstico 13) (Figs. 5-13) mantiene una alta correspondencia sólo con la muestra de *N. major*. Este carácter es mencionado en la descripción de la especie, pero no se considera en su diagnosis (Arredondo, 1970). Su comportamiento, acompañado del de otros caracteres que expresan tamaño (LT y ARC), puede servir para diagnosticar esta especie.

El comportamiento de los caracteres diagnóstico de *N. major* llevó a que Morgan (1977), tras un examen de los mismos, planteara que esta especie era una forma extrema dentro del rango de tamaño alcanzado por *N. micrus*. Sin embargo, *N. major* aparece en los mismos depósitos de *N. micrus*, asociada a iguales contextos, según el análisis tafonómico de los mismos, lo que descarta la posibilidad de que estemos en presencia de paleoespecies (Berovides y Alfonso, 1995). Teniendo en cuenta que *N. major* aparece tempo-espacialmente relacionada con *N. micrus*, además de que su mayor tamaño en todas las piezas es más apreciable que entre *N. micrus* y *N. submicrus*; y por otra parte, que presenta determinados caracteres distintivos; principalmente en el cráneo (Figs. 5-13), consideramos apropiada la reelaboración de la diagnosis de *N. major*, sobre la base del material tipo y los nuevos hallazgos.

Mandíbula

Esta parte del esqueleto se utilizó en las descripciones de *N. micrus, N. submicrus y N. superstes.*

Dos de los caracteres diagnóstico utilizados en la descripción de *N. micrus* se expresan en todas las especies del género por lo que consideramos necesario eliminarlos de esta diagnosis (presencia de cíngulo en la parte media anterior del aspecto externo del primer y segundo molar (M1 y M2) y protocónido más alto que metacónido, el cual queda casi oculto en vista lateral, aunque esta cúspide es muy poco posterior, con respecto a la del metacónido) (Allen, 1917). Por su parte en *N. submicrus*, que se asemeja en talla a las formas más pequeñas de *N. micrus*, el autor menciona la anchura del cuerpo mandibular (Carácter Diagnóstico 3), que varía en *N. micrus* de manera amplia, según lo obtenido en el ACP de Condis *et al.* (en prensa). En este análisis también se puede apreciar que la altura de las coronas de los molares no está relacionada con la altura del cuerpo mandibular, lo cual unido a la variabilidad que muestra el carácter altura de las coronas igualando la del cuerpo mandibular (Carácter Diagnóstico 4), que se presenta en algunos individuos de pequeña talla de *N. micrus*, permite afirmar que esta relación no debe usarse como diagnóstico. Lo mismo sucede con la distancia del tercer molar (M3) a la rama mandibular (Carácter Diagnóstico 8) y la forma de la apófisis coronoides (Carácter Diagnóstico 9) (Figs. 15-19), que se presentan indistintamente en mandíbulas de *N. micrus* y *N. major*, como se aprecia en el gráfico de frecuencia de caracteres mandibulares de Condis *et al.* (en prensa).

También *N. superstes*, según su autor, se asemeja a *N. micrus* en talla y forma general. El único carácter diferencial que se plantea es la posición oblicua del P_3 y el P_4 (Carácter Diagnóstico 10), que se presenta indistintamente en numerosos individuos de *N. micrus* y principalmente de *N. major*, con todas las formas intermedias que este carácter puede presentar (Fig. 20) (Condis *et al.*, en prensa).

Por esta razón, Condis *et al.* (en prensa) obtuvo en el ACS de estos caracteres que los mismos no permiten discriminar las especies en cuestión, lo que nos lleva a considerar que *N. superstes* y *N. submicrus* son sinónimos de *N. micrus*, ya que estas han sido descritas a partir de caracteres variables de la mandíbula y no contamos con ninguna otra pieza del esqueleto que pueda sustituir a la usada.

Dado que la diagnosis de *N. micrus* también está basada en la mandíbula, consideramos oportuno reelaborar la misma, aprovechando que se conoce ampliamente el cráneo de esta especie.

Nuevas diagnosis de *Nesophontes major* y *Nesophontes micrus*.

Dada la variabilidad de algunos de los caracteres considerados con anterioridad como diagnósticos y al demostrarse anteriormente en este trabajo, tras lo obtenido por Condis *et. al.* (en prensa), que *N. longirostris*, *N. submicrus* y *N. superstes* son sinónimos de *N. micrus*, se hace necesaria la rediagnosis de *N. micrus* y *N. major*.

Las nuevas diagnosis de *N. major* y *N. micrus* se basan principalmente en el material de cráneo y mandíbula, ya que los huesos largos disponibles no pueden ser atribuidos con seguridad al material de cráneo y mandíbula.

Nesophontes major

Material Examinado: 9 cráneos y 20 ramas mandibulares.

Diagnosis: Especie de *Nesophontes* con un cráneo notablemente menor que el de *N. edithae* y ligeramente mayor que los de las otras dos especies conocidas. Menor abultamiento del supraoccipital que *N. micrus*. Mayor longitud y anchura del rostro en relación con *N. micrus*. Con un mayor desarrollo de los molares y el P_3 de la mandíbula que *N. micrus*.

Nesophontes micrus

Sinonimias:

N. longirostris Anthony, 1919, nuevo sinónimo.
N. submicrus Arredondo, 1970, nuevo sinónimo.
N. superstes Fischer, 1977, nuevo sinónimo.

Pieza: Cráneo y Mandíbula

Material Examinado: 16 cráneos y 32 ramas mandibulares.

Diagnosis: Especie de *Nesophontes* con un cráneo considerablemente más pequeño que *N. edithae* de Puerto Rico y ligeramente menor que *N. major*, en dimensiones generales, pero cuya mandíbula es evidentemente similar en la forma general del angular y la rama mandibular. El cuerpo, sin embargo, se muestra proporcionalmente más delgado que la de *N. edithae*, sin la curva profunda bajo los molares. Los molares difieren de los de la especie tipo de *Nesophontes*: 1) En que son menos elongados en el eje del cuerpo mandibular. 2) En que decrecen en tamaño del M_1 al M_3. 3) Ante la falta de cierta "robustez" se asemejan en forma a la encontrada en *Solenodon*. Con un menor desarrollo de los molares y el P_3 de la mandíbula, que en *N. major*. Sus cúspides son puntiagudas. El hipocónido, en ocasiones presenta un pequeño hipoconúlido. El tamaño del lacrimal es largo, independientemente del tamaño del cráneo y expandido hasta una apertura atrompetada, a diferencia de *N. edithae*, donde el lacrimal se reduce con la reducción del cráneo. El maxilar en el borde orbital es redondeado, mientras que en *N. edithae* presenta una expansión, como un saliente. El cráneo presenta un mayor abultamiento del supraoccipital y menor longitud y anchura del rostro, con respecto a *N. major*.

Es necesario continuar los estudios sobre la sistemática del género *Nesophontes*, reforzando los correspondientes a la morfología funcional en este grupo y la taxonomía del mismo.

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11

PIGEONS AND PELAGICS: INTERPRETING THE LATE PLEISTOCENE AVIFAUNAS OF THE CONTINENTAL 'ISLAND' OF GIBRALTAR

Joanne H. COOPER

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Resum

Quatre jaciments espeleològics del Pleistocè tardà (la balma de Devil's Tower i les coves de Gorham, Vanguard i Ibex) han lliurat alguns dels conjunts ornítics més abundants i diversos del Paleàrtic Occidental, incorporant devers 130 taxa. Les associacions d'espècies sense equivalents moderns esdevenen a tots els jaciments, però semblen poder-se atribuir amplament als efectes combinats del temps promig de deposició i a la conducta migratòria, i no a l'existència d'ambients no anàlegs als actuals. S'ha confirmat que un total de 18 espècies han criat a la regió de Gibraltar durant el Pleistocè tardà. A més d'espècies típiques de les comunitats modernes d'ocells ibèrics, incloent *Cyanopica cyanus*, s'han identificat restes immadures de dues ànneres, *Melanitta nigra* i *M. fusca*, que actualment crien a les regions Àrtica i Boreal. La presència com a reproductors d'altres espècies marines nord-atlàntiques, com *Pinguinus impennis*, no s'ha pogut confirmar.

Paraules clau: Pleistocè tardà, Gibraltar, avifaunas, migració, cria, *Melanitta nigra, M. fusca.*

Abstract

Four Late Pleistocene cave sites; Devil's Tower Rock Shelter and Gorham's, Vanguard and Ibex Caves, located on the southern Iberian peninsula of Gibraltar, have yielded some of the most abundant and diverse avifaunal assemblages in the Western Palearctic, incorporating some 130 taxa. Species associations with no modern equivalents occur throughout the sites, but appear to be largely attributable to the combined effects of depositional time-averaging and migratory behaviour and not the former existence of non-analogue environments. A total of 18 species are confirmed as having bred in the region of Gibraltar during the Late Pleistocene. In addition to species typical of modern Iberian bird communities, including *Cyanopica cyanus*, immature remains were identified of two ducks, *Melanitta nigra* and *M. fusca*, that currently breed in Boreal-Arctic regions. Breeding presence of other North Atlantic marine species, including *Pinguinus impennis* cannot be confirmed.

Key words: Late Pleistocene, Gibraltar, avifaunas, migration, breeding, *Melanitta nigra, M. fusca.*

INTRODUCTION

The Late Pleistocene encompasses the last interglacial-glacial cycle, from around 130,000-12,000 years before present (BP). It is a period characterised by rapid climatic fluctuations, culminating in the last glacial maximum and subsequent amelioration between approximately 24,000-12,000BP. Understanding the nature of these fluctuations and their impacts is not only important in terms of understanding possible future climatic changes, but also in coming to understand the development of modern faunal communities. Remains of vertebrates are one source of evidence of both climate change and faunal development. Mammalian faunas have traditionally dominated Late Pleistocene vertebrate research, however more attention is now being given to exploring the palaeoecological potential of other classes. Foremost amongst these are birds, now shedding a widespread reputation of being both scarce and uninformative (cf. Lowe & Walker, 1997; see also Tyrberg, 1998).

Bird remains are in fact regular, if not necessarily abundant, components of Late Pleistocene vertebrate assemblages, and may be found in a wide range of depositional situations, (Tyrberg, 1998; Morales Muñiz 1993). Recovery of Late Pleistocene bird material is frequently associated with the excavation of archaeological sites, whether Neanderthal or Anatomically Modern Human (Tyrberg, 1998). Consequently, there is a strong tendency for interpretation to focus primarily on taphonomic issues, considering them in relation to human activities (cf. Stewart, 2002). However, there is a growing awareness of the intrinsic value of avian assemblages, particularly as palaeoecological proxies.

One key advantage of birds in palaeoecological applications is the availability of a vast modern ornithological literature, from which detailed analogue information can be drawn for Pleistocene populations (Baird, 1989; Morales Muñiz, 1993). Modern analogues can be used at various levels of interpretation, from examining an individual taxon to comparing the overall species composition of an assemblage with modern biogeographic regions. Where modern equivalents exist, this approach can be very successful (e.g. Tyrberg, 1999). However, a phenomenon widely recognised in Late Pleistocene research is the occurrence of faunal associations with no modern equivalents. Known as non-analogue faunas, these are of considerable interest as possible evidence of environments unknown at the present day (Lowe & Walker, 1997). They are regularly encountered in avian assemblages, where species now characteristic of contrasting habitats or climate are found in association. In the Mediterranean region, such associations have been interpreted as evidence of compression of biomes during the Late Pleistocene, for example of Mediterranean and tundra habitats in southern France (Covas & Blondel, 1998). Whilst non-analogue species associations may undoubtedly represent non-analogue environments, it is also possible that they could be relicts of taphonomic processes, or even reflect certain aspects of avian behaviour. Alternative explanations for their origins must be considered before a non-analogue environment can be invoked.

Modern analogues of bird species are primarily based upon habitat and climate preferences, frequently of species' breeding ranges. Implications of the behaviour of modern species, and the resulting interactions with their environment tend to be given less emphasis. Yet, certain aspects of species' behaviour can have profound implications on the understanding of an assemblage's palaeoecological signal.

Paramount amongst these behaviours is migration, which in birds may occur across a wide range of temporal and geographic scales. However, it is the various seasonal movements of many species which are the most obvious manifestation of the behaviour, and which also have the greatest potential impact on the palaeoecological signal of an assemblage. It should be noted that far from affecting a minority, seasonal migration is in fact demonstrated by the majority of bird species in the Western Palearctic (Alerstam, 1990). As a result, most modern temperate continental avian communities are extremely fluid in their species composition throughout the year. Migratory behaviour represents a particular palaeoecological problem, as a migrant occurring in an assemblage may potentially represent one of several situations: its summer breeding grounds, its wintering grounds or its route of passage. This can have habitat implications, but most importantly it has climatic significance, as the majority of migratory movements primarily reflect seasonal conditions.

In addition to species that migrate along fairly well defined routes, others may disperse very widely from their breeding ranges over a large, generalised area (Wernham *et al.*, 2002). This dispersal migration is characteristic of many pelagic seabirds, whose wanderings may potentially bring them within the range of terrestrial localities far beyond their established breeding range. As a result, in addition to non-analogue climatic associations, such behaviour introduces potential for extreme contrasts in habitats to occur within a single assemblage (e.g Stewart, 2002).

The aim of this paper is to examine the implications of introducing possible effects of migration and other aspects of avian behaviour into palaeoecological interpretation, using examples drawn from a group of localities in Gibraltar, southern Iberia, where non-analogue species associations are a hallmark of their Late Pleistocene avifaunas.

Located on the north-east coast of the Strait of Gibraltar, the small peninsula of Gibraltar itself lies within a region significant in modern ornithology as the junction of two major migration bottlenecks. Terrestrial species passing north or southwards between the continents of Europe and Africa seek a relatively short sea-crossing over the Strait, only 14 km at its narrowest; marine and coastal species are funnelled through the Strait as they pass east or westwards between the western Mediterranean and the Atlantic. From a palaeontological perspective, the physical geography of the region means that even during Late Pleistocene changes in sea-level or in the precise nature and extent of migration, the Strait of Gibraltar would have remained a bottleneck that migrating birds would have been constrained to use. Both the Strait of Gibraltar and the great limestone outcrop of the Rock of Gibraltar that dominates the peninsula are today classed as Important Bird Areas, in direct recognition of their significance to migrating birds (Heath & Evans, 2000).

Furthermore, Southern Iberia also has biogeographic significance as having been one in a chain of Late Pleistocene temperate refugia located along the southern edge of Europe, characterised by modern associations of largely non-migratory residents with restricted ranges, often including endemic species or subspecies (Harrison, 1982). In a lesser way, the Rock of Gibraltar itself can be regarded as a refugium, providing a montane habitat 'island' within a lowland coastal plain. Although Gibraltar has no endemic birds, it does have an endemic plant species, Gibraltar Candytuft *Iberis gibraltarica* (Cortés & Finlayson, 1988).

The combination of Late Pleistocene refugium and migration bottlenecks have created some of the richest, most diverse and dynamic avian communities in the Western Palearctic. At present, some 75% of Western Palearctic bird species may occur within the region of the Strait of Gibraltar during the course of a year (Finlayson, 1992). This represents a total of some 400 species known from the Strait region, of which 186 are breeding residents or summer migrants; 91 are wintering or passage migrants; and the remainder are accidental vagrants (Finlayson, 1992).

Certain caves on Gibraltar have yielded abundant bird remains from the Late Pleistocene, offering the prospect of detailed proxy evidence of Gibraltar's Late Pleistocene palaeoenvironments. Non-analogue species associations occur regularly throughout the stratigraphic sequences of these sites. However, given the fundamental importance of migration to the region's modern avifauna, the phenomenon must be given due consideration as a possible cause of non-analogue associations, in addition to other taphonomic factors.

MATERIAL AND METHODS

Gibraltar's Late Pleistocene avifaunas have been examined in a number of previous works, most important of which are the original publications on the bird remains from Devil's Tower Rock Shelter, recovered during the 1920s (Bate, 1928) and those from excavations at Gorham's Cave during the 1950s (Eastham, 1968). Whilst no material has been retrieved from Devil's Tower since the original work, a number of excavations have been carried out at Gorham's Cave, adding considerably to knowledge of the site and its fauna (Stringer *et al.*, 2000).

The present paper primarily considers material recovered from Gorham's Cave and the two previously unexplored sites of Ibex and Vanguard Caves during a series of excavations conducted between 1994-1998 under the auspices of the Gibraltar Museum and The Natural History Museum, London (Stringer, 2000; Stringer *et al.*, 2000; Finlayson *et al.*, 2000). Identifications of the avian assemblages were made using the recent comparative collections of The Natural History Museum, Tring, supplemented by the collections of the Museo Nacional de Ciencias Naturales, Madrid and the Institut Mediterrani d'Estudis Avançats, Palma de Mallorca. The recently excavated bird material from Gorham's and Vanguard Caves is now mainly held by the Department of Palaeontology, The Natural History Museum, London; further Gorham's and Vanguard specimens and the entire Ibex Cave assemblage are held by the Gibraltar Museum.

Avian taxonomy used here follows Dickinson (2003). Grid references are given in Universal Transverse Mercator.

RESULTS

In its present form, Gibraltar is a small peninsula, 5.2 km long, 1.6 km wide (natural maximum) and about 6 km^2 in area. It is dominated by the vast outcrop of Jurassic limestone known as the Rock, which extends roughly 2.5 km along the peninsula, rising to over 400 m at its highest point. At least 143 caves have been discovered within the Rock (Rose & Rosenbaum, 1991), in which varied archaeological and palaeontological assemblages have been preserved. A summary is given below of each site considered here, Gorham's, Vanguard and Ibex Caves, and Devil's Tower Rock Shelter (Fig. 1), in geographic order from north to south.

Devil's Tower Rock Shelter

Devil's Tower Rock Shelter (approximately TF 89270293) lay at the base of the cliffs of the North Face of the Rock. In addition to the cave chamber itself, a narrow fissure some 1.2 m wide and 4 m deep, the original excavations encompassed the emerging talus slope and the *in situ* deposits it covered (Garrod *et al.*, 1928). A stratigraphic sequence of over 10 m was recorded, comprising various tufas, sands and speleothems overlying a raised beach. Faunal remains, particularly mammals and birds, were abundant throughout the site. Bate (1928) identified 33 species of bird, but did not appear to have studied the entire collection (Cooper, 1999). Re-examination of the complete Devil's Tower bird assemblage has increased this to some 80 species. Notable avian finds here are various pelagic species, including both *Alle alle* Little Auk and *Pinguinus impennis* Great Auk, and well over a thousand bones of *Tachymarptis melba* Alpine Swift (Cooper, 1999). However, most famous of the fossils unearthed here is the fragmentary skull of a Neanderthal child, found within the cave itself (Garrod *et al.*, 1928). In general though, evidence of human activity was relatively scarce and the site seems to have been used only occasionally. Recent attempts to date material from Devil's Tower have been made difficult by low collagen levels in the bones, but the majority of the sequence does in fact appear to lie beyond the range of radiocarbon (C. B. Stringer, pers. com.).

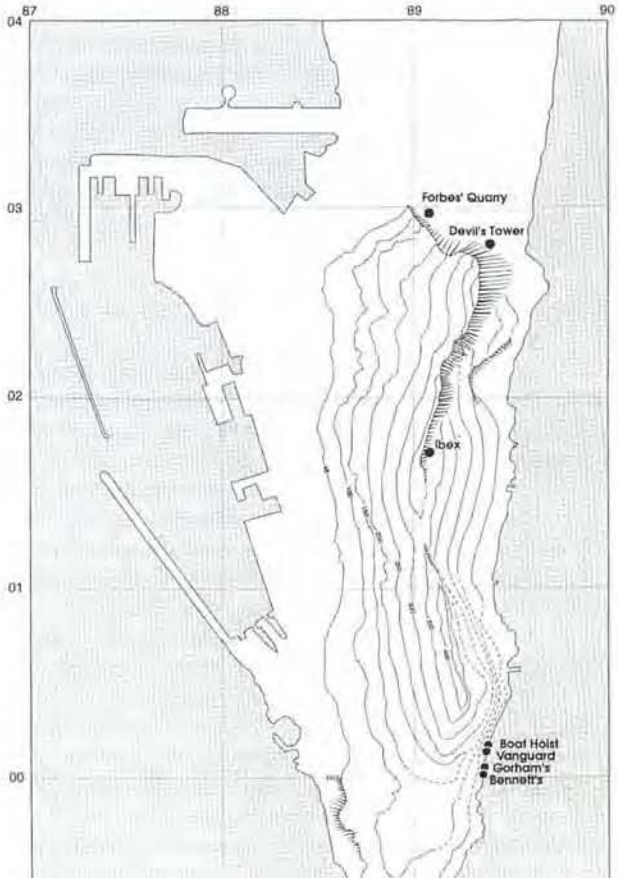

Fig. 1. Map of Gibraltar, southern Iberia, indicating cave sites described in text. Reproduced courtesy of R.N.E. Barton.

Fig. 1. Mapa de Gibraltar, sud de la Península Ibèrica, indicant els jaciments espeleològics descrits al text. Reproduït per cortesia de R.N.E. Barton.

Ibex Cave

Ibex Cave (approximately TF89050172) is located on the eastern side of the Rock, some 250-300 m above sea-level. It is a small cave, about 5 m wide at its mouth and about 5 m deep, lying at the base of limestone cliffs above thick deposits of wind-blown Pleistocene sands. During the only excavation at this site, in 1994, a sedimentary sequence approximately 3 m deep was excavated; this was dominated by silty sands, and included some small blocks of breccia. Despite the relatively small scale of the site, a diverse faunal assemblage was recovered, largely from the single, least disturbed, unit. The assemblage included abundant remains of both large and small mammals, and numerous fragments of tortoise (Fernandez-Jalvo & Andrews, 2000). In terms of birds, some 240 remains were recovered, of which some 75 were identified at least to family, representing at least 25 species (Cooper, 1999; 2000a). These included a complete left femur of *Pinguinus impennis* Great Auk, and an almost complete skull of *Morus bassanus* Northern Gannet (Cooper, 1997, 1999).

A variety of lithics were recovered, predominantly flakes and cores, but these have been interpreted as representing a single episode of human activity at the site, and it is primarily regarded as having been a carnivore den (Barton, 2000; Fernandez-Jalvo & Andrews, 2000).

Electron Spin Resonance dating placed the *in situ* fauna of the undisturbed unit within the mid-last glaciation, approximately between 37,100 ± 3,300 (early uptake model) to 49,400 ± 3,200 (late uptake model) BP (Rhodes *et al.*, 2000).

Vanguard Cave

Vanguard Cave (TF 89360021) is one of a suite of caves that also includes Gorham's Cave, along the eastern coast of the Gibraltar peninsula. It possesses a huge overhanging double entrance and narrow chamber, developed along a fissure, of at least 20 m in length. A second considerably smaller chamber is located to the north of the cave's inner entrance. A total depth of some 16 m of sediments was recorded in the main chamber, consisting mainly of massive coarse sands interspersed with thin units of brown silts and silty sands. Micromorphological examination of the sediments suggests that the cave maintained a relatively dry environment throughout its depositional history (Macphail & Goldberg, 2000). Avifaunal remains were abundant, though not in the quantities found at Gorham's Cave. However, this may reflect the fact that excavations in Gorham's were located relatively deeper within its chamber. Evidence of human activity suggested a relatively low intensity of use, though well preserved discrete hearths were found in several horizons (Barton, 2000).

To date, only the 1995 and 1996 seasons' assemblages have been studied in detail. From an overall collection of some 2,900 remains, about 900 were referable at least to family, with a total of approximately 70 species identified (Cooper, 1999). The pattern of occurrence of bird bones through the sequence revealed a few high-diversity horizons amid units with relatively sparse assemblages. Reflecting the smaller number of recovered specimens in comparison to Gorham's, fewer non-analogue species associations were identified in single horizons, but overall the avifaunas did include species characteristic of both climate and habitat contrasts, such as *Fulmarus glacialis* (Northern Fulmar) and *Coracias garrulus* (European Roller) (Cooper, 1999).

The majority of Vanguard's sequence fell outside the limits of AMS radiocarbon dating, though a few dates in the uppermost levels suggested that the cave had filled by approximately 45,000 BP (Pettit & Bailey, 2000). Additionally, a charcoal sample from a discrete hearth in the side-chamber gave an AMS radiocarbon date of >44,100 BP. To provide a chronology for the main chamber, luminescence dating was applied. Samples from the middle and lowest excavated levels gave ages of 93,380 ± 7,300 BP and 111,850 ± 10,020 BP (Pettit & Bailey, 2000).

Gorham's Cave

Gorham's Cave (TF 89340007) lies adjacent to Vanguard Cave. Of a similar form to its neighbour, it has a very wide, high entrance enlarged by wave-action and tapers back into a passage-like chamber in excess of 40 m length. The 1995-1998 excavations concentrated on deposits lying approximately within the first 20 m of the main chamber.

The exposed sedimentary sequence of some 16-18 m depth, consisted of largely sandy units in the lower sections, with the middle and upper levels dominated by dark, organic rich clays and sandy silts. A particular characteristic of these upper levels was a high degree of local variation in the sediments, with complex relationships between individual units. Also notable was evidence of intense biological activity, including burrowing, human occupation and significant quantities of guano (Macphail & Goldberg, 2000).

A very wide range of palaeontological remains were recorded from this site, including a diverse mammalian assemblage and an abundant herpetofauna in addition to the thousands of bird bones recovered (Currant, 2000; C. Gleed-Owen, *in litt.*). Extensive evidence of human occupation was found, including hearths with charcoal and charred bones, butchered bones and numerous lithics.

Only the avifaunal remains recovered during the 1995 and 1996 seasons have been studied in their entirety. From some 9,000 remains, about 2,600 were identifiable at least to family level, representing approximately 90 species (Cooper, 1999). Typically, bird remains were relatively scarce in most levels, but a few units yielded assemblages of considerable diversity and abundance. Without exception, these units included non-analogue species associations, usually of 'warm' Mediterranean species with 'cold' boreal or arctic species, e.g. *Upupa epops* Hoopoe and *Melanitta fusca* Velvet Scoter, or *Falco naumanni* Lesser Kestrel with *Clangula hyemalis* Long-tailed Duck.

A dating program using AMS radiocarbon targeted the upper levels of the sequence, due to their high archaeological interest. Most dates unfortunately did not coincide with the majority of the bird-yielding units, however one particularly high-diversity unit yielded two dates from charcoal samples; 45,300 ± 1,700 BP from within a hearth and 51,700 ± 3,300 BP at the unit's base (Pettit & Bailey, 2000).

The bird assemblages studied by Eastham (1968) were recovered during excavations directed by John Waechter from 1951-54. However, although this collection still constitutes an important record of birds from Gorham's Cave, Waechter's stratigraphic scheme is now known to be seriously flawed, thus compromising the use of these birds in detailed palaeoecological analyses (Currant, 2000). Consideration of these assemblages is therefore not included here.

DISCUSSION

Together, the combined avifaunal assemblages from Gorham's, Vanguard, Ibex and Devil's Tower Caves represent the richest Late Pleistocene avifauna known from the Iberian peninsula, and one of the richest in the Western Palearctic (cf. Tyrberg, 1998). In total, remains from at least 130 species, in 98 genera from 38 families are now known from the sites (Cooper, 1999). This paper cannot provide a comprehensive review of the complete avifaunal assemblage, but will focus instead on the presence of selected species.

As noted, non-analogue species associations occur throughout the sites, though are most reliably recorded in Gorham's and Vanguard Caves due to the better resolved stratigraphies of these sites. Two broad categories of non-analogue associations can be identified. Firstly, there are juxtapositions of climatic preferences, typified by associations such as *Falco naumanni* and *Melanitta fusca* at Gorham's and secondly, there are contrasts in typical habitat requirements, such the pelagic *Pinguinus impennis* or *Pterodroma* sp. with terrestrial partridges *Alectoris* sp. or *Columba livia/oenas* (Rock/Stock Dove).

The species list of an avian assemblage, be it for an entire site or a single horizon, can be regarded in some ways as the equivalent of a modern regional checklist. All species observed during the period from which records began are included; residents, migrants, vagrants listed together (e.g. Finlayson, 1992: Appendix 1). When using such a list, it is taken as a given that not everything will occur together in time and space, and a good checklist will often include some indication of the seasonal status of each species, and even how frequently it may occur. A fossil species list is simply a checklist without this supplementary data, but is equally as complex (if not more so) and therefore must not be interpreted at face value. To produce this additional, palaeoecological information requires further analysis of the avifauna; the temporal resolution of the site must be examined and each individual species' potential seasonal status considered.

Temporal resolution of an assemblage is dependent on the depositional processes that may have affected its accumulation. Of particular concern are the processes of time-averaging, as they may cause remains from different time intervals to be preserved together, potentially giving rise to palaeoecologically misleading combinations (Kidwell & Behrensmeyer, 1993). The extent of time-averaging will also determine the precision with which an avifauna records climatic fluctuations, which are known to have occurred regularly on a millennial scale throughout the Late Pleistocene (Roucoux *et al.*, 2001).

In Gibraltar, it is noticeable that the high-diversity units in Gorham's and Vanguard Caves are typically more developed humic horizons, which in Gorham's are characterised with considerable organic inputs, especially bird guano (Macphail & Goldberg, 2000). The nature of these levels strongly suggests depositional hiatuses, which would also allow for extended development of their avian assemblages and a corresponding increase in the time-averaging effect. Furthermore, bioturbation is an additional complication evident in the sites. Unfortunately, at present it is not possible to suggest the precise intervals that each of these high diversity units may represent, but it seems likely that temporal resolution in any horizon is potentially on a scale of several millennia or more.

Therefore the validity of any non-analogue associations must be immediately be suspect, as although birds may have responded sensitively to rapid climatic fluctuations, these events are in fact likely to be represented by a succession of generalised assemblages. Evidence of climatic shifts clearly is preserved by the Gibraltar avifaunas in the occurrence of Arctic and Boreal breeding species such as *Clangula hyemalis*. However, it cannot be determined whether these species would have occurred in close temporal association (i.e. during the course of a year) with Mediterranean migrants such as *Falco naumanni*.

The habit of migration is not considered a recent phenomenon, although the routes and patterns followed by modern birds have probably developed within the past 10,000-5,000 years (Alerstam, 1990). If it is assumed that Late Pleistocene species possessed broadly the same migrational tendencies as their modern counterparts, it is possible to consider the potential seasonal status of Gibraltar's Late Pleistocene birds using a simple deductive technique based on the predicted effects of a southerly retreat in response to climatic deterioration on present Palearctic seasonal distributions. Admittedly, this is rather crude, but it is a useful device for beginning to categorize an assemblage and for identifying potentially valuable indicator species.

Four categories of seasonal status can be defined for Gibraltar Late Pleistocene species as follows:

- Residents: species with non-migratory populations still occurring in southern Iberia.
- Summer migrants: species presently occurring in southern Iberia *only* as summer migrants, and therefore unlikely to have been present outside this season under cooler conditions.
- Probable winterers: species that currently winter well to the north of southern Iberia and are recorded only rarely, if at all, in the Strait region at present.

Species presently wintering in the Strait region and breeding in more northerly territories are classed as indeterminate, as under conditions similar to those at present could have been wintering, or in cooler phases could have been breeding. Also regarded as indeterminate are species which may have a resident population, but also a seasonal migratory population.

Taxa falling into the categories of resident and summer migrant are of great interest, as these would have been part of the region's communities of breeding birds. As far as palaeoecological interpretation of birds is concerned, positive identification of a breeding population is the ultimate achievement for two fundamental reasons. Firstly, it establishes the seasonal status of a given species and secondly, the breeding distributions of modern species can often be more clearly defined in terms of ecological parameters than their wintering regions, therefore giving a more precise signal (e.g. Voous, 1960). Although likely breeding species can be identified on the basis of their predicted seasonal presence, including both summer migrants and residents, physical evidence is obviously preferable to informed speculation. In birds, this may be provided by the remains of juveniles or immatures, medullary bone in adult remains or even eggshells (providing they can be identified).

Some 18 species are represented by positive evidence of breeding in the Gibraltar assemblages (Table 1). Sixteen of these species still breed in southern Iberia at present, reflecting a long-term stability in the region's avifaunas. This stability is also apparent in the mammalian remains and plant macrofossils recovered from Gorham's and Vanguard Caves, which include various characteristic elements such as Spanish Ibex *Capra pyrenaica* and Olive *Olea* sp. (Currant, 2000; Gale & Carruthers, 2000).

If breeding species are ideal palaeoecological indicators, one in particular appears to provide especially strong indications of habitat and climate. Remains of the endemic Iberian subspecies of Azure-winged Magpie *Cyanopica cyanus*, have been found in both Gorham's and Vanguard Caves, including those of immature birds (Cooper, 2000b). The occurrence of *C. cyanus* is interesting for both biogeographical and palaeoecological reasons, and is a good example of the need to avoid overemphasising what could potentially be an anomalous palaeoenvironmental signal.

The modern Iberian population of *C. cyanus* is both sedentary and has fairly specific ecological preferences in terms of vegetation types and climate, suggesting that it would be an ideal source of detailed palaeoecological information (e.g. Finlayson & Pacheco, 2000). However, interpretation of this species in fact requires some careful consideration.

At present, *C. cyanus* has an extremely disjunct distribution, occurring across China, Japan and Korea, and in the Western Palearctic, only in the Iberian Peninsula, with no intervening populations. Previously, its fossil record was confined to China (Tyrberg, 1998), but its origins in Iberia as a relict rather than a recent introduction have been confirmed by the Late Pleistocene Gibraltar finds (Cooper, 2000b). Molecular evidence of the genetic divergence of the eastern and western populations have

Taxon	Status	Devil's Tower	Ibex Cave	Vanguard Cave	Gorham's Cave
Alectoris sp.	R	B/M	—	B	B
Melanitta fusca	W	—	—	—	B
Melanitta nigra	I	—	—	—	B
Gyps fulvus	I	—	—	B	—
Falco naumanni	S	B	—	B	B
Falco cf. tinnunculus	I	M	—	—	—
Columba cf. *livia*	R	—	—	—	B
Columba cf. *oenas*	I	—	—	B	—
Columba livia/oenas	I	B/M	—	B	B/M
Columba palumbus	I	—	—	B/M	—
Bubo bubo	R	—	—	—	B
cf. *Strix aluco*	R	B	—	—	—
Tachymarptis melba	S	—	—	B	—
Apus apus/pallidus	S	—	—	B	B/M
Hirundo sp.	I	—	—	B	B
Cyanopica cyanus	R	—	—	B	—
Pyrrhocorax pyrrhocorax	R	B	B	B	B
Corvus monedula	I	—	—	B	—
cf. *Corvus corone/frugilegus*	I	—	—	—	B

Table 1. Bird species in Late Pleistocene Gibraltar represented by positive evidence of breeding. R - predicted resident; S – predicted summer migrant; W – predicted winter migrant; I – indeterminate. B - presence of juvenile or immature bones; M - presence of medullary bone.

Taula 1. *Espècies d'ocells al Pleistocè tardà de Gibraltar amb evidència positiva de cria. R – resident predit; S – migrant estival predit; W – migrant hivernal predit; I – indeterminat; B – presència d'ossos immadurs o juvenils; M – presència d'os medul·lar.*

corroborated the fossil discoveries (Fok *et al.*, 2002). It seems likely that the absence of its remains from other Iberian sites may be explained in part by taphonomic biases, in that the majority of these sites do not include significant inputs from the woodland situations favoured by *C. cyanus* (Cooper, 1999, 2000b). A second possibility is that its absence from other sites is an indication of a highly restricted range within the refugium area.

Within Iberia, the species seems to have quite a narrow set of ecological preferences, but in its considerably larger eastern range, its requirements are somewhat different. It still favours open woodlands, particularly broadleaf ones, but is less restricted by climate, occurring in areas with deep winter snow (Cramp & Perrins, 1994). It is also worth noting that if *C. cyanus* once had a range across the entire Palearctic, it must have been a reasonably adaptable species. When compared with the species' overall characteristics, the more restricted preferences of the present Iberian population seem somewhat atypical. It therefore seems possible that the present Iberian population's ecological needs have been altered through isolation. The extinction of all intervening populations suggest that the species came under severe environmental pressure in its western territories,

	Devil's Tower	Ibex Cave	Vanguard Cave	Gorham's Cave
Procellaridae				
Fulmarus glacialis	—	—	1	1
Pterodroma sp.	—	—	4	31 (4)
Calonectris diomedea	8 (3)	—	—	2
Puffinus ?mauretanicus	2	—	2	3
Hydrobatidae				
Hydrobates pelagicus	—	—	1	4 (2)
Alcidae				
Pinguinis impennis	1	1	—	1
Alle alle	1	—	—	—
Uria aalge	3	—	2	—
Alca torda	1	—	2	3
Fratercula arctica	1	—	9 (2)	3

Table 2. Number of identified specimens of Petrels, Shearwaters, Storm-petrels and Auks (Families: Procellaridae, Hydrobatidae and Alcidae) in Late Pleistocene sites, Gibraltar. Figures in brackets indicate minimum number of individuals (MNI), where MNI >1

Taula 2. *Nombre d'espècimens identificats de petrells, baldritges, virots, aus de les tempestes i alques (Famílies: Procellaridae, Hydrobatidae i Alcidae) als jaciments del Pleistocè tardà de Gibraltar. Les xifres entre parèntesi indiquen el nombre mínim d'individus, quan MNI >1.*

	Devil's Tower	Ibex Cave	Vanguard Cave	Gorham's Cave
Anatidae (marine species only)				
Tadorna tadorna	—	—	—	1
cf. *Aythya fuligula*	1	—	—	1
Somateria sp.	1	—	—	2
Melanitta nigra	10 (3)	—	—	6
cf. *Melanitta nigra*	—	—	—	7
Melanitta fusca	—	—	—	3 (2)
cf. *Melanitta fusca*	—	—	—	1
Clangula hyemalis	1	—	1	19 (4)
cf. *Clangula hyemalis*	1	—	2	26 (9)
Mergus cf. *merganser*	2	—	—	—
Mergus cf. *serrator*	1	—	—	—

Table 3. Number of identified specimens of marine ducks (Family: Anatidae) in Late Pleistocene sites, Gibraltar. Figures in brackets indicate minimum number of individuals (MNI), where MNI >1.

Taula 3. *Nombre d'espècimens identificats d'ànneres marines (família: Anatidae) als jaciments del Pleistocè tardà de Gibraltar. Les xifres entre parèntesi indiquen el nombre mínim d'individus, quan MNI >1.*

leaving a small remnant population – perhaps even confined to a single refugium. The degree of isolation and environmental pressure may have had a bottleneck effect on the relict population, causing both ecological and morphological divergence from the original ancestral population. As a result, although its survival in Iberia is an indication that ecological conditions have remained within certain parameters, as once extinct it could not have re-colonised the region, it is misleading to identify those parameters too closely with the needs of the modern population (cf. Finlayson & Pacheco, 2000). Nevertheless, it can be regarded as a certain indicator of open woodlands in the Gibraltar region during the Late Pleistocene, alongside other species from the Gibraltar assemblages rarely found on Iberian sites such as *Dendrocopos ?major* and *Picus viridis* (Cooper, 1999; Cooper, 2000b). From such an example, the benefits of including ecological analogues from multiple species can be appreciated.

In the absence of positive evidence of breeding, determining seasonal status becomes more subjective. In my view, it then becomes critical to consider not only the habitat and climatic preferences of a given species, but also its behaviour; again, drawing on modern populations as analogues. Perhaps the best illustration of this can be found in the interpretation of the continental occurrence of pelagic species, i.e. birds that spend the majority of their lives at sea, normally only returning to land to breed. This is an area that has generated some controversy, with particular attention paid to the implications of Pleistocene finds of the extinct, flightless *Pinguinus impennis* (Cooper, 1997; Mourer-Chauviré, 1999; Stewart, 2002). It is a debate to which the Gibraltar assemblages can make an important contribution, as between them the four sites record one of the most diverse assemblages of pelagic species known from the Late Pleistocene. Auks (Family Alcidae) and petrels, shearwaters and storm-petrels (Families Procellaridae and Hydrobatidae) are particularly well represented, with a total of 10 species present in the sites' combined fossil record (Table 2). In addition to *P. impennis*, notable recoveries included the first Pleistocene Northern Hemisphere continental records of as yet unidentified species of gadfly petrel, *Pterodroma* sp. (Tyrberg, 1998; Cooper, 1999).

In addition to the offshore species, a range of seaducks were also recovered (Table 3). Together with certain other marine species, these constitute the most critical avian evidence of the climatic fluctuations of the Late Pleistocene. Climatic deterioration is not similarly recorded in the terrestrial avifauna; finds identified by Eastham (1968) as *Nyctea scandiaca* (Snowy Owl) have proved to be referable to *Bubo bubo* (Eurasian Eagle Owl) (Cooper, 1999).

Therefore, from a palaeoecological perspective it is extremely important to try and establish whether these northern marine species were present in breeding colonies, as this would have markedly different climatic implications than records of wintering individuals.

At the core of the debate is the proposition that pelagic species would only be available to terrestrial predators and scavengers when they return to land to breed. Therefore, it is argued, terrestrial fossil finds can be equated with former breeding distribution. In the case of *P. impennis*, this argument has been extended to implicate prehistoric humans in the disappearance of former breeding colonies on the Mediterranean and Portuguese coastlines (Mourer-Chauviré, 1999; Mourer-Chauviré & Antunes, 1991). Whether or not humans were involved, the underlying issue remains whether or not breeding colonies were present.

Most modern populations of the pelagic species represented show a marked preference for breeding on offshore islands, often in substantial colonies. Historically, this is also known to apply to *P. impennis* (Montevecchi & Kirk, 1996). This strong tendency towards isolation is in no small part the result of the vulnerability of such colonies to mammalian predators, the impacts of which are extremely well documented. Petrels and shearwaters are particularly vulnerable; *Pterodroma* species notoriously so, with a global record of many populations driven either extinct or close to it by mammalian disturbance (BirdLife, 2000, Worthy & Holdaway, 2002).

Whilst modern populations can provide direct comparisons for extant species, alternative sources are required for extinct species, such as *P. impennis*. Montevecchi & Kirk (1996) reviewed historical and Holocene archaeological evidence of *P. impennis* in the north Atlantic, but did not conclusively identify mainland breeding sites. Indeed, it was concluded that remoteness from mainland mammalian predators was one of the most important factors governing the location of the species' breeding sites. Why this should be the case, is easily demonstrated by a comparison from the Southern Hemisphere; that of the interaction of penguin rookeries with mammalian predators, as the ecologically convergent penguins are an excellent analogue for the large, flightless *P. impennis*. In both New Zealand and Australia, penguin colonies are preyed upon by cats, foxes, dogs, rats, pigs, ferrets and even goats; adults, chicks and eggs are all taken. Some colonies in farmed regions on New Zealand's South Island of *Megadyptes antipodes* (Yellow-eyed Penguin), similar in size and weight to *P. impennis*, have experienced annual chick mortality in excess of 90% due to mammalian disturbance (Marchant & Higgins, 1990). These examples refer to the impact of introduced predators on 'naïve' prey; they nevertheless serve to demonstrate the great potential vulnerability of accessible breeding colonies of large, flightless marine birds to mammalian predation. However, it may be further noted that in South Africa, breeding colonies of the endemic *Spheniscus demersus* (African Penguin), which has evolved its breeding strategies in the presence of mammalian predators, are predominantly located on offshore islands. Where predators have reached such colonies, e.g cats on Dassen Island, they represent a significant problem (del Hoyo *et al.*, 1992).

Many of the predators listed above, and others, were present in the Gibraltar region during the Late Pleistocene (Currant, 2000). Undoubtedly, accessible breeding colonies of pelagic birds would have represented a significant source of easily caught prey to Gibraltar's mammalian predators, human or otherwise. The fossil evidence of exploitation of such colonies has been found on many sites throughout New Zealand, with the bones of pelagic species present in significant quantities, including those of juveniles (Worthy & Holdaway, 2002).

The scale of archaeological New Zealand 'mutton-birding' undoubtedly surpasses what might have been possible in Late Pleistocene Europe, but does serve to demonstrate in particular what occurs when a resourceful human population encounters a ready supply of attractive prey. Another taphonomic comparison comes from Holocene archaeological sites in North America and northern Europe, where numerous remains of *P. impennis* have been found as evidence of human exploitation of offshore breeding colonies (Montevecchi & Kirk, 1996).

Within the Gibraltar sites' pelagic assemblage, each taxon is represented by only very low numbers of identified specimens and correspondingly low minimum numbers of individuals. None of the Gibraltar auks, petrels or shearwaters are represented by any juvenile or immature remains. The fossil signature of known exploitation of pelagic colonies seems a complete contrast to the pelagic fossil record found in the Gibraltar sites. Therefore, in my view, if both taphonomic and behavioural evidence are taken into account, on the basis of current evidence the Gibraltar remains cannot be interpreted as representing predation on mainland breeding colonies of auks, petrels or shearwaters and an alternative explanation should be considered.

It is noticeable that most of the marine species present are regularly found washed upon European beaches. Additionally, sea-ducks such as *Somateria mollissima* (Common Eider), *Melanitta nigra*, *M. fusca* and *Clangula hyemalis* and a variety of waders are affected by beaching and all may be found in the Gibraltar assemblages (Heubeck, 1987; Granadeiro *et al.*, 1997; Cooper, 1999). Occasionally, beached casualties may be found in considerable numbers as a wreck event, which can occur over a geographically very wide area and may be related to extreme weather conditions (Avery, 1989). Fossil remains of wrecked migrant pelagics, notably Procellaridae, have been identified from a number of dune deposits in New Zealand, though formerly some had been interpreted as evidence of breeding (Worthy & Holdaway, 2002).

If wreck events occurred in the Strait of Gibraltar during the Late Pleistocene, they would have represented important carrion bonanzas for local scavengers. Humans are also known to have exploited beached birds as a food resource (Avery & Underhill, 1986). The balance of fossil evidence, both in Gibraltar and from comparative localities, combined with behavioural habits of pelagic species strongly suggests that the remains of such birds in the Gibraltar sites represent scavenging of occasional beached carcasses.

Taking into account their modern distribution patterns, the majority of these remains are probably those of migrant birds wintering in the Strait region. However, it is clear that at least two boreal-arctic aquatic species were breeding relatively close to Gibraltar at some point during the Late Pleistocene. One tarsometatarsus each of *Melanitta nigra* and *M. fusca* were recovered from Gorham's Cave, both in a relatively late stage of fusion (Fig. 2). Though *M. nigra* is a regular winter presence in the Strait (Finlayson, 1992), the majority of both species' populations presently breed above 55ºN (Cramp & Simmons, 1977). The Gibraltar finds represent the most southerly direct evidence of breeding of *Melanitta* species, but juvenile specimens of *M. nigra* and also *Clangula hyemalis* are known from Portugal (Mourer-Chauviré & Antunes, 2000). Together, these specimens constitute irrefutable evidence of major southerly displacements in breeding distribution. The Gibraltar remains may represent breeding grounds within the Strait region, but there remains the possibility that they might have been from individuals already at sea (cf. Stewart, 2002).

However, a second tarsometatarsus from Gorham's of *M. nigra* with an unfused proximal epiphysis (Fig. 2) is strongly suggestive of breeding grounds somewhere within the immediate Gibraltar region. Unfortunately, this specimen was found in the cave's superficial sediments and its original stratigraphic and temporal context cannot be assessed.

Southerly displacement of these and other 'cold' marine species reflects regular extensions of Boreal water masses, at least in colder months, into the latitude of the Strait region, and possibly even into the western Mediterranean. Arguably, certain of these specimens may well record the impact of Heinrich Events on the avifaunas of the North Atlantic. At least four of these ice-rafting episodes are known to have occurred during the accumulation of the deposits in Gorham's and Vanguard Caves (Roucoux *et al.*, 2001). Part of the stratified immature specimen of *Melanitta nigra* was recovered from the unit underlying the base of the high-diversity unit dated by AMS radiocarbon to 51,700 ± 3,300BP (Cooper, 1999; Pettit & Bailey, 2000). This may suggest a correlation with a Heinrich Event at approximately 57,000BP (Roucoux *et al.*, 2001) but further analysis is required.

Fig. 2. Immature tarsometarsi of *Melanitta fusca* (left - 'Gor 1996, sample 276') and *Melanitta nigra* (centre - 'Gor 1996, sample 92' [proximal] and 'Gor 1995, sample 293' [distal]; right - 'Gor 1996, sample 5') from Gorham's Cave, Gibraltar. Photo: The Natural History Museum, London.

***Fig. 2.** Tarsometatarsos immadurs provinents de la cova de Gorham, Gibraltar, de* Melanitta fusca *(esquerra - 'Gor 1996, mostra 276') i* Melanitta nigra *(centre - 'Gor 1996, mostra 92' [proximal] i 'Gor 1995, mostra 293' [distal]; dret - 'Gor 1996, mostra 5'). Fotografia: The Natural History Museum, London.*

CONCLUSIONS

The Late Pleistocene avifaunas of Gibraltar are amongst the richest and most diverse avian assemblages of this age known from the Western Palearctic. The combined assemblages from the four sites investigated; Devil's Tower Rock Shelter and Ibex, Gorham's and Vanguard Caves, are characterised by a succession of generalised, superficially unchanging avifaunas, including frequent examples throughout of non-analogue species associations, both of habitat and climatic contrasts.

However, the sites appear to demonstrate relatively poor temporal resolution. Although birds could have responded rapidly to the brief, sharp climatic fluctuations known to have occurred during the accumulation of the Gibraltar assemblages, deposition at the sites could not record anything but the broadest of distributional changes. For the most part, the non-analogue associations must be regarded as taphonomic relicts.

Migration further complicates the interpretation of the Gibraltar avifaunas, as to resolve any palaeoecological signal requires some assessment of each species' seasonal status – which might have changed over time. Whilst predicting possible status by deduction can be helpful, only positive evidence of breeding can confirm a species' presence in a particular season. Identification of breeding ranges, which may be either of residents or summer migrants, must therefore be given priority.

In Gibraltar, 16 out of 18 known Late Pleistocene breeding species still breed in the region, including the endemic Iberian subspecies of *Cyanopica cyanus*, reflecting the region's role as a temperate refugium. However, even with reliable evidence of breeding, it is important not to over-emphasize the importance of any single species, such as *C. cyanus*, thus avoiding the danger of skewing interpretations with potentially anomalous ecological indications.

The stability of the terrestrial species contrasts with the presence of various boreal-arctic marine taxa throughout the assemblages, indicating the impacts of climatic fluctuations and associated oceanic changes, on the distributions of North Atlantic birds. The remaining two species represented by juvenile or immature specimens, *Melanitta nigra* and *M. fusca*, both presently breed in boreal-arctic regions, and are incontrovertible evidence of significant displacement of their breeding ranges into southerly latitudes by as yet unspecified periods of climatic deterioration. However, a tentative correlation may exist between one specimen of *M. nigra* and a Heinrich Event at approximately 57,000 BP. By contrast, remains of other pelagic and coastal species, including *Pinguinus impennis* and *Pterodroma* sp., cannot be taken as evidence of former breeding grounds. Instead, comparison of Gibraltar's fossil finds with the behaviour of modern pelagics and other fossil assemblages of such birds, strongly suggests that the Gibraltar finds represent occasional wrecks, probably of wintering individuals.

Gibraltar's location on the converging major migration routes of the Strait of Gibraltar does mean that the effects of migration on its Late Pleistocene avifaunas may be exaggerated. Each site has been influenced by a unique set of depositional processes that may or may not be similar to those encountered elsewhere. However, given that non-analogue species associations are recorded throughout Late Pleistocene assemblages in the Mediterranean and beyond, issues of interpretation raised by the Gibraltar avifaunas are certainly of wider relevance. It is apparent though, that significantly different situations do exist. Gibraltar's non-analogue associations are primarily contrasts between aquatic and terrestrial species; elsewhere non-analogue associations of only terrestrial species occur (Tyrberg, 1998). It is my view nevertheless, that any associations involving one or more species of known migratory habits must be considered with extreme caution.

Increasingly, birds are being used in modern studies as environmental indicators, and there is a growing understanding of their response to climatic change (e.g. Wernham *et al.*, 2002; Butler, 2003). This body of knowledge is a valuable resource for enhancing our understanding of the Late Pleistocene fossil record of birds, offering insights into avian behaviour that may shape future palaeornithological research. Equally, modern ornithologists should be encouraged to refer more frequently to palaeontological and archaeological works (e.g. Harrop, 2004), as remains of Late Pleistocene birds are the physical evidence of species and communities during this critical period in the biogeographic history of modern avifaunas. Only by this two-way flow of information can the full palaeoecological potential of Late Pleistocene birds be explored.

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12

THE GEOLOGICAL CONTEXT OF MIDDLE PLEISTOCENE CRATER LAKE DEPOSITS AND FOSSIL BIRDS AT ULUPAU HEAD, OAHU, HAWAIIAN ISLANDS

Paul J. HEARTY, Helen F. JAMES & Storrs L. OLSON

Alan ZIEGLER, retired vertebrate zoologist at the B. P. Bishop Museum, Honolulu, had an abiding interest in the fossil vertebrates of the Hawaiian Islands and in fostering public education about them. He made many collecting trips to Ulupau Head and personally collected hundreds of fossils there. He died 16 September 2003, on the first day of the symposium of which this volume is the proceedings. It gives us great pleasure to acknowledge his enormous contribution and to remember his many years of unstinting generosity, collegiality, and friendship.

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Resum

Els dipòsits pleistocènics llacunars del cràter Ulupau, a Oahu, contenen les restes fòssils més antigues d'ocells conegudes a les Illes Hawaïi. Aquests fòssils són importants per documentar les taxes evolutives a una varietat de línies d'ocells terrestres i aquàtics de les illes. L'anàlisi estratigràfic detallat revela diferents cicles deposicionals que comporten dipòsits llacunars interestratificats, colluvium i paleosòls. La conca volcànica va ser oberta per l'erosió marina prèvia al pic del darrer interglacial (estadi isotòpic marí, o 'MIS' 5e), fa 125 ka, restringint l'edat dels sediments del llac al Pleistocè Mitjà. Els tres cicles de deposició (Unitats III, IV i V) semblen estar estretament lligats a pujades interglacials amb una ciclicitat de 100 ka. Donada la complexitat de la successió dels sediments del cràter i el temps requerit per a la seva formació, es probable que la conca del llac s'omplís al llarg de diferents interglacials, assolint una extensió màxima de més de 50 ha durant l'estadi MIS 11, fa uns 400 ka. Aquesta és també la màxima edat probable de les capes fossilíferes més riques de la Unitat III, però no es pot excloure que siguin del MIS 9 (fa 300 ka). Els requeriments d'hàbitat probables de diferents elements de l'avifauna donen llum sobre la paleoecologia de la localitat durant el Pleistocè Mitjà.

Paraules clau: llacs de cràter volcànic, sedimentació llacunar, cicles de llacs, ocells fòssils, paleoecologia, racemització d'aminoàcids, Illes Hawaii.

Summary

Pleistocene lake deposits in Ulupau Crater on Oahu contain the oldest fossil bird remains known from the Hawaiian Islands. These fossils are important for documenting evolutionary rates in a variety of lineages of land and water birds from the islands. Detailed stratigraphic analysis reveals distinct cycles of deposition involving interbedded lacustrine deposits, colluvium, and paleosols. The volcanic basin was breached by marine erosion prior to the peak of the last interglaciation (marine isotope stage or 'MIS' 5e) over 125 ky ago, constraining the age of the lake sediments to the middle Pleistocene. The three cycles of deposition (Units III, IV, and V) appear to be closely linked with interglacial highstands with 100 ky cyclicity. Given the complexity of the succession of crater sediments and the time required for their formation, it is probable that the lake basin filled over several interglacials, reaching a maximum extent of over 50 ha during MIS 11, about 400 ky ago. This is also the likely maximum age of the richest fossil beds in Unit IV, but MIS 9 (300 ky) also remains a possibility. Probable habitat requirements of the various elements of the avifauna provide insights into the paleoecology of the site during the middle Pleistocene.

Keywords: volcanic crater lakes, lacustrine sedimentation, lake cycles, avian fossils, paleoecology, amino acid racemization, Hawaiian Islands.

INTRODUCTION

The Hawaiian Islands (Fig. 1) originated as the oceanic lithosphere of the central Pacific was perforated by a hotspot plume (Wilson, 1963). The chain of islands provides classic examples of Darwin's three-stage model of island evolution, progressing from (1) volcanic eruption, to (2) fringing reef and carbonate platform development, to (3) coral atoll. The early development of carbonate platforms is poorly documented, however, as many of these deposits are submerged, buried, or eroded on older islands, and rarely interbedded with extrusive volcanics (Hearty *et al.*, 2005). Carbonate platforms are sometimes pierced by rejuvenation (late stage) volcanoes, which may result from lithospheric flexure due to shield-

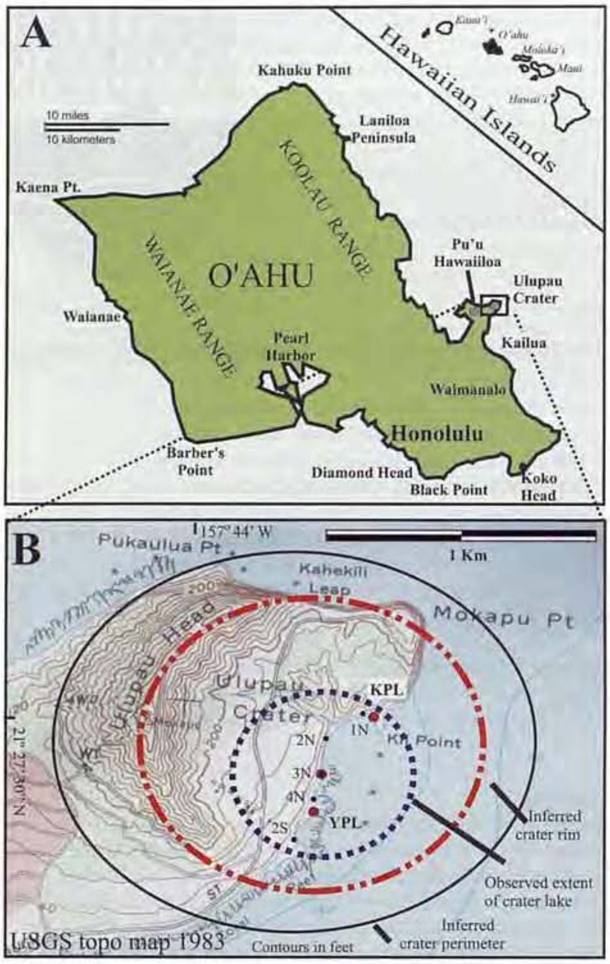


Fig. 1. A. Map of the island of Oahu showing the location of Ulupau Crater (box) and neighboring Pu'u Hawaiiloa on the Mokapu Peninsula along the northeast coast. Inset shows the position of Oahu (solid) relative to the other Hawaiian Islands. B. Topographic map of Ulupau Crater showing reconstructed crater perimeter (solid line), crater rim (red dash-dot line), and inferred area of crater lake (blue dotted line). Small black dots identify locations of the sections in the correlation diagram (Fig. 7), while larger red circles indicate key sections. KPL = Ki'i Point Limestone. YPL = Yellow Point Limestone.

Fig. 1. A. Mapa de l'illa d'Oahu on es mostra la localització del cràter Ulupau (rectangle) i el veïnat Pu'u Hawaiiloa a la Peninsula Mokapu Peninsula al llarg de la costa nord-est. El requadre mostra la posició d'Oahu (solid) respecte les altres Illes Hawaii. B. Mapa topographic del crater Ulupau que mostra el perímetre reconstruït del cràter (línia sòlida), la vorera del cràter (línia vermella de punts i ratlles), i l'àrea inferida del llac del cràter (línia de punts blava). Els punts negres petits identifiquen les localitzacions de les seccions al diagrama de correlació (Fig. 7), mentre que els cercles vermells més grans indiquen seccions clau. KPL = Ki'i Point Limestone. YPL = Yellow Point Limestone.

building eruptions over the Hawaiian hotspot to the southeast (Jackson *et al.*, 1980). After eruption, volcanic craters may host bogs, lakes, or embayments. Lakes are rare and poorly understood in the Hawaiian Islands (Maciolek, 1982) and elsewhere among the Pacific islands. The crater of Ulupau Head, a tuff cone that formed during the rejuvenation stage eruptions on Oahu, may have sustained one of the longest and largest lacustrine systems in the Hawaiian Islands. The spectacular modern crater lake Rano Kau on Rapanui or Easter Island (Fig. 2; see Flenley *et al.*, 1991) is probably a close modern analog of certain stages of development of the Ulupau crater lake. Lacustrine and colluvial sediments preserved in the crater are the source of an important assemblage of fossil birds from the Pleistocene of Oahu (Fig. 3, James, 1987).

This paper will review the complex processes that brought Ulupau Crater to its current condition, with particular attention to the formation of lakes in the crater and the occurrence of abundant avian fossils in the lacustrine and colluvial sediments (James, 1987), an aspect that was overlooked in previous geological descriptions of the crater (Stearns & Vaksvik, 1935; Wentworth & Hoffmeister, 1939). The Pleistocene bird bones from the site are a valuable resource for understanding rates of morphological evolution and species turnover in an isolated island avifauna, and providing fossil calibration points to estimate nucleotide substitution rates in avian genes. Fundamental to these research applications is a reasonably accurate knowledge of the age of the fossils.

Consequently, the overall objective of this paper is to identify constraints on the geologic age of the fossil birds through the reconstruction of the landscape evolution in and around Ulupau Head. Ancient paleoenvironments of the lake and surrounding crater are further reconstructed by inference from the habitat requirements of the birds identified in faunal assemblage.

Questions fundamental to this study include: (1) approximately when did the crater form, and how much time was required for the lacustrine and colluvial sediments to accumulate in the crater basin? (2) what geological time constraints can be implicated relative to the avian fossils contained in the lake sediments? (3) under what paleoenvironmental conditions were the fossil birds deposited? and, (4) how long ago was the crater breached, finalizing the lacustrine phase at Ulupau? Most of these questions can be addressed through interpretation of the outcrop geology, combined with new geochronologic and fossil data from the site.

EVOLUTION OF ULUPAU CRATER

Geological Setting of Ulupau Head.

Ulupau Head forms the headland of the Mokapu Peninsula along the northeast coast of Oahu (Fig. 1B) at approximately 27° 30' N Lat by 157° 44' W Long on the Marine Corps Base Hawaii at Kaneohe, about 5 km NE of the town of Kailua. After the initial shield-building phase of volcanic eruptions on Oahu (Fig. 1A), which ended c. 2 My (McDougall, 1964), the island experienced several notable geologic episodes in and around Ulupau Crater. These include carbonate platform development, rejuvenation volcanics, collapse, basin formation and lacustrine sedimentation, colluvial episodes, crater breach, and coral reef development. The remnant crater is about 1300 m in diameter, with the west rim (Ulupau Head) rising to about 210 m. The Ulupau Head tuff cone is one of several dozen "rejuvenation" volcanoes on Oahu, referred to as the Honolulu Volcanic Series (HVS). Two previous studies of K-Ar dates from the HVS vents have con-

Fig. 2. Photograph of Rano Kau on Rapanui (Easter Island), a possible analog for one stage in the development and ultimate breaching of Ulupau Lake Crater. Depths are generally 5-10 m, while floating vegetation mats cover the lake surface. The eastern wall of the crater (right of photo) is near the point of breaching.

Fig. 2. Fotografia de Rano Kau a Rapanui (Illa de Pàsqua), un possible anàleg per a un estadi en el desenvolupament i trencament final del cràter Ulupau. Les profunditats són generalment 5-10 m, mentre que tapisos de vegetació flotant cobreixen la superfície del llac. La paret oriental del cràter (a la dreta de la foto) es troba a prop del punt de trencament.

cluded that this post-shield-building explosive volcanic phase on Oahu took place after 0.8 to 0.6 My, although the picture is clouded by several older K/Ar readings that are rejected by the original authors due to contamination by xenoliths apparently containing excess argon (Gramlich *et al.*, 1971; Lanphere & Dalrymple, 1980). The accepted dates on the HVS correlate roughly with the period of major shield building on the island of Hawaii (<0.6 My, in Macdonald *et al.*, 1983), which apparently caused lithospheric flexure beneath Oahu. Lithospheric flexure and fracturing are thought to be closely linked to the fundamental causes of rejuvenation volcanic activity (Jackson *et al.*, 1980). Carbonate platforms must have been forming between the shield-building and rejuvenation intervals of volcanism, as blocks and fragments of marine limestones are common in tuff cones around Oahu (Wentworth & Hoffmeister, 1939; Stearns, 1978). These limestone traces are evidence of HVS eruptions penetrating through carbonate deposits.

After its formation, Ulupau Crater intermittently filled with either fresh, salt, or a mixture of waters, and accumulated both colluvial and lacustrine deposits below and well above present sea level. Soils formed on these deposits during periods of stability. At its maximum size, the crater may have held a lake of up to 50-60 ha, by far the largest lake known in the Hawaiian Islands. Subsequently, the eastern half of the crater wall and lake sediments were removed, forming a sea cliff against which coral reefs of last interglacial age formed (Muhs & Szabo, 1994; Szabo *et al.*, 1994).

Fig. 3. Middle Pleistocene bird bones from Ulupau Head, Oahu, lake deposits, Unit IVa. **A.** Humerus of a small duck *Anas* aff. *wyvillia-na/laysanensis*, BPBM 178731. **B.** Maxilla of the large extinct finch *Chloridops regiskongi*, USNM 528523. **C.** Coracoid of a goose *Branta* sp., BPBM 159074. **D.** Tarsometatarsus of the extinct flightless waterfowl *Thambetochen xanion*, BPBM 159751. **E.** Tarsometatarsus of a hawk *Buteo* sp., USNM 394270. **F.** Ulna of an extinct crow, *Corvus* sp. USNM 528524.

Fig. 3. Ossos d'ocells fòssils del Pleistocè Mitjà provinents d'Ulupau Head, Oahu, sediments llacunars, Unitat IVa. **A.** *Húmer d'un ànnere petit* Anas *aff.* wyvilliana/laysanensis, *BPBM 178731.* **B.** *Maxil·lar del gran pinçà extingit* Chloridops regiskongi, *USNM 528523.* **C.** *Coracoid d'una oca* Branta *sp., BPBM 159074.* **D.** *Tarsometatars de l'oca avoladora extingida* Thambetochen xanion, *BPBM 159751.* **E.** *Tarsometatars d'un aligot* Buteo *sp., USNM 394270.* **F.** *Ulna d'un corb extingit,* Corvus *sp. USNM 528524.*

Post-Shield Building and Pre-eruption Phases at Ulupau

Shield building took place at different times in western and eastern Oahu. Buildup of the Waianae western shield volcano occurred between about 3.5 and 2.5 My, while the eastern Koolau volcano developed somewhat later between about 2.5 and 1.8 My (McDougall, 1964). The shield-building phases of Oahu (Waianae and Koolau Volcanic Series) ended around 1.8 My. Carbonates presumably began to accumulate soon after, leaving at least 1 My of the early and middle Pleistocene for carbonate platforms to form before the eruptive phase of the HVS. Although many carbonate and reef deposits are known from Oahu (Stearns, 1978), most of them date from middle and late Pleistocene intervals (Ku *et al.*, 1974; Szabo *et al.*, 1994; Muhs & Szabo, 1994; Hearty *et al.*, 2000). Exposed early Pleistocene platform remnants are known only from southeastern Kauai (Hearty *et al.*, in press).

Eruption

Ulupau Head is a tuff cone formed by hydromagmatic eruptions near sea level (Stearns in Macdonald *et al.*, 1983), inferring synchrony with an interglacial highstand of sea level. The tuffs overlie nephelinite lava flows from Pu'u Hawaiiloa (a neighboring tuff cone, Fig. 1), which is thus older than Ulupau. Pu'u Hawaiiloa is terraced at 30 m above present sea level (noted as "+30 m"), probably equating with the Kaena Highstand (Stearns, 1978), which is interpreted to have occurred during MIS 11, around 400 ky (Hearty, 2002a). Because of the K/Ar age uncertainty created by the volcanics contaminated with xenoliths of the area (Gramlich *et al.*, 1971; Lanphere & Dalrymple, 1980) the Ulupau tuff has not been directly dated, and it is only possible to infer the age of crater formation. Assuming the lake developed penecontemporaneously with the development of the volcanic basin, crater formation probably occurred toward the end of the period between about 0.6 and 0.4 My.

The Ki'i Point Limestone and the Ulupau Eruption

Near the center of the original Ulupau basin (Fig. 1B, 4) are two isolated and discontinuous outcrops of carbonate rock whose stratigraphic position and relative ages are perplexing. These two fossiliferous limestones are sedimentologically distinct and are comparable only in their high-angle bedding dipping inward toward the ancient center of the crater.

The Ki'i Point Limestone (KPL; Fig. 4A, B) is an *in situ* oyster (*Ostrea hanleyana* Sowerby) and barnacle reef with a matrix of fine-grained, parallel-bedded carbonate marl, interbedded with diatom ooze, carbonate silt and minor volcanics. The bedding dips southward at between 25º and 35º. Wentworth & Hoffmeister (1939) describe an overlying "calcareous sandstone composed of beach detritus", but we did not observe a distinct unit of this description (collapse is evident and frequent at the site).

The Yellow Point Limestone (our name, or YPL; Fig. 4C), was considered part of the Ki'i Point Formation by Wentworth & Hoffmeister (1939) despite the fact there are few similarities between the units. The YPL is a coarse-grained foraminiferal carbonate sand, containing <25% volcanics. The deposits contain large coral and well-rounded volcanic tuff fragments, and nearshore hard-substrate-associated fossils (limpets, top shells, etc). Considering the large clasts and littoral marine fossils, the YPL was probably deposited in a nearshore, moderate to high energy, shallow, subtidal sandy environment, in proximity of rocky outcrops. A rib of a small whale (*Globicephala* sp.) was also found within the YPL (Wentworth & Hoffmeister, 1939) confirming a connection of this unit with the open ocean.

Either or both of these limestone units were formed (1) as part of carbonate platforms previous to the eruption of Ulupau Crater and were subsequently rotated and incorporated into the volcanic mass; or (2) during the initial stages of volcanic eruption, and are nearly in place, with minor displacement, perhaps caused by collapse of the caldera. Stearns & Vaksvik (1935) and Wentworth & Hoffmeister (1939) concluded that the KPL and YPL were formed in place within Ulupau Crater. Without question, however, they predate and are succeeded by lake sediments.

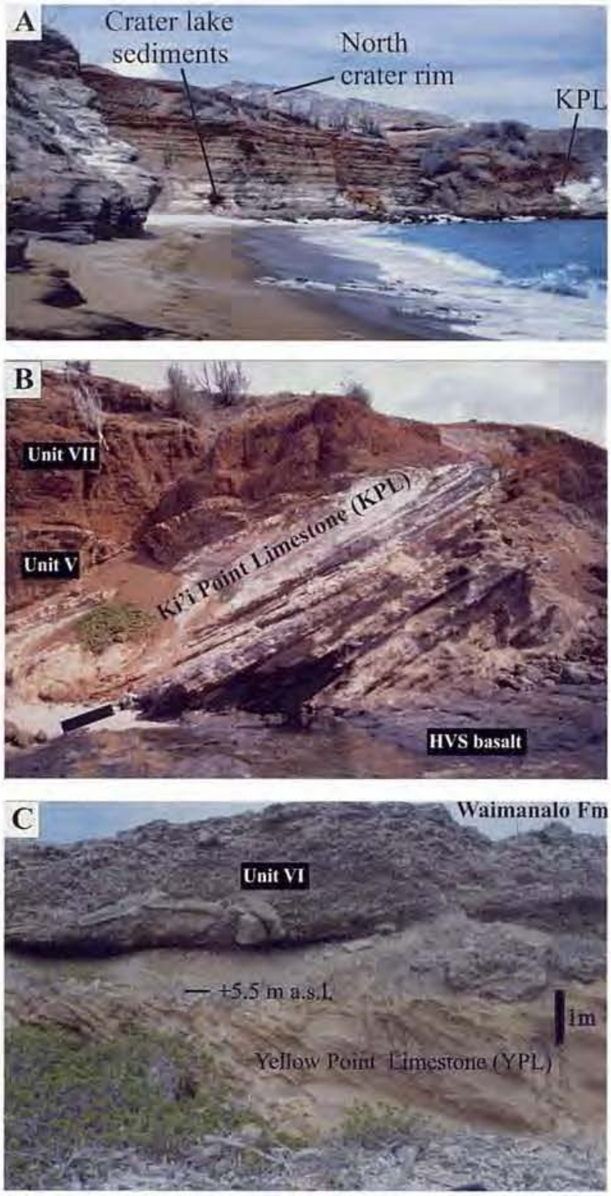


Fig. 4. Photographs of sea cliff and lake sediments at Ulupau Crater. A. View of crater rim in background and lake sediments in mid and foreground. B. Detail of the Ki'i Point Limestone and adjacent lake-filling colluvial units. C. Detail of the Yellow Point Limestone and overlying Waimanalo Fm conglomerate and reef.

Fig. 4. Fotografies del penya-segat mari i dels sediments llacunars del cràter Ulupau. A. Vista de la vorera del cràter a darrera i dels sediments llacunars enmig i a davant. B. Detall del Ki'i Point Limestone i unitats col·luvials adjacents que rebleixen el llac. C. Detall del Yellow Point Limestone i el conglomerat i esculls de la formació Waimanalo que el cobreixen.

Lake Formation and Sedimentation

Lake Depositional Model

Maciolek (1982) identified three types of lakes in the Hawaiian Islands: (1) high altitude (elevations are 2040 m for Wai'ele'ele, and 3969 m for Waiau) perched aquifers; (2) salt lakes or ponds in topographic depressions adjacent to the sea, and receiving a regular supply of marine phreatic water; and (3) fresh to salt water lakes or embay-

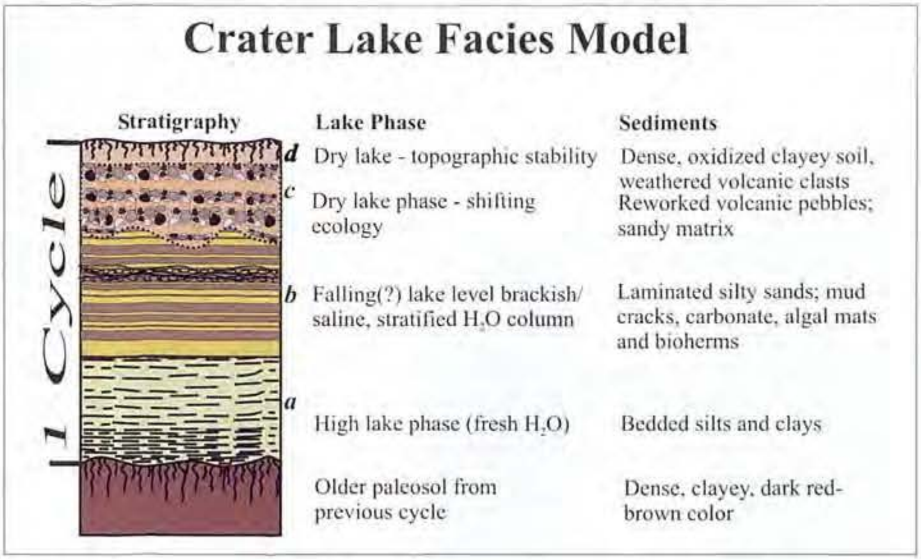


Fig. 5. Crater lake facies model. Units reflect a cyclical sedimentation progressing from (a) high fresh lake; (b) high saline lake; (c) dry lake with erosion and deposition of colluvium (shifting ecology); and (d) dry lake with topographic stability (forested?) and soil development.

Fig. 5. Model de fàcies llacunar a un cràter. Les unitats reflecteixen una sedimentació cíclica progressant des de (a) un llac d'aigua dolça alt; (b) un llac salí alt; (c) un llac sec amb erosió i deposició de col·luvium (ecologia canviant); i (d) un llac sec amb una estabilitat topogràfica (forestal?) i amb desenvolupament de sòl.

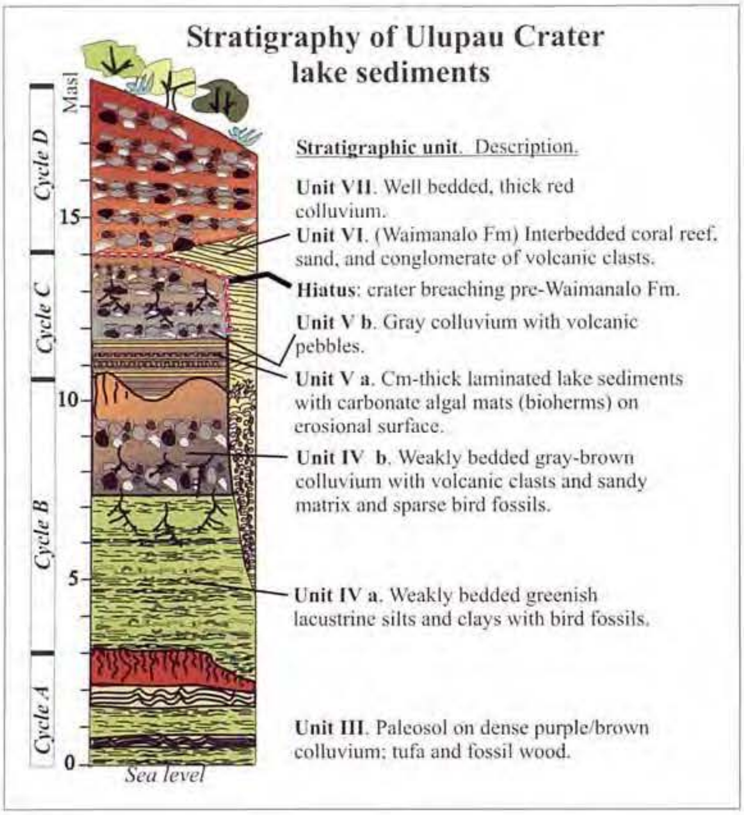
ments in craters lying at or near the sea, with the local or regional groundwater table dictated by sea level. Ulupau Crater would fall in the last category. Because of the permeable nature of the volcanic tuff, it would be unlikely that a lake at Ulupau could be perched at an elevation significantly above sea level. There are no perched lakes at lower elevations anywhere in the Hawaiian Islands today. Therefore it is reasonable to assume that rising and falling sea levels would have dominated the hydrology of the Ulupau crater lakes, and that such lakes would tend to fill the crater basin during stable highstands.

It is possible to infer some of the conditions in the lakes of Ulupau Crater by comparision with Wai a Pele (or Green Lake), currently the largest freshwater lake in Hawaii, located 2 km inland of Cape Kumukahi in a windward position on the easternmost point of the Big Island of Hawaii. The lake, which occupies the inactive Kapoho Crater, is about a hectare in area, over 6 m deep, and rises to an elevation of about +1 m (Maciolek, 1982). Wai a Pele occurs in an area of moderate precipitation (250 cm per yr), and has a dissolved mineral content of 300 mg per liter. The lake is stratified between 22º and 25ºC, and becomes anoxic at a thermocline about 3 m deep. The hydrologic stratification persists most of the year, turning over with cooler winter temperatures. We assume that the Ulupau lakes may have operated similarly in the earlier stages of development of the basin. Later stages of development in Ulupau basin may have resembled Rano Kau on Rapanui (Fig. 2), which currently supports a 8-m-deep lake with floating vegetal mats, and is near the point of breaching on its southern rim (right of photo in Fig. 2).

Lake and Colluvial Sedimentation in Ulupau Crater

Despite the limitations of the geochronological methods and less than optimal sample material, it is still possible to understand the history of basin filling in Ulupau Crater by interpretation of the exquisite exposures in the cliffs. Furthermore, we recognize and have dated various sea-level highstands from the Hawaiian Islands (e.g., Hearty *et al.*, 2000; Hearty, 2002a), and seek to correlate them with high lake stands. With these considerations, we developed a facies model representing the major elements of crater basin sedimentation (Fig. 5) based on an extensive survey of the strata exposed in Ulupau Crater. The stratigraphic evidence indicates rapidly shifting and diverse environments of deposition within the crater. The sediments indicate deposition in fresh, salt, and mixed lake waters, with significant fluxes of colluvium on slopes during unstable (thinly vegetated?) intervals, and stable intervals of soil formation. Analyses have identified four main types of sediments (as per Fig. 5): ***(a)*** massive or weakly stratified, fissile and compact greenish (reduced anoxic conditions?) silts and clays = high fresh water lake phase, anoxic with depth; sea-level highstand, but sufficiently separated by stratigraphic barriers to influence, but not dominate the lake water chemistry. The presence of abundant carbonate sediments and rocks in the KPL and YPL as well in pre-existing carbonate platform beneath the crater, would have provided ample buffering in the subsequent lake sediments; ***(b)*** laminated and oxidized silty sands with carbonate bioherms = high level anoxic lake with input of marine groundwater; ***(c)*** volcanic colluvium = low sea level; no lake, and unstable crater landscape and slope wash due to shifting plant ecology; and ***(d)*** dense, oxidized soil development = stable landscape; vegetated, perhaps forested. It appears that the deposition of these types of sediments occurred in a *cyclical* succession from lacustrine sediment, to colluvium, to soil.

A representative stratigraphic section logged from near the center of the Ulupau Crater basin (Section OKP3N, Fig. 6) contains a variety of sediment types and sedimentary structures related to different processes. This section has been subdivided into units from the base to the top of the section. Five units (III to VII) have been identified within OKP3N and adjacent sections (Fig. 7). Each of the units contains facies variations and subunits, indicative of changing environments within larger sedimentary cycles. Some subunits are missing locally due to topographic irregularities in the basin. In all crater-filling units, colluvial beds become finer and thinner toward the center of the basin, while lake sediments are thickest in



Stratigraphic unit. Description.

Unit VII. Well bedded, thick red colluvium.

Unit VI. (Waimanalo Fm) Interbedded coral reef, sand, and conglomerate of volcanic clasts.

Hiatus: crater breaching pre-Waimanalo Fm.

Unit V b. Gray colluvium with volcanic pebbles.

Unit V a. Cm-thick laminated lake sediments with carbonate algal mats (bioherms) on erosional surface.

Unit IV b. Weakly bedded gray-brown colluvium with volcanic clasts and sandy matrix and sparse bird fossils.

Unit IV a. Weakly bedded greenish lacustrine silts and clays with bird fossils.

Unit III. Paleosol on dense purple/brown colluvium; tufa and fossil wood.

Fig. 6. Interpretation of representative stratigraphy of lake sediments (Section OKP3N) in Ulupau Crater illustrating three cycles of lake deposition. The earliest lake level was near present sea level (Unit III), followed by a deep-lake phase over +15 m (Unit IV), and a final high lake phase (Unit Va) to around +12 m. Removal of the eastern rim and breaching of the crater wall occurred previous to MIS 5e. Unit VII (Cycle D) represents only a colluvial cycle as no lake sediments are present.

Fig. 6. Interpretació de l'estratigrafia representativa dels sediments llacunars (Secció OKP3N) al cràter Ulupau, il·lustrant tres cicles de deposició llacunar. El nivell llacunar més primerenc estava a prop del nivell marí actual (Unitat III), va ser seguit per una fase llacunar fonda a devers +15 m (Unitat IV), i una fase final de llac alt (Unitat Va) a devers +12m. La substracció de la vorera oriental i el trencament de la paret del cràter va ocórrer abans del MIS 5e. La Unitat VII (Cicle D) representa només un cicle col·luvial ja que no s'hi troben sediments llacunars.

the center of the basin, and thin laterally (Fig. 7). Facies transitions (lake to colluvial) are generally conformable with the exception of minor cut and fill probably associated with the development of small gullies within the basin formed during heavy rainfall events.

1. *Unit III, 1st lake, colluvial, and pedogenic cycle.* The lowest deposit exposed in the crater is Unit III, which, along with Units IV and V, onlap the Ki'i Point Limestone in angular unconformity (Fig. 4B). Subunit IIIa is a dense clayey colluvium, interbedded with tufa beds (IIIb). The colluvium thickens considerably in more northerly sections. The tufa beds on the southern edge of the lake basin expose organic structures (root traces and algal mat) as well as fossil wood. The succession of deposits is capped by a dense, dusky-red mature clayey paleosol found across the basin (Figs. 7 and 8). The lower beds exhibit short-term switching of lake and colluvial deposition, perhaps indicating the waning phases of the crater lake. This cycle of deposition is marked by a substantial, well-developed paleosol suggesting an extended interval of topographic and ecologic stability, perhaps under forest cover.

2. *Unit IV, 2nd lake and colluvial cycle.* This comprises two subunits, with Subunit IVa consisting of lake sediments. Its five meters of green to buff colored silts and clays form Subunit IVa and the base of the second cycle of lake deposition. There is weak, compact, fissile bedding but no profound visual lamination of the sediments. Thin lenses of pebbles and some whitish hardpans are observed. Before compaction, the sediments of Unit IVa may have been considerably thicker, indicating a much greater height of the lake level during deposition, than indicated by their current height of +7 to +8 m.

Unit IVa contains bones of seabirds, shorebirds, waterbirds, land birds, and bats, but few other macrofossils (James, 1987). Because abundant bird bones are preserved in the unit, it is evident that the pH of the lake was sufficiently basic to prevent their dissolution, so the lake waters apparently were buffered either by marine phreatic groundwater leaking through the crater walls, or by the influence of carbonates within and beneath volcanic tuff. Root traces are observed in the uppermost beds penetrating the lacustrine unit, indicating growth of vegetation probably in the overlying colluvial deposit. The uppermost beds of Subunit IVa grade conformably to the overlying colluvium.

The sediments of Subunit IVb are composed of alternating lenses of weakly to strongly bedded, very coarse volcanic breccia and medium sand and pebble textures. Fossil bird bones occur in this subunit but are less common than in subunit IVa. Trace fossils of root structures are abundant throughout this subunit and extend into the lower subunit. At OKP3N, the upper contact of the colluvial unit exposes an undulating surface showing scouring and removal by erosion. Although absent in this section, a moderately-developed paleosol capping IVb is observed in more northerly sections OKP1N and OKP2N (Figs. 7 and 8).

Deep lake levels persisted over a considerable time period during the deposition of Subunit IVa. The 5 m of tightly compacted sediment may represent a much grea-

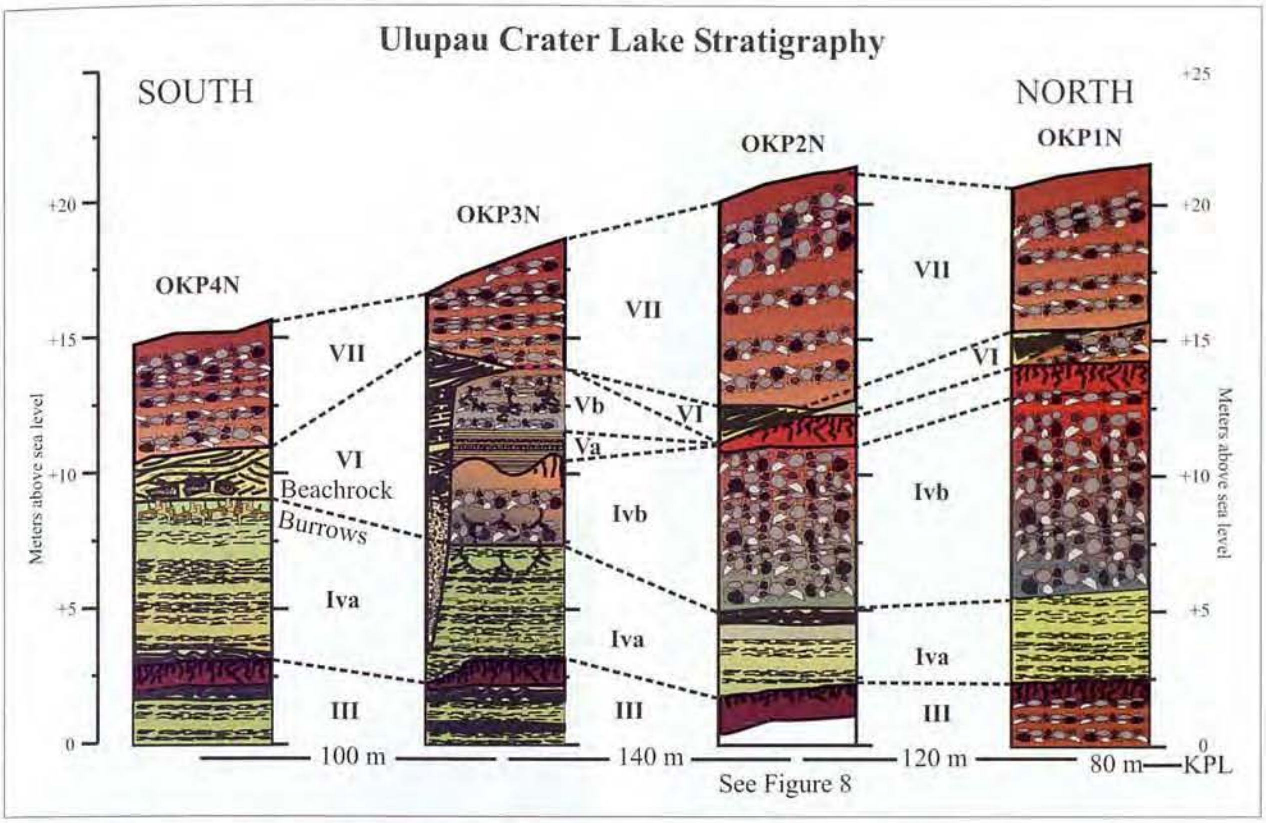


Fig. 7. Correlation of four logged stratigraphic sections in lake sediments of Ulupau Crater. The sections transit the lake exposure from north to south, representing most of the existing strata and units.

Fig. 7. Correlació de quatre seccions estratigràfiques en columna dels sediments llacunars del cràter Ulupau. Les seccions recorren l'exposició del llac de nord a sud, representant la majoria d'estrats i unitats existents.

ter original thickness (perhaps double), and thus significantly higher elevation of the lake level of perhaps between +15 to +20 m. A stratified water column and generally anoxic conditions produced a reducing environment. It is reasonable to assume that anoxia occurred at similar depths of ~3 m as in the modern Wai a Pele. The area attracted abundant bird life, whose fossil remains accumulated primarily in the lake sediments in Unit IVa, and less so in the colluvium of Unit IVb. The presence of root casts indicates termination of the lake phase, growth of vegetation, and ecological transition from the high lake to dry lake and colluvial phases. Colluvial Subunit IVb represents a major depositional event within the crater walls. It is apparent that lake levels fell quickly, after which there was rapid flux of colluvial debris from the flanks, thinning near the center of the crater. According to our model, this transition occurred at the onset of a glacial period as sea level fell. Rapid drying of the lake accompanied marine regression, which lowered the level of the Ghyben-Herzberg lens, so that the crater no longer functioned as a hydrographic window.

3. *Unit V, 3rd lacustrine phase and colluvium.* Subunit Va overlies an erosional contact and is characterized by thinly-laminated silty and clayey layers averaging about 5 mm thick (Fig. 9A) and rising to about +10 to +12 m. These lake facies are present only near the center of the basin at OKP3N (Figs. 6 and 7). The laminations contain lenses and intercalations of carbonate algal structures and desiccation cracks (Figs. 9B and 9C). A sample of the algal material has been dated by the ICPMS U/Th method (discussed below). A red oxidation stain fills an irregular and undulating zone in the upper 1 to 2 m of the unit. The laminated lake sediments make a conformable and thinly-interbedded transition to the overlying colluvial unit.

The grey colluvium of Subunit Vb is 2 to 3 m thick and gray in color. The deposits are moderately to strongly bedded and contain multiple-cm thick lenses of pebbles.

The laminations in Unit Va indicate stratified anoxic (brackish?) water ranging from dry (mudcracks) to ca. 2 m deep. Unit Va is absent from OKP1N, 2N, and 4N logs (Fig. 7), indicating that the lake was much smaller than during Unit IVa, as the basin had largely filled with sediments from previous higher highstands. The clast-supported coarser sediments would have been compacted less than the matrix-supported silts and clays of Unit IV. Because of their carbonate composition, the algal mats may have formed by the leakage of marine phreatic water through the perhaps thinning eastern crater wall. Further support of this inference comes from the reddening by oxidation of the volcanic minerals in Unit Va. This may indicate that the sediments, rich in ferric minerals, were initially deposited in a reducing lake environment (deeper water), and subsequently exposed to marine waters and occasional desiccation. This partial marine incursion by percolation or piping may have also contributed to the sustained higher pH of the groundwaters in the crater.

CRATER BREACHING AND SUBSEQUENT EROSIONAL AND DEPOSITIONAL EVENTS

Crater Breaching

1. *Premises and givens.* A high eastern rim of Ulupau Crater must have been present in order for the lake sediments to accumulate to nearly +20 m thickness. Assuming a circular or slightly oblong crater geometry, as inferred from the remaining structure (Fig. 1), and similarly shaped HVS volcanoes of Oahu, it is possible to estimate that between 300 and 500 m of horizontal erosion from the eastern flank has taken place. Holocene and recent erosion would account for only a fraction of the removal. The existing sea cliff exposes lake sediments for approximately 0.5 km along a N-S axis. Coral reef, shore and marine conglomerate of the Waimanalo Fm abut the sea cliff (Fig. 10) and armor it from erosion, particularly along the southern part of the crater. Once reef deposits are removed, however, erosion of the friable lake sediment occurs quickly, as observed along more northerly reaches of the coastline.

2. *Interpretation of timing of crater breaching events.* At some point in Oahu's history, an enormous landslide ripped a major portion of the island away from the northeastern coast, leaving a dramatic headwall, the Nuuanu Pali. The "Nuuanu Debris Avalanche" was one of the most massive of the submarine slides described in the Hawaiian Islands by Moore *et al.* (1989), covering 23,000 km^2, and extending about 230 km from the headwall on Oahu across the Hawaiian Deep (depth 4600 m) and up the opposite rising flank. Those authors propose that the largest and most extended slides occurred during "the final stages of the shield building cycle when volcanic production peaks" (Moore *et al.*, 1989, p. 17,482), probably around 2.5 My ago. Thus, the entire HVS, coastal plain development, and carbonate platform construction, and breaching of Ulupau Crater all most likely occurred subsequent to the Nuuanu Debris Avalanche.

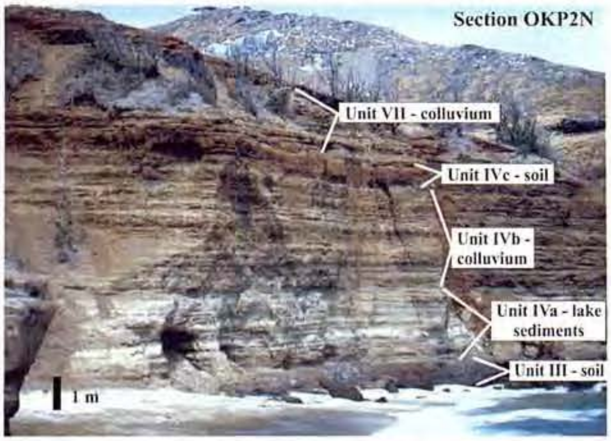


Fig. 8. Photograph of OKP2N (noted as "2N" on Fig. 1) showing a full cycle of deposition (paleosol → lake sediments → colluvium → paleosol).

Fig. 8. *Fotografia de OKP2N (indicat com a "2N" a la Fig. 1) que mostra un cicle complet de deposició (paleosòl → sediments llacunars → col·luvium → paleosòl).*

The modern shelf, about 6 km wide (to 100 m depth) east of Ulupau Crater, is intact and does not indicate any bathymetric evidence of mass wasting. Relatively shallow platform and islands surround Ulupau Head on all sides (Fig. 1), additional evidence that no significant mass wasting events have affected the peninsula during the latter part of the Quaternary. Inspection of USGS Pacific Seafloor Mapping shaded relief and backscatter images of the ocean floor east of Ulupau Head (http://wrgis.wr.usgs.gov/dds/dds-55/pacmaps/ou) provides further confirmation of this view.

Removal of one-third to one-half of the crater diameter (300 - 500 m) of Ulupau Crater and exposure of lacustrine beds must have occurred prior to the deposi-

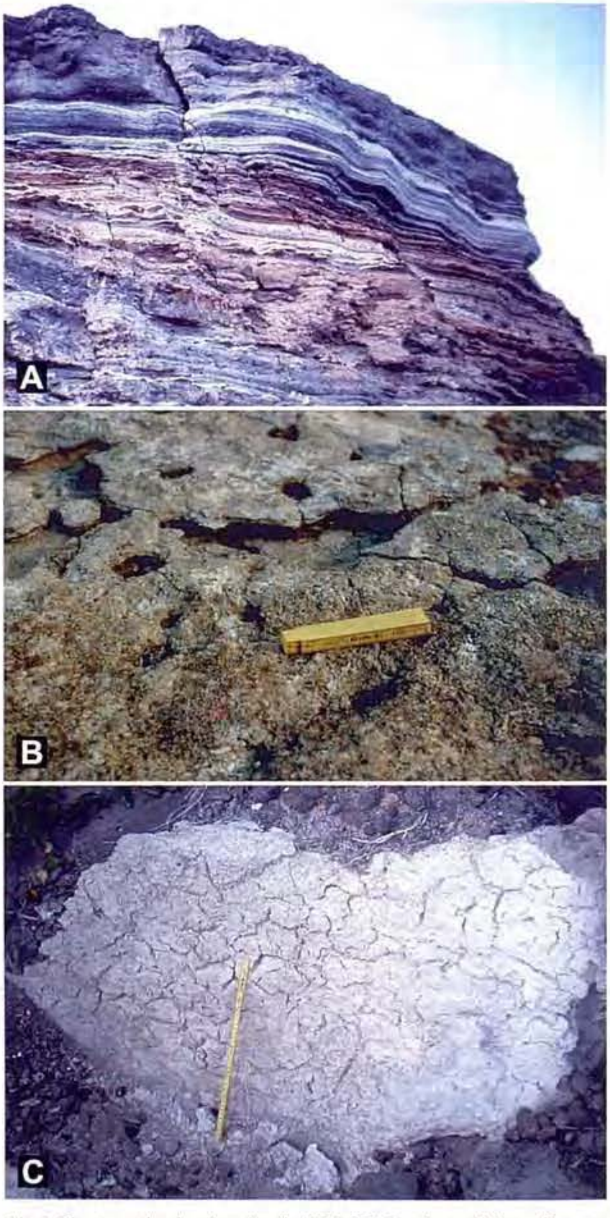


Fig. 9. Photographs showing detail of Unit V. **A.** Laminated lake sediments and colluvium. **B.** Carbonate algal mat (dated at 240 ± 10 ka by U/Th). **C.** Mud cracks in algal mat in Unit V.

Fig. 9. *Fotografies que mostren detalls de la Unitat V.* ***A.*** *Sediments llacunars laminats i col·luvium.* ***B.*** *Tapís algal carbonatat (datat a 240 ± 10 ka by U/Th).* ***C.*** *Crulls de fang a el tapís algal a la Unitat V.*

tion of the Waimanalo Fm. Wave erosion would require a long period of time to accomplish this work, while large-scale mass wasting could have effectively removed the material very quickly. Opportunities for removal by marine erosion occurred during highstands post-dating the formation of the crater 0.3 to 0.5 My and preceding MIS 5e. The most likely highstands involved in erosion of the Ulupau crater wall would thus have been MIS 11, 9, and 7. Removal of the eastern rim and lake sediments by marine erosion may have taken more than one interglacial (>100 ka). Within the lake sequence, the removal of the eastern rim is represented by a major angular unconformity between Units III, IV and V, and Unit VI the Waimanalo Fm (Figs. 4B and 10). Vertical reef growth and accumulation of sediments built a wall plastered against sub-horizontal lake beds (Fig. 8).

Unit VI, Waimanalo Erosion and Marine Highstand Cycle

A coral reef (Waimanalo Fm) and cemented sediments abut directly against a sea cliff eroded in Ulupau lake sediments (Units IV and V) in the southern part of the study area (Fig. 10). Unit VI consists of laterally discontinuous lenticular geometry of coral reef, coral rubble, volcanic conglomerate facies with some fossil mollusk and calcareous algae, marine sands, and minor eolian deposits. Our new MC-ICPMS U/Th ages on corals from this unit range in age from 131 to 115 ka (Table 3), largely in agreement with previous U-series determinations (Szabo *et al.*, 1994; Muhs & Szabo, 1994). Coral reefs rise to +5 and +8.5 m, while marine subtidal sands are present to +11 m (Hearty *et al.*, 2000). The Waimanalo deposits are succeeded by Unit VII. Remnants of the bioconstructional coral reef and shore deposits still remain along the sea cliff, indicating that Holocene events have removed only a small fraction of the lake deposits over the past 6,000 to 7,000 years (see below). A flat shelf surface at less than 6 m below sea level c. 200 to 300 m wide (USGS 1:24,000 topographic maps) east of Ulupau Crater, marks the extent of what is probably the cumulative erosion from both MIS 5 and 1.

Unit VII – Final Colluvial/Alluvial Phase

Subunit VIIa is an accumulation of more than 10 m (over 20 m in places) of interbedded fine to coarse colluvium. Throughout the crater, these deposits are oxidized to a reddish brown color (Fig. 4B). The red colluvium slopes at low angles <10° to the east in amphitheater form within the existing half of the Ulupau Crater. This unit buries all previous sediments except in the modern sea cliff. This final phase of sedimentation occurred after the Waimanalo highstand, and may be active up to the present. Multiple weak soils (Subunit VIIb) are interbedded within the unit, with greater soil development near the top of the unit.

It appears that this major colluvial event was initiated soon after the Waimanalo highstand, and continued throughout the following glacial lowstands (MIS 4 to 2) and into the Holocene. Most of this sediment flux could probably be attributed to ecological disturbance in the transition between wetter interglacial vegetation and more xeric types during glacial periods (Hotchkiss et al., 2000). The degree of influence of anthropogenic changes in plant cover on the sediment flux is unknown, but by analogy with other Hawaiian basins, this could have been a significant source of colluvial flux (Burney *et al.*, 2001; Burney, 2002).

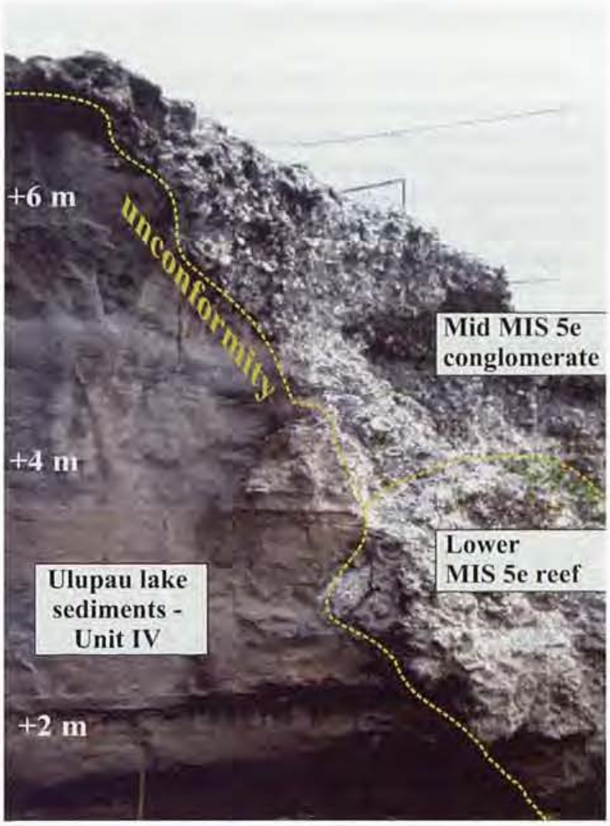


Fig. 10. Detailed stratigraphic log of the Waimanalo Fm plastered against the Ulupau Crater lake sediments at OKP2 (section 2 in Fig. 1). The section shows lake sediments adjacent to a near vertical plaster of reef/conglomerate-reef of Waimanalo age (134 to 118 ky). Between 300 and 500 m of crater wall and lake sediments were removed from the eastern margin of Ulupau Crater *previous to initiation* of deposition of Waimanalo deposits.

Fig. 10. *Columna estratigràfica detallada de la Formació Waimanalo enfront dels sediments llacunars del cràter Ulupau a OKP2 (secció 2 a la Fig. 1). La secció mostra els sediments llacunars adjacents a un pegat quasi vertical de escull/conglomerat-escull d'edat Waimanalo (134 a 118 ka). Entre 300 i 500 m de la paret del cràter i sediments llacunars varen ser trets de la vorera oriental del cràter Ulupau* abans de començar *la deposició dels dipòsits Waimanalo.*

APPARENT AGE OF ULUPAU LAKE SEDIMENTS, CARBONATES, AND FOSSILS

The isotope curve from ODP Site 677 (Shackleton *et al.*, 1990) provides a template and time frame for the geological events and evolution of Ulupau Crater over the past half-million years (Fig. 11). The curve also serves as a *relative* sea level indicator based largely on ice volume changes. *Measured* sea-level highstands from stable carbonate platforms (Hearty & Kaufman, 2000) are compared to those of Oahu (Hearty *et al.*, 2000; Hearty, 2002b) over the past half-million years, the interval when high lake stands occurred (Table 1).

Age Sequence of Ulupau Crater

No direct dating of Ulupau volcanics has been successful (Gramlich *et al.*, 1971; Lanphere & Dalrymple, 1980). Based on the extent of weathering and erosion, Winchell (1947) concluded that Ulupau Crater and neighboring Pu'u Hawaiiola were among the oldest of the HVS, perhaps approaching 0.6 My. Amino acid racemization (AAR) analyses of whole-rock carbonate sand from the YPL and oysters from the KPL indicate ages between 0.3 and 0.6 My (Table 2). The equilibrium ratio from the KPL (A/I = 1.30 ± 0.03) is beyond the range of age calculation by apparent parabolic kinetics (Mitterer & Kriausakul, 1989). It thus constrains a *minimum* age of 0.4 to 0.6 My. The estimated age of the whole-rock sample from the YPL, determined from A/I = 0.80 ± 0.09, is between 0.3 and 0.5 My. In summary, the AAR data from the KPL and YPL, which are stratigraphically older than lake sediments of Units III to V, give a general estimate of lake sedimentation beginning somewhere between 0.3 and 0.5 My. These independent age estimates fit well with the succession of events interpreted from the physical geology of Ulupau crater.

Based on the complexity and time-requirements for formation and development of the units (particularly deep paleosols), the lack of "perched" low-elevation lakes in Hawaii, and probable modulation by sea-level highstands, we suggest that lake cycles are tied to 100 ka sea-level cycles (Fig. 11). The dense and well-developed capping paleosol and complex stratigraphy of Unit III supports a significant length of time of development, far more than could be accomplished during shorter obliquity or precession cycles (20-40 ka duration). Likewise, the >5 m accumulation of fine silts in Sub-unit IVa, source of the greatest concentration of bird fossils, alone must encompass a significant interval of time. We suggest up to 25 ka for this unit to form.

Given that the 125 ka Waimanalo reef abuts a cliff of lake sediments located midway across the lake basin (Fig.10), and the estimated maximum age of the crater, all of the lake sediments must be of middle Pleistocene age. Based on the complex stratigraphy, including three lake phases, three colluvial phases, and well-developed paleosols between, the duration of the entire lake sequence must have encompassed multiple sea-level cycles.

MIS 7 was a less influential highstand on the lake evolution as growth-position corals from the west coast of Oahu, dated at ca. 225 ka, indicate maximum MIS 7 sea level was below –10 m (Sherman *et al.*, 1999), too low to support a groundwater lake in the crater. Tectonic uplift was not factored into the MIS 7 datum, implying that original sea level may have been even lower. Indeed, considering that the marine platform created by marine erosion is less than 6 m below current sea level, we can infer that the bulk of erosion of the crater must have occurred before MIS 7.

We have obtained a U/Th age of 240 ± 10 ka on algal carbonate material from Unit V. Because the sample contained a small fraction of detrital material, we can consider the age only an estimate (Table 3). Despite this, it appears to fit reasonably well with other data. Most importantly, the date indicates the lake represented by Unit V was intact up until the upper-middle Pleistocene.

If the 240 ka age were taken at face value, it would indicate the lower part of Unit V was formed at the onset of MIS 7. However, because MIS 7 sea level probably never attained an elevation greater than –10 m in Oahu (Sherman *et al.*, 1999), it is highly unlikely that the algal mat formed during this particular highstand. There are no known tectonic processes on the island that can raise the highstand deposits 20 m in 200 ka, and a younger age is not an option for reasons discussed below. However, given an uplift rate of 3 m/100 ka, generally accepted for Oahu (Muhs & Szabo, 1994; Hearty *et al.*, 2000), combined with an approximate +3 m sea level during MIS 9, relative sea level would have been about +12 m. This level for the algal mat in Unit V would be in better agreement with a late MIS 9 correlation (Hearty & Kaufman, 2000). If this is the case, then the older and thicker lake deposits

Isotope Stage	Oahu, HI (Stearns, 1978; Hearty *et al.*, 2000; Hearty, 2002a)	Bahamas (Hearty & Kaufman, 2000)	Bermuda (Hearty, 2002b; Hearty *et al.* 1999)	Uplift Rate (m/ky)
Late 5e	+9 to +11 m (Waimanalo)	+6 to 8.5 m	+6 to +9.2 m	0.025 ± 0.005
Mid 5e	+5.5 m (Waimanalo)	+3.0 m	+2.5 m	0.024 ± 0.003
7?	-10 to –20 (Olomana?)	0 to +1 m	<0m	Insufficient data
9?	+12 m (Waialae?)	+3	Above present	Insufficient data
Late 11	+28 m (Kaena)	+21 m	+20 m	0.020 ± 0.003
Mid 11	+13.5 m (Kaena)	+7.5 m	+5 to +7m	0.015 ± 0.001
Early 11	+5 to +6 m (Kaena)	0 to +1.5 m	+1m	0.012 ± 0.005

Table 1. Comparison of sea-level indicators between Oahu, Bermuda, and the Bahamas used to estimate uplift rates since MIS11. These data indicate that a fairly consistent or slightly increasing uplift rate averaging 0.020 m/ky has affected Oahu over the past 410 ky. Uplift rates calculated in previous studies (Muhs & Szabo, 1994; Grigg & Jones, 1997) were greater by a factor of 2 to 3, attributing all 30 m elevation of the Kaena deposits to uplift, rather than only 8 to10 m, given a global highstand of sea level at 400 ky at +20 m.

Taula 1. Comparació dels indicadors de nivell marí entre Oahu, Bermuda i les Bahames emprats per estimar les taxes d'aixecament des de l'estadi MIS11. Aquestes dades indiquen que una taxa d'aixecament bastant consistent o lleugerament incrementada d'un promig de 0,020 m/ka va afectar Oahu durant els darrers 410 ka. Les taxes d'aixecament calculades a estudis anteriors (Muhs & Szabo, 1994; Grigg & Jones, 1997) eren més grans per un factor d'entre 2 i 3, i atribuïen totes una elevació del 30 m al dipòsits de Kaena, enlloc que només 8 a10 m, donat la situació més alta del nivell marí, a +20m, a nivell global fa 400 ka.

of Unit IV may either have formed during early MIS 9 (c. 320 ka), or more likely during the previous MIS 11 (c. 400 ka). The MIS 11 highstand is known to have risen to 18-20 m on stable coastlines (Hearty *et al.*, 1999), and is found up to 30 m during the Kaena Highstand of Oahu at 400 ka (Hearty, 2002a) because of a 3 m/100 ka uplift rate. No traces of the Kaena Highstand are evident on the flanks of Ulupau Head, although preservation of such geomorphology would be unlikely in the friable and unstable volcano-clastic materials of the crater. We conclude therefore that the evolution of lakes in Ulupau Crater was in synchrony with, and modulated by 100 ka sea-level oscillations (Fig. 12) from MIS 13 onward.

AVIFAUNA OF ULUPAU CRATER LAKE.

Twenty-six species of birds were identified in a preliminary study of approximately 750 bones from Unit IV (James, 1987). Subsequent collecting has increased the number of fossil bones from the site considerably, although further morphological and systematic studies of the collection have not been completed. The fossil collections from Ulupau Head are accessioned primarily at the B. P. Bishop Museum, Honolulu, with a smaller number of bones accessioned at the National Museum of Natural History, Smithsonian Institution, Washington, DC.

Lab #	Sample type	Sample #	Run 1	Run 2	Average	±1σ	N
Mokapu – Waimanalo Formation (c. 125 ka) – *Ostrea*							
2507A	*Ostrea*	OKP2a	0.980	0.940	0.960	0.028	2
2507B	*Ostrea*	OKP2a	0.716	0.719	0.718	0.002	2
							Mean: 0.84 ± 0.17 (n =4)
Ki'i Point Limestone (KPL) – age unknown – *Ostrea*							
2506A	*Ostrea*	OKP1a	1.279		1.279		1
2506B	*Ostrea*	OKP1b	1.313	1.329	1.321	0.011	2
							Mean: 1.30 ± 0.03 (n = 3)
Mokapu – Waimanalo Formation (c. 125 ka) – Whole-rock							
2511A	W-R	OKP2a	0.550	0.532	0.541	0.013	2
2511B	W-R	OKP2a	0.532		0.532		1
							Mean: 0.54 ± 0.01 (n = 3)
Yellow Point Limestone (YPL) – age unknown – Whole-rock							
4267A	W-R	OKP3aa	0.722	0.751	0.737	0.021	2
4267B	W-R	OKP3aa	0.858	0.868	0.863	0.007	2
							Mean: 0.80 ± 0.09 (n = 4)

Table 2. Amino acid ratios (D-alloisoleucine/L-isoleucine or A/I) from oyster and whole-rock samples from last interglacial Waimanalo, Ki'i Point and Yellow Point Limestone units. Mollusks (*Ostrea* in this case) epimerize at substantially faster rates compared to whole-rock samples (Hearty *et al.*, 1992; Hearty, 2002b), as indicated from the equal-age samples from the Waimanalo Formation. Age estimates are based on "apparent parabolic kinetics" (Mitterer & Kriausakul, 1989).

Taula 2. *Proporcions d'aminoàcids (D-aloisoleucina / L-isoleucina o A/I) de mostres d'ostres i de roques senceres del darrer interglacial, Ki'i Point and Yellow Point Limestone. Els mol·luscs (*Ostrea *en aquest cas) epimeritzen en taxes substancialment més altes , en comparació a les mostres de roques completes (Hearty* et al.*, 1992; Hearty, 2002b), com s'indica a partir de mostres d'edat idèntica de la Formació Waimanalo. Les estimes d'edat estan basades en la "cinètica parabòlica aparent" (Mitterer & Kriausakul, 1989).*

Sample number	Material	U ppm	^{230}Th ppt	δ ^{234}U	δ ^{234}U	[^{230}Th/ ^{238}U]	[^{230}Th/ ^{238}U]	[^{230}Th/ ^{232}Th]	Age (ka)	± 1σ	Initial	δ ^{234}U
OHE 1c	Coral	2.506	30.74	114.85	0.71	0.7547	0.0022	20917	**119.4**	**0.6**	161.1	0.93
OHE 2a 1	Coral	2.275	27.38	115.21	1.55	0.7403	0.0042	38643	**115.4**	**1.2**	159.8	2.01
OHE 2a 2	Coral	2.204	26.82	111.94	1.23	0.7487	0.0031	135934	**118.3**	**0.9**	156.6	1.59
OKP 2a	Coral	2.216	28.78	119.63	0.87	0.7987	0.0012	53242	**131.2**	**0.4**	173.6	1.16
OKP 2c	Coral	2.449	32.13	111.5	0.81	0.791	0.0013	273	**130.9**	**0.5**	161.6	1.07
OKP 3c	Coral	2.482	31.83	108.39	0.79	0.7887	0.0015	18865	**131.0**	**0.5**	157.1	1.05
OKP3n Unit V	Algal mat	1.694		28.210	2.140	0.922	0.016	4	**240**	**15**	55.7	4.4

Table 3. New U/Th ages of corals and algal limestone on Oahu[1]. All corals from OHE and OKP are from Unit VI, the last interglacial Waimanalo Formation. The algal mat is from Unit V.

Table 3. *Noves edats U/Th de coralls i calcàries algals a Oahu[1].Tots els coralls de OHE i OKPsón de la Unitat VI, la Formació Waimanalo del darrer interglacial. El tapís algal és de la Unitat V.*

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[1] Analyses were performed on a multi-collector, inductively coupled plasma mass spectrometer (MC-ICPMS) at The Australian National University (Canberra, ACT).

Taxon	Habitat characteristics
SEABIRDS	
Pterodroma cf. *hypoleuca*	Nests near the sea in burrows that it excavates in sandy or other soft substrates (Seto & O'Daniel, 1999).
Puffinus newelli	Nests in excavated burrows or crevices usually at higher elevations. Recorded between 160 and 1200 m asl. in open canopy forest with dense understory (Ainley *et al.*, 1997). Fossils *of P. newelli* are rare in lowland sites (Olson & James, 1982), suggesting that the species has always preferred to nest in upland forest.
Procellaridae, undetermined large species	Unknown.
Nesofregetta fuliginosa	Nests in burrows that it excavates in sandy substrates with low vegetation, or in natural crevices in rocky substrates (BirdLife International, 2000).
Fregata cf. *minor*	*Fregata minor* nests in colonies on remote islands, usually near shore but sometimes up to 8 km inland (Metz & Schreiber, 2002). Nests are preferably placed in the tops of bushes such as beach naupaka (*Scaevola*). A few pairs currently nest on Moku Manu Island near Ulupau Head.
Sula sp.	Species undetermined but possibly conspecific with *Sula sula*, which currently has a breeding colony on the crater rim of Ulupau Head. *Sula sula* places nests in shrubs or trees.
SHOREBIRDS	
Pluvialis cf. *fulva*	In the Hawaiian Islands, winters in open habitats of many varieties, such as grasslands, mudflats, beaches, salt marshes, and small clearings in forest, and is found from seashore to at least 2,500 m asl (Johnson & Connors, 1996).
Numenius tahitiensis	During winter occurs on Pacific islands in a variety of habitats, both near shore and inland, including wetlands, saltpans, open grassy areas, vegetated dunes, and coconut groves (Marks *et al.*, 2002). Feeds on marine and terrestrial invertebrates, small vertebrates, seabird eggs, carrion, and fruits.
WATERBIRDS	
Branta sp.	The bones from Ulupau Head are similar in morphology to those of *Branta canadensis*, which winters in North America in coastal wetlands, wet grasslands, freshwater marshes, lakes, rivers, and agricultural fields (Mobray *et al.*, 2002). *Branta canadensis* feeds on aquatic plants, grazes on grasses and other terrestrial plants, and takes seeds and berries.
Anas aff. *wyvilliana*/ *laysanensis*	*Anas wyvilliana* prefers freshwater habitat, including coastal and ephemeral wetlands, upland rivers, streams, bogs, and pools at the base of waterfalls (Engilis *et al.*, 2002). Its upland haunts can be heavily forested. It feeds mainly on aquatic invertebrates and plants. *Anas laysanensis* currently inhabits Laysan Atoll, where brine shrimp and brine flies in a hypersaline lake are important foods (Moulton & Marshall, 1996). *Anas laysanensis* is not strictly a wetland bird, as it formerly occurred in upland forest in the main Hawaiian islands (Cooper *et al.*, 1996), where it may have fed on terrestrial invertebrates such as snails and arthropods.
Fulica sp.	The coot from Ulupau Head is probably a distinct species from *Fulica americana* (James, 1987). To breed, *Fulica americana* requires freshwater wetlands with heavy emergent vegetation at least partly surrounded by open, standing water. When not breeding coots also make use of coastal brackish and marine wetlands. *Fulica americana* feeds primarily on aquatic vegetation, and also takes aquatic invertebrates and vertebrates (Brisbin & Mowbray, 2002).
TERRESTRIAL BIRDS	
†*Thambetochen xanion*	Bones of the species are common in Holocene sites in karstic pits and caves on the lowland `Ewa Plain of Oahu (Olson & James, 1991). Fossils of its sister species, *Thambetochen chauliodous*, of Maui, Molokai and Lanai, occur in a wide variety of terrestrial habitats from seaside dunes to upland forest (James & Burney, 1997).
†? *Buteo* sp.	The hawk from Ulupau Head is similar in morphology to the extant *Buteo solitarius* though somewhat larger. *Buteo solitarius* occurs in a variety of upland habitats from pastures to tall forest on the island of Hawaii, where it feeds on rodents, birds, and invertebrates (Clarkson & Laniawe, 2000).
†*Porzana* spp., two species of flightless rails	Flightless insular rails may occur in wetlands but are also often found in broad range of terrestrial habitats. Of the two Hawaiian species of flightless *Porzana* that survived into historical times, one inhabited Laysan Atoll where it fed on insects, seabird eggs and carrion, and the other inhabited Hawaii Island, where it reportedly was found in open and bushy habitat below the closed canopy forest belt (Olson, 1999b).
†*Grallistrix orion*	Owl pellet accumulations in Holocene fossil sites indicate that members of this endemic genus of owls specialized in eating forest birds and flightless rails (Olson & James, 1982, 1991).
†*Corvus* sp.	Bones of *Corvus* are common in Holocene sites in the `Ewa Plain of Oahu. On Hawaii Island, the only surviving species of Hawaiian *Corvus* lives in native dry to wet forest, where fleshy fruits are important in its diet, and it also takes seeds, nectar and flowers, arthropods, and eggs and nestlings of smaller forest birds (Banko *et al.*, 2002).
Chasiempis sandwichensis	Most abundant in tall, mesic forest with well developed understory; absent from dry scrubland (Vanderwerf, 1998). Occurs as a fossil in Holocene sites on the lowland 'Ewa Plain of Oahu (Olson & James, 1982). Feeds on arthropods.
†*Chaetoptila* sp.	Fossils of the species are abundant in the Holocene sites on the `Ewa Plain (Olson & James, 1982). The species was probably primarily nectarivorous.
†*Rhodacanthis* sp.	This represents an extinct species of a koa finch (James & Olson, 2005). The two species of koa-finches (*Rhodacanthis*) that survived into historical times on the island of Hawaii fed mainly on pods and seeds of the koa tree *Acacia koa* (Olson, 1999a).
†*Chloridops wahi*	The only species in the genus of koa finches that survived into historical times, *C. kona* of the island of Hawaii, fed mainly on seeds of the naio tree *Myoporum sandvicense* (Olson, 1999a).
†*Chloridops regiskongi*	Fossils of the species are fairly common in Holocene sites on the `Ewa Plain of Oahu. The large and robust finch-like bill of this species indicates that it was able to crack hard seeds (James & Olson, 1991).
†*Akialoa* sp.	Species undetermined, but possibly *Akialoa ellisianus*, which survived into historical times on Oahu. The akialoas that were observed in life inhabited mesic to wet forest, although the distribution of fossils suggests that lowland shrublands were also used (Lepson & Johnston, 2000). Fed on beetle larvae and other arthropods and on nectar, primarily by probing with the long, decurved bill.
†*Aidemedia* sp.	Holocene fossils of *Aidemedia* occur in sites in the coastal lowlands of Oahu and Molokai and on the leeward slope of East Maui (James & Olson, 1991). Based on bill morphology the species is thought to have been insectivorous.
Paroreomyza maculata	Currently occurs in mesic to wet forest and shrubland (Baker & Baker, 2000). Holocene fossils of the species occur on the dry leeward `Ewa Plain of Oahu (Olson & James, 1982). The species feeds on invertebrates, primarily by probing in bark and dead wood and gleaning from leaves.
Loxops [*virens*] *chloris*	Currently occurs in dry and wet forest and more rarely in shrubland (Lindsey *et al.*, 1998). Feeds omnivorously on arthropods, nectar, and fruit. Fossils occur in Holocene sites on the lowland `Ewa Plain of Oahu.

Table 4. Habitats used by the birds in the Ulupau Head fossil assemblage (James, 1987). Daggers identify extinct species that have never been observed in life in historical times and whose habitat preferences must be inferred by analogy.

Taula 4. Hàbitats emprats pels ocells del conjunt fòssil Ulupau Head (James, 1987). Les creus identifiquen les espècies extingides que mai s'han observat en vida en temps històrics, i les seves preferències d'hàbitat s'han hagut d'inferir a partir d'analogies.

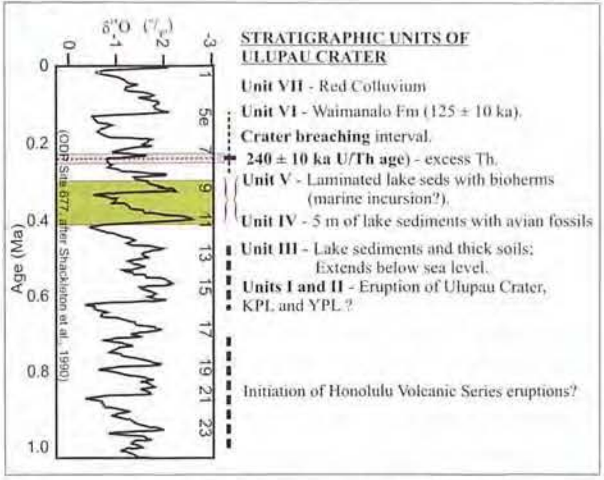

Fig. 11. Isotope curve from ODP 677 (Shackleton *et al.*, 1990) showing climate cycles and relative ice volume changes over the past million years. Events at Ulupau Crater are noted on the right of the graph.

Fig. 11. Corba isotòpica de ODP 677 (Shackleton et al., 1990) que mostra els cicles climàtics i els canvis relatius del volum de gel al llarg dels darrers milions d'anys. A la dreta de la gràfica s'indiquen els esdeveniments al cràter Ulupau.

In the present paper, we assess the paleoecological setting of Unit IV by evaluating the habitat requirements of the 26 avian taxa identified by James (1987). The habitat requirements and diets of the avian taxa are summarized in Table 4, in which the taxonomic nomenclature has been updated to reflect the names for Hawaiian fossil birds introduced by Olson & James (1991) and James & Olson (1991). In the light of findings by Cooper *et al.* (1996), the bones formerly referred to *Anas* cf. *wyvilliana* are now identified as belonging to *Anas laysanensis* or *A. wyvilliana*. A species of goose previously listed as Anserinae sp. is now assigned to *Branta* sp. In the revised faunal list we also grant full species status to the Pacific Golden Plover (*Pluvialis dominica* emended to *P. fulva*, see Connors *et al.*, 1993), and to Newell's Shearwater (*Puffinus puffinus newelli* emended to *P. newelli*).

Bones of seabirds are uncommon in the deposit in proportion to those of waterbirds and terrestrial species, suggesting that seabird breeding colonies were not situated near the lake shore. However, it is likely that the lake was not far from the sea, because the seabirds in the assemblage include taxa that rarely stray inland (*Sula* sp., *Fregata minor*). *Sula sula* and *Fregata minor* breed near the site at the present time. If we assume these species were nesting nearby when the fossils were accumulating, we can infer that the surrounding habitat probably included their preferred nesting habitat of shrubland or low trees. The two species of shorebirds in the deposit still winter in the Hawaiian Islands, where they are found along the coast and also inland in open habitats including various types of wetlands.

A small duck that is similar in morphology to the two extant species of endemic Hawaiian ducks is the most abundant species in the Ulupau Head assemblage. Bones of the duck, a goose *Branta* sp., and a coot *Fulica* sp., probably represent birds that fed or rested in the lake. Modern taxa that closely resemble the fossils are *Fulica americana* and *Branta canadensis*, which may feed in water or on adjacent dry land. Modern populations of *Anas wyvilliana* and *A. laysanensis* feed primarily on aquatic invertebrates, especially insects, and secondarily on aquatic plants. The numerical dominance of birds that feed in freshwater habitats in the faunal assemblage supports the inference that a lake and perhaps at times a shallow wetland existed when Unit IV was accumulating. However, waterbirds have a tendency to expand their ranges into terrestrial habitats after colonizing islands that lack native mammalian ground-dwelling predators.

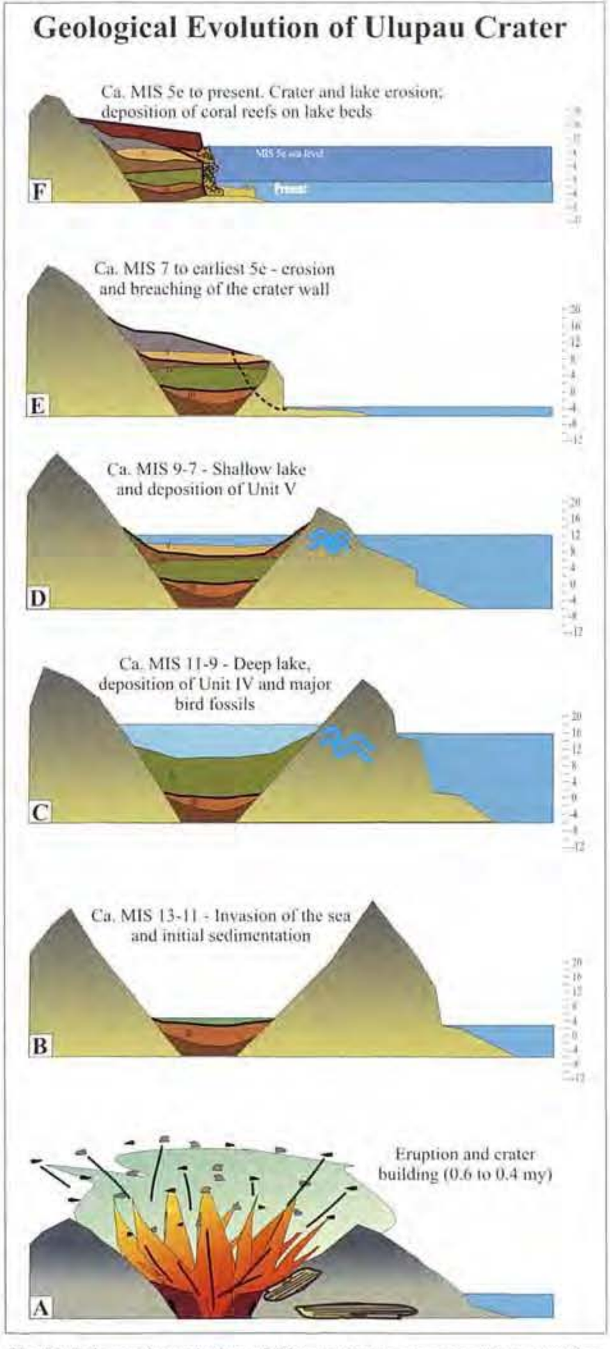

Fig. 12. Schematic evolution of Ulupau Crater encompassing eruption, lake phases, and breaching over the past several hundred thousand years.

Fig. 12. Evolució esquemàtica del cràter Ulupau, que inclou l'erupció, les fases llacunars, i l'obertura d'una bretxa al llarg dels darrers centenars de milers d'anys.

Holocene fossils of *A. laysanensis* occur in upland lava tubes on the island of Hawaii, far from coastal wetlands, for example (Cooper *et al.*, 1996). For this reason, we rely on the abundance of birds that prefer to feed in lakes, rather than their mere presence, to support our paleoecological interpretation of Unit IV.

A species of hawk *Buteo* is common in the assemblage (Olson & James, 1997). By analogy with the extant species of *Buteo* from the island of Hawaii, the Pleistocene hawk of Oahu may have occurred in a wide range of terrestrial habitats from grassland to canopy forest. An abundance of hawk bones appears to be a taphonomic signature of lake deposits in the Hawaiian Islands. The only other avian fossil assemblage in the islands with abundant hawk bones is from the lake deposit in Makauwahi Cave on Kauai (Burney *et al.*, 2001). Both the hawk and an extinct bird-eating owl, *Grallistrix orion*, probably contributed to the fossil assemblage by depositing prey remains of smaller forest birds and flightless rails.

The ground-dwelling terrestrial birds in the Ulupau Head assemblage include two species of flightless rails *Porzana* spp., and a flightless goose-like duck *Thambetochen xanion*. If *T. xanion* were similar in habit to *Thambetochen chauliodous*, a very similar species known from the islands of Molokai, Maui and Lanai, then it was a widely distributed browsing herbivore that fed on broadleaf understory vegetation (James & Burney, 1997). The ground-dwelling birds in the assemblage, and likewise the predatory species, are not particularly helpful for characterizing the plant communities near the site, because they tend to make use of a broad range of habitats. Although avian faunal assemblages are useful for paleoenvironmental reconstructions on continents (Olson & Rasmussen, 1986; Behrensmeyer *et al.*, 2003), the tendency of endemic island birds to have broad habitat tolerances may reduce their informative value for ecological purposes.

Five of the small forest birds in the assemblage belong to the insectivore or nectarivore/insectivore feeding guilds. The presence of this suite of birds suggests that the habitat surrounding the lake included forest or at least shrubland with nectar-producing plants, and habitat for insects. Some of the insectivorous birds in the assemblage forage by probing in bark, plant bracts, and epiphytes (*Akialoa* sp., *Paroreomyza*). Crow bones in the deposit may indicate that plants with fleshy fruits grew in the area, considering that fruit is an important part of the diet of the extant *Corvus hawaiiensis* on the island of Hawaii. Finally, the three species of finches in the assemblage indicate that plants with hard seeds grew in the area. The koa-finch (*Rhodacanthis* sp.) may have been feeding on koa pods, or perhaps on pods of kanaloa (*Kanaloa kahoolawensis*), a leguminous shrub that no longer occurs on Oahu but is abundant in the Holocene lowland pollen record of the island (Athens, 1997). The two species of *Chloridops* in the deposit are finches with very robust bills, suggesting that other trees or shrubs with hard yet nutritious seeds were present near the lake.

In one respect the vertebrate assemblage from Unit IV is distinctly different from the only other vertebrate assemblage from a lake deposit in the Hawaiian Islands, that from the central sinkhole of Makauwahi Cave on Kauai (Burney *et al.*, 2001). Fish bones are abundant in the Makauwahi deposit, whereas they are all but absent from the lacustrine sediments at Ulupau Head, indicating that fish failed to colonize the Ulupau lakes. Marine and freshwater shells are also absent, or nearly so, although one worn and fragmentary bone of a marine mammal was found (James, 1987). The virtual absence of marine shell supports the interpretation that the lake of Unit IVa had no surface connection to the ocean, and was protected from overwash by either a high crater wall or a more distant shoreline.

In summary, the vertebrate assemblage provides support for interpreting Unit IV and as lake and wetland sediments, particularly because waterbirds and hawks are common. The seabird bones in the lake deposit are suggestive that breeding colonies were present although probably not adjacent to the lake. From the species of seabirds represented we can infer that the site was not far from the ocean and that scrublands or low trees were probably nearby. We cannot infer that open habitat such as grassland or herbland was present, because the birds in the deposit that favor such areas can also be expected to occur near lakes and other wetlands and along shore lines. The forest birds in the deposit indicate that the local plants provided nectar, seeds, and probably fleshy fruits, as well as habitat for bark-dwelling insects. A leguminous tree or shrub, either koa or kanaloa, was probably present. Ulupau Head most likely supported mixed forest and perhaps shrublands surrounding a lake when Unit IV was deposited.

The Ulupau Head tuff cone lies on the windward side of Oahu, where it currently receives enough rainfall to support mesic lowland forest (c. 900 cm per yr). Weakening of the trade winds during glacial periods may have reduced precipitation at the site (Hotchkiss & Juvik, 1999; Hotchkiss *et al.*, 2000), so that forest and shrubland might have been replaced with dry grassland or herbaceous groundcover, which could not have sustained the forest birds present in the assemblage. The paleoecological evidence from the avian assemblage is thus consistent with our sedimentological arguments in favor of interglacial timing of high lake stands, although it is by no means decisive.

SUMMARY OF EVOLUTION OF ULUPAU CRATER AND ITS FOSSIL AVIFAUNA

1. The extensive exposures of lake sediments, colluvium, and paleosols in Ulupau Crater allow the interpretation and reconstruction of paleoenvironments in the basin over several hundred thousand years. The deposits show cyclicity and complexity indicating a dynamic setting with periodic lakes, floods of colluvium, and intervals of ecological stability (Fig. 12) marked by thick, well-developed soils. The primary modulating agent was the rise and fall of sea level during multiple middle Pleistocene events.

2. High lake levels appear to coincide with sea-level highstands. Three major cycles of lacustrine sedimentation occurred in Ulupau Crater. The largest lake may have occupied 50-60 ha during late MIS 11 (c. 400 ka) or early

MIS 9 (c. 300 ka), but was greatly reduced as the basin had filled with sediments, and as sea-level highstands progressively lowered during MIS 9 and 7 interglacials.

3. Crater breaching occurred previous to MIS 5e as the result of progressive attack of the eastern rim by marine erosion over multiple sea-level highstands.

4. If taken at face value, the U/Th age of 240 ka would constrain the age of the three lake cycles between about 400 and 200 ka. However, if we consider the amplitude of sea-level cycles that would best correspond with a succession of high lake levels, and the optimal times of crater breaching, the "best fit" scenario equates Units IV and V with either two separate highstand episodes during MIS 11, or MIS 11 and 9, respectively. Thus, the concentration of bird fossils at the base of Unit IV would have been deposited between 400 and 300 ka.

5. The fossil bird remains from Ulupau Crater are the oldest known for the Hawaiian archipelago and may be among the oldest recovered from any relatively small oceanic island. Their significance derives in part from the fact that they constitute a large fossil assemblage representing many species lineages with diverse ecological and trophic specializations. A few of the species appear to be closer to continental ancestral taxa that may have given rise to endemic Hawaiian species in the interval since the fossils were deposited, which could provide one of the most precise estimates of divergence times for any vertebrate lineage in the fossil record. This could potentially be extremely valuable for calibrating molecular divergence times. On the other hand, numerous other lineages appear not to have changed at all morphologically over several hundred thousand years and provide striking examples of evolutionary stasis.

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13

CONTRASTING TAPHOFACIES IN OCEAN ISLAND SETTINGS: THE FOSSIL RECORD OF MASCARENE VERTEBRATES

Julian Pender HUME

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Resum

Les Illes Mascarenyes, que comprenen Mauritius, La Réunion i Rodrigues, estan situades a l'Oceà Índic sud-occidental i són d'origen volcànic. Històricament, les illes estaven habitades per un nombre d'espècies endèmiques, el millor exemple de les quals és el dodó de Mauritius, *Raphus cucullatus*. Encara que hi ha referències sobre l'ecologia de Mauritius als diaris i quaderns de bitàcola dels vaixells, no fou fins el descobriment dels primers materials fòssils que es va poder percebre la composició faunística original. A Mauritius, als aiguamolls de Mare aux Songes, el 1865 varen ser descoberts nombrosos materials fòssils, mentre que es varen fer altres col·leccions a coves de valls poc fondes, particularment a la cadena muntanyenca de Le Pouce. A Rodrigues, les coves calcàries situades a la Plaine Corail han subministrat centenars de fòssils, principalment recol·lectats a les darreries del segle XIX. A La Réunion, les primeres restes fòssils varen ser descobertes el 1974, a talls dels penya-segats; s'ha trobat material subfòssil a aiguamolls i a localitats cavernícoles. Totes les restes fòssils són de l'Holocè. Alguns dels dipòsits fossilífers de les Mascarenyes presenten biaixos tafonòmics; en concret, els dipòsits dels aiguamolls són pobres en restes de petits vertebrats, com, per exemple, passerins. A Mauritius quasi no s'han trobat materials esquelètics a cap cova o tub volcànic, i els dipòsits de Mare aux Songes presenten biaixos elementals. A Rodrigues s'han conservat ocells marins, el solitari, *Pezophaps solitaria*, i la tortuga gegant, *Cylindraspis* sp., i relativament pocs ocells terrestres. Els sistemes cavernícoles i els tubs de lava són rars a Mauritius i La Réunion, i, a partir de les restes d'animals introduïts descobertes als tubs de lava de La Réunion, és clar que els elements esquelètics es degraden molt aviat. A més, als dipòsits d'aiguamolls s'han trobat centenars de restes de tortugues, mentre que, pel contrari, els ocells petits i de mida mitjana virtualment no s'hi troben.

Aquest treball descriu la situació tafonòmica de diferents localitats fossilíferes i fa comparacions, emprant el microscopi electrònic d'escandallatge, entre espècimens fòssils de cada dipòsit. Es presenta evidència de la geologia, topografia, estratigrafia i sedimentologia, i es discuteixen els paleoambients, vida mitjana, carronyeig, activitat antropogènica, biaixos de recol·lecció i probabilitat d'entrampament, en relació amb la preservació dels elements. Malgrat els materials de les Mascarenyes són holocènics, els problemes que comporten són complexes, i la interpretació de qualsevol registre fòssil aparentment recent s'ha d'emprendre amb molta cura.

Paraules clau: Mauritius, La Réunion, Rodrigues , localitats fossilíferes, tafonomia, biaixos en el registre fòssil.

Summary

The Mascarene Islands are situated in the southwest Indian Ocean and are volcanic in origin. Historically, the islands were inhabited by a number of endemic species, and although references were made about Mascarene ecology in ships' logs and journals, it was not until the discovery of the first fossil material that the diversity of the original fauna could be established. All of the fossil remains are Holocene. Some of the Mascarene fossil deposits exhibit marked taphonomic bias; in particular; the marsh and Réunion cave deposits are depauperate in small vertebrate remains, e.g. passerines, despite their presence being known from other evidence. On Rodrigues, comparatively few land birds other than solitaire *Pezophaps solitaria* and giant tortoise *Cylindraspis* sp. have been preserved. Cave systems and lava tunnels are rare on Mauritius and Réunion, and it is clear from the remains of introduced species found in such lava tunnels on Réunion that skeletal elements decay rapidly.

This paper describes the taphonomic setting of the various fossil sites and makes comparisons using SEM and light microscopy between fossil specimens from a range of deposits. Evidence from geology, topography, stratigraphy and sedimentology is presented and bioerosion, geochemistry, scavenging, collecting bias, entrapment and time-averaging are discussed in relation to element preservation. Although the Mascarene material is relatively young <5,000 years, the problems that can be encountered are complex; thus interpretation of any fossil record including recent ones must be approached with caution.

Keywords: Mauritius, Réunion, Rodrigues , fossil localities, taphonomy, bias in the fossil record.

INTRODUCTION

The Mascarene Islands comprise Réunion, Mauritius and Rodrigues and are situated in the southwestern Indian Ocean (Fig. 1). Although they share a volcanic origin (Courtillot, 1999), each is significantly different both geologically and biologically. Vertebrate endemism is high within the Mascarenes (Adler, 1994), epitomised by the family Raphidae, comprising the dodo, *Raphus cucullatus* and solitaire *Pezophaps solitaria*. Knowledge of the fossil record of Mauritius began with the discovery of a richly fossiliferous horizon in the Mare aux Songes marsh (Fig.2a) in 1865 (Clark, 1866; Owen, 1866). Most of the now extinct vertebrate species were discovered at this time although additional material was collected from the Mare aux Songes by Théodore Sauzier in 1889 (Newton & Gadow, 1893) and in the early 1900s by the amateur naturalist Etienne Thirioux (Carié, 1916) between 1897-1908. Thirioux collected important material in boulder fields and cliff undercuts at Le Pouce and various other unspecified localities on Mauritius. On Rodrigues, the first skeletal material was discovered, but not described, in the limestone caverns of the Plaine Corail (Fig.2c) in 1789 (Strickland & Melville, 1848; Newton & Newton, 1869). It was not until the 1860s, however, that a thorough survey of the caverns was undertaken (Slater, 1879a,b) and the fossil material described (Milne-Edwards, 1873; Günther & Newton, 1879). Remarkably, fossil localities were unknown on Réunion until 1974 (Kervazo, 1979; Cowles, 1987; 1994; Mourer-Chauviré *et al.*, 1999), when fossils were found in a large cavern on the northwest coast; subsequently new cave (Fig.2b) and marsh deposits have been discovered on Réunion (Mourer-Chauviré *et al.*, 1999).

Unlike many other oceanic islands, Mascarene ecology was comparatively pristine upon its discovery by western man, and although the fossil record is certainly incomplete, contemporary accounts derived from ships' logs and journals provide some indication of the original faunal diversity. Historical records are not necessarily accurate, but fossil remains can corroborate the existence of species mentioned in such accounts.

Each Mascarene Island has or had a comparable fossil depositional environment, i.e. marsh deposits and lava tunnels on Réunion and Mauritius, and cave infillings on all three islands. Here I compare the different fossiliferous deposits from each island and address some of the problems associated with the present Mascarene fossil record, particularly concerning a perceived lack of small vertebrates. The influences of sedimentology, taphonomic presence, topography, time-averaging, geochemistry and collecting bias are examined. Emphasis is placed on avian fossil remains, but data from mammals and reptiles is considered when available.

Abreviations

The following abbreviations are used: BMNH, The Natural History Museum, London, England (formerly the British Museum (Natural History)); UMZC, University Museum of Zoology, Cambridge, England; MHNH, Muséum National d'Histoire Naturelle, Paris, France; UCB, Université Claude Bernard-Lyon 1, France; MI, Mauritius Institute.

Geological setting

The Mascarene Islands were created from the same hotspot that produced the vast Deccan Traps lava fields of India, leaving a trail of plateaux, island groups and seamounts across the southwestern Indian Ocean as the Indian plate drifted north (Courtillot, 1999). The hotspot is presently situated approximately 5 km southeast of Réunion (Duncan and Richards, 1991). Mauritius is thought to have developed between 7-9 My and comprises old lavas (> 7My) to young lavas (> 20 000 years); sand and coral deposits are comparatively recent (< 20 000 years) and the island is almost completely surrounded by actively growing reef formations (Montaggioni & Nativel, 1988; Saddul, 1995). Réunion is very much younger with the oldest lavas dated at 3 My (Rivals, 1989). It rises from a 4000m deep oceanic floor to a height of 7000m, but reef formation is extremely limited (Montaggioni & Nativel, 1988). Réunion is also volcanically active; the volcano *Piton de la Fournaise* continues to reshape the southwestern coast, whilst the other major volcano *Piton des Nieges*, although now dormant, catastrophically destroyed much of the island between 300,000 and 200,000 years ago (Mourer-Chauviré *et al.*, 1999). The geology of Rodrigues is less well understood and dating of the island stems from just one study (McDougall *et al.*, 1965). Although the island is presently considered the youngest Mascarene Island at 1.5 My, the faunal composition suggests it is the oldest. Rodrigues is dominated by a central ridge running W.S.W. parallel to its longer axis and is completely surrounded by a vast reef and lagoon extending beyond the shoreline. It reaches 6.5 km to the south, 3.2 km to the west and 6.5 km to the north; no reef is developed on the east side (North-Coombes, 1971; Saddul, 1995). The Mascarenes are basaltic islands and the basalts are transitional between tholeitic and alkalic; both rock suites contain olivine in proportions >5% (olivine basalt) plus plagioclase feldspars and pyroxenes (Saddul, 1995). Other basaltic rocks present throughout the Mascarenes include Oceanite, Ankaramite, Hawaiite, Mugearite and Trachyte (McDougall *et al.*, 1965; Saddul, 1995).

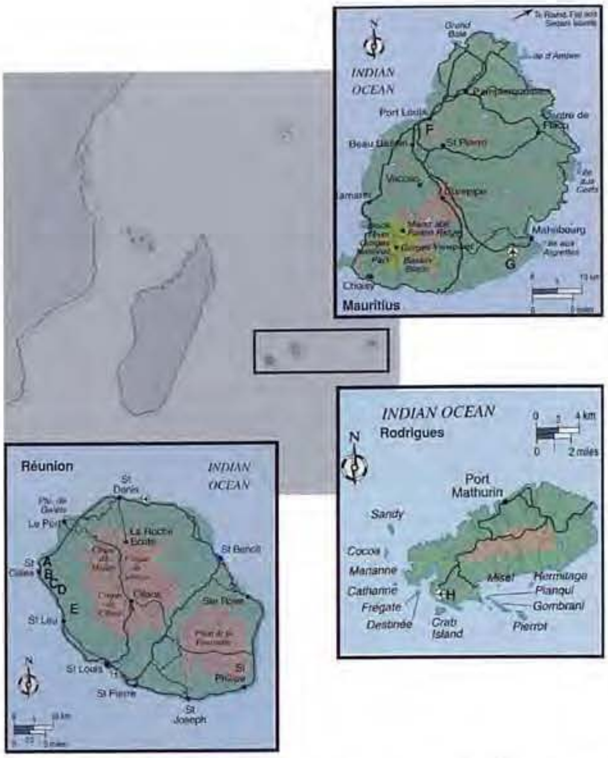


Fig. 1. Map of the Indian Ocean with Mascarenes (inset, middle left). On Mauritius, Réunion and Rodrigues, letters approximate fossil localities.

Fig. 1. Mapa de l'Oceà Índic amb les Mascarenyes (al centre esquerra, emmarcades). A Mauritius, La Réunion i Rodrigues les lletres indiquen la localització aproximada de les localitats fossilíferes.

Pre-colonisation ecology of the Mascarene Islands

Despite the fact that no serious study of the island ecology was attempted until the 19th century, long after the initial ravages of human colonisation and rapid destruction of the forests (Cheke, 1987), some contemporary accounts describe Mascarene ecology in considerable detail for the time.

Early accounts from Mauritius describe dry, semi-open woodland dominated by palms around the leeward coastal plains, whilst dense climax forest dominated by ebony grew within the interior and on the windward side (Het Tweede Boeck, 1601). Wybrandt Warwicjk's account from 1598 (Het Tweede Boeck, 1601; see also Strickland & Melville, 1848; Barnwell & Tousaint, 1949), which is now known as the first description of Mauritius, notably stated:

"the island is uninhabited and very mountainous. The soil is extremely rocky but fertile as can be judged from the large number of trees, which are so close to each other that one can hardly walk in the forest. The trees are mostly black ebony. There are also a large number of palms, the palms and palmistes are edible"

Much of the original forest has been cleared, where it still remains, the same conditions still persist (Hume *pers. obs*). Records of the original fauna exist only for the coastal and lowland plains on the dry leeward side of the island and it is not unreasonable to postulate that the larger vertebrates, including the flightless species, may have been confined to this more open zone.

The majority of near pristine surviving forests within the Mascarenes are found on Réunion. This is largely a consequence of the topography as the island is extremely mountainous, with 61% of the land surface situated above 600 m (Blanchard, 2000). As on Mauritius, the vertebrate fauna was probably most abundant in the lowland region or leeward side (this was certainly the case for the endemic giant tortoise *Cylindraspis borbonica* (Mourer-Chauviré *et al.*, 1999)) and unfortunately easily accessible to man. Dry open woodland dominated by palms was present on the coasts and lowlands of Réunion upon its discovery (Charpentier de Cossigny, 1799; Rivals, 1952; Cadet, 1977) becoming climax wet forest a short distance into the interior (Cadet, 1977). A small remnant of dry forest survives on the south coast (less than two acres), which represents the only extant pristine forest of this type (Strasberg pers.comm).

Rodrigues lacks true mountains and can be best described as 'hilly.' Fire and agriculture have now removed almost all of the original forest, but two contemporary accounts describe the ecology in some detail (Leguat, 1708; Tafforet, 1726 [Dupon, 1969]). The rapid destruction of the forests can be ascertained from the account of Balfour (1879), the first botanist to record details about the flora of Rodrigues and who described the island as 'a dry and desolate place' as early as 1875! However, Francois Leguat (1708), marooned on Rodrigues for 2 years in 1691-2, described the forests as open woodland, dominated by palms and the Mascarene trees, Bois d'olive, *Cassine orientale*, and Fig, *Ficus* sp. Today, free-roaming goats and cattle heavily graze the island and have created open grassland with dense patches of introduced scrub (Cronk, 1995). The land is also divided into a mosaic of plots by small-scale farming. A few endemic plants survive amongst the exotics, most noticeably at the heads of the valleys and on the tops of the largest hills (Strahm, 1989). In June 2000, a Malais trap was set up to collect insects in the last remaining forested localities on Rodrigues. After analysis, the collections lacked endemics and comprised only pantropical or introduced species with low diversity (Noyes, pers. comm). This suggests that unlike Mauritius and Réunion, Rodrigues has suffered almost complete extinction in some aspects of the invertebrate faunas. The lack of refugia, e.g. mountain tops, montane forests etc, that have survived on Mauritius and Réunion, is almost certainly the main reason.

FOSSIL LOCALITIES

The Mare aux Songes (S20^{O} 27', W57^{O} 41), Mauritius (Fig. 1G)

The Mare aux Songes marsh is situated approximately 0.5 km south-east of the Plaisance airport on the south-eastern side of Mauritius and is less than 100 m above sea level. Despite suggestions to the contrary (e.g., Cowles, 1987), the marsh has not been completely destroyed by development of Plaisance airport. The deposit consists of peaty sediments overlying a rocky basaltic base with sediment depths ranging from 0.2-1 m and now covers an area of 106 m x 44 m compared with 4 or 5 acres when discovered by Clark (1866). The marsh is surrounded by gently undulating hills with a shallow outlet at the southern end. This outlet eventually reaches a lagoon 0.5 km to the southeast but fluvial energy is low and there is little evidence of erosion *en route*, e.g. undercut river banks, steep sided valleys etc. In the winter (dry season), the marsh is predominantly dry and only the southern end of the marsh remains damp and boggy. In the summer (wet season), the marsh can be immersed in 1m+ depth of water. Some intertidal invertebrates, which are still extant within the lagoon surrounding Mauritius, are present in the Mare aux Songes marsh sediments. This indicates that the marsh may have been subject to lagoonal influences in the past but the marsh must now be considered 'made-ground' and any conclusions concerning its evolution are difficult to ascertain. According to Clark (1866), the marshy deposits were deep, at least 3 springs were present and endemic trees were abundant. Today Sugar cane completely surrounds the vicinity with small stands of introduced trees situated along the edges of the marsh, thus, it is now difficult to discover new localities within the area without the aid of heavy duty digging machinery.

Le Pouce (exact coordinates undetermined), Mauritius (Fig.1F)

The mountainous regions of Le Pouce comprise sheer escarpments often incised by steep v-shaped valleys. Situated along the contact zone between escarpment and valley are a number of small undercuts, and vast boulder fields/scree cover the base of the escarpment and the valley sides. Some of the larger material within the scree also forms small caves or fissures. The area is now completely overgrown by exotic plants, particularly gauva (*Psidium cattleyanum*) and Acacia (*Leucaena leucocephala*) and collecting from old sites or discovering new sites on a casual basis has so far proved difficult. The Le Pouce valley has proved to be richly fossiliferous (see below) and the many holes and fissures proved to be excellent natural faunal traps and fossil depositional sites.

One of the greatest, yet much maligned, collectors of Mauritian fossil material was Louise Etienne Thirioux (1846-1917). He was a hairdresser by trade but diligently searched for fossil remains in his free time. Thirioux collected at a number of localities, e.g. Corde de Garde, but most of his material stems from Le Pouce and he often simply states '*Le Pouce valley*' on his collecting labels. Thirioux's fossil collection is by far the most important from Mauritius as it contains a high proportion of small <5 cm elements of vertebrate species that are almost unknown from the fossil record elsewhere in the Mascarenes (Table 1). The collection also includes the only associated dodo, *Raphus cucullatus* skeleton, an almost complete skeleton of the red rail, *Aphanapteryx bonasia* a unique skeleton of the Mauritian giant skink, *Leilopisma* (*Didosaurus*) *mauritiana*. After initially sending material to Alfred Newton in Cambridge and to the Paris Museum via Paul Carié (Carié, 1916), he deposited the remainder of his collection, including the dodo, skink and rail skeletons, in the Mauritius Institute at Port Louis, where they still reside.

Caverne de la Tortue (S21^{0} 04,'W55^{0} 16), Réunion (Fig.1E)

The Caverne de la Tortue is situated on the northwestern side of Réunion approximately 3.2 km from the coast and 250 m above sea level. The caves are not karstic, but a lava tunnel system developed within vesicular basaltic lava (Mourer-Chauviré *et al.*, 1999). The cavern system is complex, with many branches and narrow caves with shallow infilling sediments and extends for 200 metres (Brial, 1996). The main entrance is sheer and accessible only by rope ladder; a second entrance is accessible only by crawling. The first cavern forms a large chamber but quickly grades into narrow, shallow passages. Fallen blocks of basalt litter the main entrance but further in the floor is covered by very fine sediments, with thickness from 50 mm – 1.5 m approximately 2 m from the entrance. This sediment is continuous through the cave system. At 20 m from the main entrance, a small area approximately (4 x 4 m) has produced unusual formations of a 1-2mm layer of limestone developed around a central core of basalt. This peculiar formation represents the only known limestone deposit on Réunion (Brial, pers. comm). The cave atmosphere is extremely humid and some of the cave floor deposits show evidence of high-energy fluvial activity, most notably ripple marks on shallow compact sediments. This cave acted as a natural pit-fall trap for a number of endemic species, particularly tortoises and flightless birds (Mourer-Chauviré *et al.*, 1999); although the preservation of bone material is generally very poor.

Marais de L'Ermitage (S21 40', E55 16.5), Réunion (Fig.1D) (after Mourer-Chauviré *et al.*,1999 and pers.obs)

This marsh is found 0.7 km from the coast, between St-Gilles and St-Leu and is situated in a low-lying <50 m above sea level sedimentary basin. Unfortunately, recent road construction has now destroyed the locality (Mourer-Chauviré pers. comm). A 0.8 m layer of fossil-poor peaty sediment, overlies a breccia 0.3-0.4 m deep, comprising abundant vertebrate fossils, volcanic rocks, coral and shelly fragments. This layer in turn overlies a layer of marine sediments comprising coralline sands, coral and marine mollusc fragments. The area is waterlogged and rapidly infills with water once test pits have been dug. Many hundreds of bones of the endemic giant tortoise *Cylindraspis borbonica* have been recovered, but bird and bat bones are extremely rare (see Mourer-Chauviré *et al.*,1999).

Grotte des Premiers Français (1.5 km southeast of Saint Paul) (Fig.1A); **Grotte "aux Sable" (1 km south of Saint Gilles)**(Fig.1B); **Grotte de l'Autel (2 km south of Saint Gilles)**(Fig.1B), **Réunion** (after Mourer-Chauviré *et al.*,1999) (Fig.1)

These cave localities have provided numerous bones of endemic birds and seabirds that excavate burrows to nest in, e.g., *Puffinus puffinus*. Only the sediments from Grotte "aux Sable" were sieved, although small <10 mm elements were obtained from the other localities. All of the sediments have now been removed.

The Plaine Corail (S19 44.5', W63 22 to S19 45', W63 24), Rodrigues (Fig.1H)

The Plaine Corail is an extensive area of limestone (calcarenite), representing the largest carbonate terrain

Data source	Species	Number of elements		Percent of juvenile elements recovered
		Adults	Juveniles	
MI; BMNH; UMZC; MNHN	Dodo *Raphus cucullatus*	~1710	3	0.17
MI; BMNH; UMZC; MNHN	Solitaire *Pezophaps solitaria*	~2000	0	0

Table 1. A comparison between the numbers of adult and juvenile dodo and solitaire (Raphidae) remains discovered in all of the Mascarene fossil yielding localities. As yet, no solitaire and only 3 juvenile dodo skeletal elements have been discovered.

Taula 1. Comparació entre els nombres de restes d'adults i juvenils de dodò i solitari (Raphidae) descobertes a totes les localitats fossilíferes de les Mascarenyes. Fins ara, només s'han obtingut tres elements esquelètics juvenils de dodò i cap de solitari.

within the Mascarene Archipelago (Montaggioni and Nativel, 1988; Saddul, 1995). It is located on the south-western corner of Rodrigues and encompasses an area 4 km x 3 km situated between 40-50 m above sea level. It has been suggested that the formation began ~5000 years ago when the wind direction favoured the build up of coral sand deposits on the south west coast (Saddul, 1995). Groundwater percolation and underground streams have continually eroded the carbonates, producing extensive and complex caverns and, where large-scale roof collapse has occurred, steep-sided canyons are now present. The limestone area has numerous small openings, creating natural pitfall traps on the surface and, as a result, accumulation of large numbers of vertebrate species has occurred. The surrounding area is very harsh and dry with little topsoil. Sediments within the caverns vary from a depth of 0.5 mm (along active underground streams) to 1.5 m (little or no fluvial action). The flora occurring on the Plaine Corail is sparsely distributed and often comprises stunted individuals. Sedimentation rates are low within the caverns and as a large number of fossil remains are unburied, the palaeoenvironment may not have differed significantly from that of today. No other fossil locality has been discovered on Rodrigues.

Fig. 2a. Mare aux Songe, Mauritius. View looking east.

Fig. 2a. Mare aux Songes, Mauritius. Vista cap a l'est.

Fig. 2b. Caverne de la Tortue, Réunion. A view of the unique limestone deposit on the roof of the cave.

Fig. 2b. Caverne de la Tortue, La Réunion. Vista de l'únic dipòsit càrstic al sòtil de la cova.

Fig. 2c. A view from inside a cavern, Plaine Corail, Rodrigues. Note how minor roof collapse has acted as natural pitfall traps for the fauna.

Fig. 2c. Vista de l'interior d'una cova, Plaine Corail, Rodrigues. Observar com un petit abissament ha actuat com a trampa natural per a la fauna.

TAPHONOMY

Much of the fossil material collected from the Mascarenes has been obtained with little or no contextual data. Despite this, it is clear that there are highly contrasting preservational styles and faunal content between locations reflecting differing taphofacies.

The Mauritian and Réunion marsh fossil deposits comprise almost entirely larger vertebrate fossils (Fig.4a and Fig.4c), with many of the bone samples exhibiting damage due to low energy fluvial activity and plant roots. Only the material collected from the caverns on Rodrigues, Thirioux's Mauritius cave and Réunion deposits contain an abundance of small (<5cm) delicate skeletal elements (Fig,4b, Fig. 4d, and Fig.4e). Furthermore, taphonomic bias has contributed to the preservation of certain elements. For example, of the endemic family Raphidae (dodo and solitaire), the remains of over 300 individual dodos were recovered from the Mare aux Songes (Clark, 1866), but only 5 crania, 7 or 8 rostra, 4 ulnae and radii and a single carpometatarsus (Fig.4a). The majority of fossil remains comprise tibiotarsi and tarsometatarsi, which suggests that dodos were wading into the marsh and becoming trapped. Presumably, the rest of the body was washed away or scavenged leaving an abundance of lower leg bones in the deposit. This is a scenario similar to the preservation of some moa remains collected from marsh deposits on New Zealand (Worthy, pers. comm). The lack of high energy fluvial damage to the fossils specimens also suggests that the material was deposited in situ or relatively close to the locality.

In terms of juvenile dodos, only one pair of tarsi (now lost) collected by Clark (1866) and a tarsus (now lost), collected and photographed by Thirioux in 1904 have been discovered. However, not a single juvenile solitaire element, out of many thousands of fossil adult bones collected, has yet been found (Table 2). This suggests either that Raphidae nested and reared young well away from the depositional area or that due to the fragility of juvenile elements, they are much less likely to have been preserved.

The broad-billed parrot *Lophopsittacus mauritianus* was described from a partial mandible by Owen (1866)

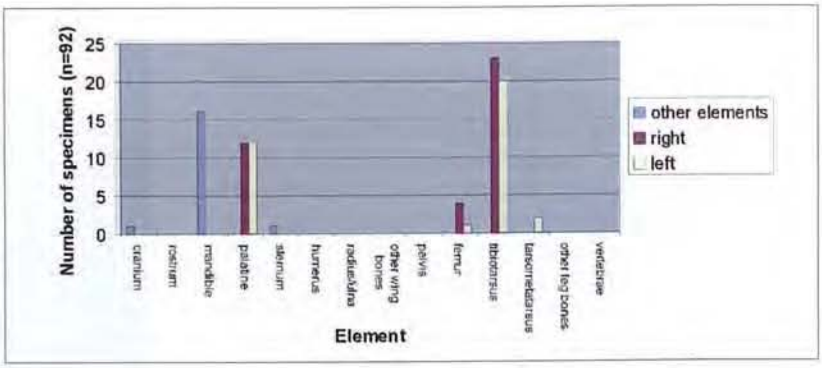


Fig. 3a. Remains of *Lophopsittacus mauritianus* collected from the Mare aux Songes, Mauritius. Note the comparatively numerous tibiotarsi, palatines and mandibles and the distinct paucity of other elements. Right and left bias of bone preservation is minimal.

Fig. 3a. Restes de Lophopsittacus mauritianus *recol·lectades a Mare aux Songes, Mauritius. Noteu els tibiotarses, pal·latins i mandíbules, relativament nombrosos, i la diferent escassesa d'altres elements. Els biaixos en la preservació dels ossos drets i esquerres són mínims.*

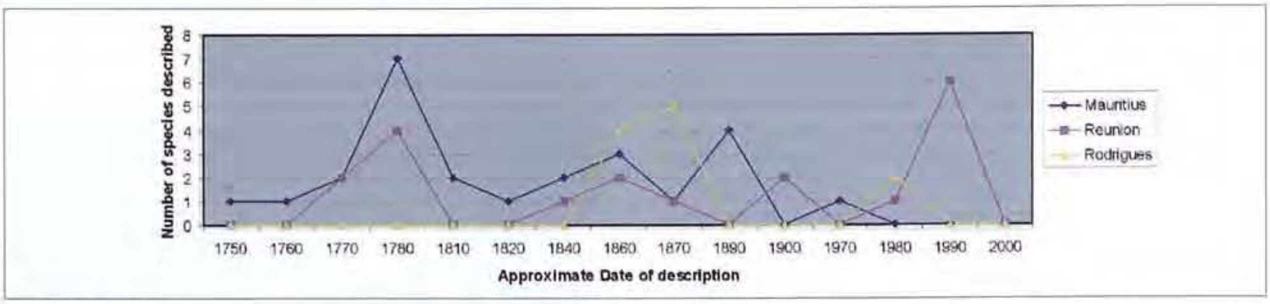


Fig. 3b. All of the Mascarene bird species described from physical (skins and fossil remains) and/or reliable historical evidence. Note the large number of passerine species from Mauritius and Réunion described between 1770-1780 (the heyday of French natural history), the 1860-1890 period (corresponding with the discovery of the Mare aux Songes, Mauritius and the caverns on Rodrigues), and the recent discoveries (e.g. Mourer-Chauviré *et al.*, 1999) on Reunion during the 1980-1990 period.

Fig. 3b. Totes les espècies d'ocells de les Mascarenyes descrites a partir d'evidències físiques (pells i restes fòssils) i/o històriques fiables. Noteu el gran nombre de passerins de Mauritius i La Reunión descrites entre 1770-1780 (l'apogeu de la història natural francesa), el període 1860-1890 (que es correspon al descobriment de la Mare aux Songes, Mauritius i de les coves a Rodrigues), i els descobriments recents (e.g. Mourer-Chauviré et al., 1999) a La Reunion durant el període 1980-1990.

and postcranial material by Milne-Edwards (1873) and Newton & Gadow (1893); Thirioux also collected some elements from Le Pouce *c.* 1904. The number of elements recovered from the Mare aux Songes indicates that at least 23 individuals are represented. However, only 1 cranium, 1 tarsometatarsus, 1 sternum and whilst no rostra, pectoral elements and foot elements have been recovered, yet at least 16 mandibles, 24 palatines and 43 tibiotarsi exist (Fig.3a). The subtle differences in fluvial energy coupled with the morphology of the individual element are likely to be responsible. When experimenting with doves (Columbidae) and gulls (Laridae), Bickart (1984) showed that the skull is one of the first parts of a corpse to detach when placed in a fluvial environment. Air spaces are present in the cranium and the rostrum of most birds, therefore, in Mauritian parrots, dodos and other avifauna, this may have been sufficient to suspend these elements in the water for longer periods and thus increase dispersal. Changes in fluvial energy are very likely to have had a serious effect on the deposition of small vertebrates as well, but defining criteria is difficult to interpret (see Ericson, 1987).

Cave material appears to lack the preservation bias associated with marsh deposits, as a significant amount of associated material has already been collected (Table 2), and fossil material comprise much larger percentages of cranial and the smaller postcranial elements, e.g. carpometacarpus etc.

The Mascarenes were once inhabited by owls of the endemic genus *Mascarenotus* (Mourer-Chauviré *et al.*,1994). However, unlike the endemic but now extinct genus *Grallistrix* of the Hawaiian Islands, *Mascarenotus* appears to have not utilised caves for breeding or feeding as owl remains are extremely scarce in all deposits and no owl pellets have yet been recognised. Owl pellets have proved essential in determining the diversity of fossil passerines on the Hawaiian Islands (Olson & James, 1991; James & Olson, 1991), and it is apparent that passerines formed a major component of Hawaiian owl prey. Conversely, however, it appears that Mascarene owls preyed heavily on reptiles (no reptiles naturally occur on the Hawaiian Islands) and convergent morphologies of the Mascarene and Hawaiian genera, e.g. short wings (forest adaptation) and long strong tarsi and pelvis (bird and reptile hunting adaptations) are a result of similar ecological niches but different prey. Evidence suggesting that *Mascarenotus* was a forest specialist and bred only in tree holes/cavities can be further extrapolated from its rapid and comparatively recent extinction (Réunion unknown; Mauritius c. 1850; Rodrigues c.1780). The last reports of the owls coincides with intense and severe deforestation that took place during the period 1800-50 on Mauritius and from 1730-1780 on Rodrigues (see Cheke, 1987).

COLLECTING OR PRESERVATION BIAS OF SMALL VERTEBRATES

Volcanic islands are notorious for the poor preservation of skeletal elements, primarily due to chemical

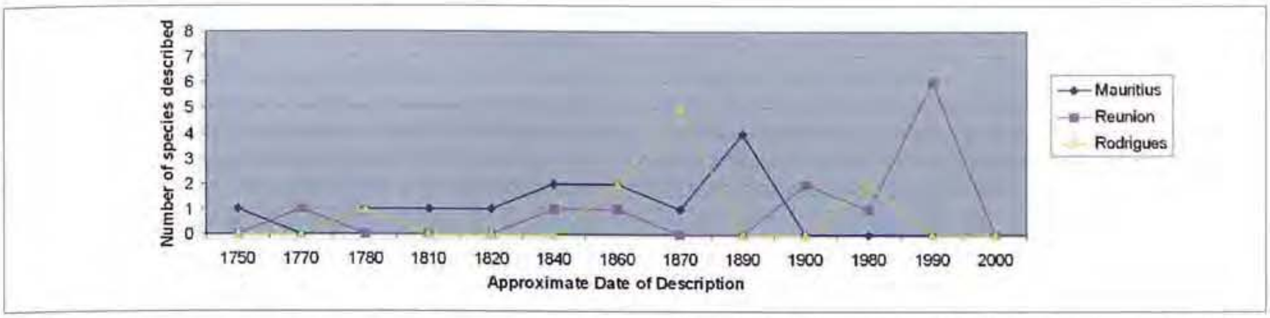
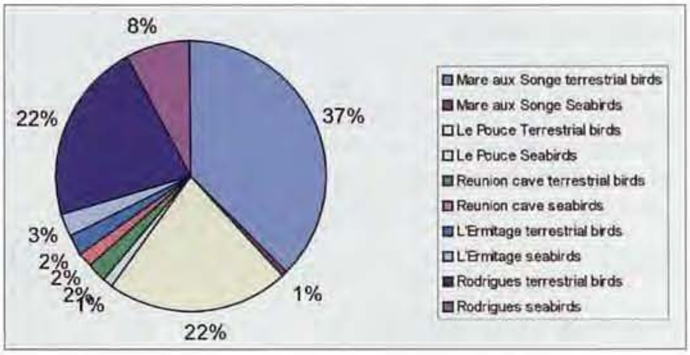


Fig. 3c. All of the Mascarene bird species described from physical (skins and fossil remains), minus all passerines described from skins. Note that comparatively few non-passerines were described before the 1860s, as it was not until the second half of the 19th century that the majority of non-passerine fossil remains were discovered. In contrast to Figure 3b, the only passerine described from the fossil record was the Rodrigues starling *Necropsar rodericanus* in 1879.

Fig. 3c. Totes les espècies d'ocells de les Mascarenyes descrites a partir d'evidències físiques (pells i restes fòssils), llevat dels passerins descrits a partir de pells. Noteu que es varen descriure relativament pocs passerins abans de la dècada dels 1860, i que no va ser fins la segona meitat del segle XIX que es va descobrir la major part de les restes fòssils d'ocells no passerins. En contrasta amb la Fig. 3b, l'únic passerí descrit a partir del registre fòssil va ser, el 1879, l'estornell de Rodrigues Necropsar rodericanus.

Fig. 3d. Comparison between seabird and terrestrial bird fossil remains collected in cave and marsh localities on the Mascarene Islands. Seabirds constitute a large percentage of Mascarene avifauna, yet are under represented in the fossil record. A large amount of Mascarene seabird fossil material remains unsorted and/or little importance has been placed on it.

Fig. 3d. Comparació entre les restes d'ocells fòssils marins i terrestres recol·lectades a les localitats espeleològiques i als aiguamolls de les Illes Mascarenyes. Els ocells marins constitueixen un gran percentatge de l'avifauna de les Mascarenyes, encara que es troben sota-representats al registre fòssil. Una gran quantitat de el material fòssil d'ocells marins de les Mascarenyes be està sense catalogat o/i be se li ha donat poca importància.



decomposition (Olson & James, 1982; Tennyson & Millener, 1994; Worthy & Holdaway, 1993) and for topograhical reasons, e.g. the steep, mountainous nature of the islands coupled with the absence of suitable sedimentary repositories encourages rapid run-off (Olson & James, 1982). It can be envisaged that a bias toward larger vertebrate bone on oceanic islands better surviving these mechanical and chemical agents as opposed to small vertebrate species may be prevalent. The techniques used to collect fossil material during the 19th century also suggest that fine sieving of the sediments was lacking (compare Figs.4a and 4c with Figs.4b and 4e), and that a bias towards the collecting of larger fossil vertebrate material is significant.

In the Mare aux Songe, only one and now lost, undescribed finch (Newton and Gadow, 1893) was collected; all the other vertebrates discovered were medium to large species, i.e. >10g. On Réunion, the marshy area of l'Ermitage has a high ratio of large bone >200 mm and only one passerine and few bat bones were discovered amongst the thousands of tortoise remains (Mourer-Chauvire *et al.*, 1999). The bias toward tortoise remains may well be explained in part by their ecology rather than preferential fossil preservation. Giant tortoises regularly wade into muddy pools (Grubb, 1971) and once there occasionally become trapped and die, therefore, increasing their representation in the fossil record. Like Réunion, Mauritius and Rodrigues once harboured large numbers of endemic tortoises and although they are not dealt with here in any detail, they constitute a major component of the known fossil remains (e.g., Clark, 1866; Arnold, 1979). Interestingly, the majority of the giant tortoise material collected from the Mare aux Songes represents bone >100mm, and smaller elements, e.g. digits, are comparatively rare.

The Plaine Corail fossil locality on Rodrigues, has fared somewhat better in terms of small vertebrate preservation. The only Mascarene passerine described from fossil material, the Rodrigues starling, *Necropsar rodericanus*, was described in 1879 (Günther & Newton, 1879) and Cowles (1987) collected two as yet undescribed passerines in 1974. Recent collections include the discovery of two *Nactus* geckos and two new geckos of unknown affinity (Arnold, 2000). Fine-mesh sieves were used to extract this extremely small, delicate material (Arnold *pers.comm*), which is in marked contrast to the 'hand-picking' techniques employed in the 1800s.

BIOEROSION

Bioerosion can be classified as the abrasion of hard surfaces through the activity of organisms (Neumann, 1966) and according to Akpan (1990) divided into two groups depending on bioerosional activities. The first group, which includes all bacteria, lichen, plants, algae, fungi and insects, can result in partial or complete destruction of solid substrates leaving empty spaces in the material. The second group includes molluscs, which mechanically abrade substrates through the action of radulae.

Methods

Methodology comprises examination of the bone material using SEM, binocular microscopy and thin section petrography on a petrological microscope. These methods can reveal the extent of bone surface textures and aid in determining the state of bone preservation or decay. Due to the very young nature of the fossil material, all of the material examined exhibited minimal diagenetic changes at a scale resolvable at microscopic level. There may well have been changes at the molecular level, however, as the bone is no longer white. Unlike any of the other material used in this analysis, the hare *Lepus* sp., has a maximum age of c.1850, as this is the time when hares were first introduced onto Réunion (Cheke, 1987). However, in comparison with the other fossil bone material used, the hare material was extremely fragile and disintegrated with extreme ease when being examined.

Thin section analysis

Thin sections of 10? thickness were produced using standard petrological techniques. Sections were produced from the following localities; Mare aux Songes, Mauritius; Caverne Gastonia, Rodrigues; and Caverne de la Tortue, Réunion and including the skeletal elements listed in table 3.

Results

Dodo *Raphus cucullatus* (Fig.5a)

BMNHmau1 – proximal end of right humerus (see Table 3) with transverse section taken proximal to mid shaft.

The periosteal surface is exhibits no visible traces of damage. However, the endosteal layer exhibits minor bioerosion with possible penetration by bacteria or fungi of the lamellar cortical layer reaching 0.4 mm in depth. The Vascular canals are visible and remain intact with no erosional damage, particularly at the periosteal surface. The trabecular layer is intact in the specimen, but not visible in thin section. Osteocyte lucanae are visible and intact, particularly within the primary (lamellar) bone. Two large fractures in the upper lamellar cortical layer have been infilled with silt. Minor cracking has occurred throughout the specimen, probably as a result of the preparation technique. This is particularly noticeable when some shrinkage of the resin has occurred during curing and can cause cracking in delicate samples.

Solitaire *Pezophaps solitaria* (Fig.5b)

BMNHrod1 – left distal end of ulna (see Table 3) with transverse section taken proximal to distal end.

Despite the morphology being well preserved, the histology is poor due to early diagenetic changes. The periosteal surface is particularly well preserved in this solitaire and the bone is enveloped in a layer of laminated radial calcite 2 mm thick. The endosteal layer is also well preserved and has a thin layer of $CaCO_3$ covering the surface. The dark layers appear to represent silt sediment intrusions and clearly defined lamellae are present (arrowed), with each representing a possible mineralising event. The initial deposits surrounding the bone comprise lamellae of $CaCO_3$ separated with very fine sediment deposits. Between the outer lamellae, a large deposit of poorly sorted sediment, which includes mollusc fragments (upper right), is separated by a very narrow mineralising events, with calcite deposits accumulating between sediment input. Small Calcite deposits have also been deposited on the endosteal layer of the bone, otherwise the trabecular layer is not infilled. Vascular canals are visible and are unaffected by erosional agencies.

Hare *Lepus* sp. (Fig.5c)

BMNHre1. Proximal end of right femur (see Table 3) with transverse section taken distal to mid shaft.

This specimen exhibits extensive damage to the periosteal surface and lamellar cortical layer. The endosteal surface is less eroded, but the trabecular bone has almost completely disappeared. The specimen has been infilled with silt where structural damage has exposed the lamellar cortical layer. Small amounts of sediment have also adhered to the periosteal and endosteal surfaces. Vascular canals are visible but have been extensively enlarged by bioerosion or possible chemical agency in the upper lamellar cortical layer.

SEM

Small 2x2 mm samples of bone were cut from identifiable elements obtained from the following localities: Mare aux Songes and Le Pouce, Mauritius; Caverne Gastonia, Rodrigues; Caverne de la Tortue, Marais L'Ermitage, and Grotte aux Sable, Réunion. All samples were mounted on 20 mm stubs using conductive carbon compound.

Results

Dodo *Raphus cucullatus* (Fig.6a)

BMNHmau1 Proximal end of right humerus. Section taken from cranial surface distal to the proximal end (see Table 3).

On the natural surface at 100 µm magnification, the periosteal surface is generally undamaged with only the occasional indentation. Sediment has adhered to the surface, and some pitting is visible but restricted. At 10 µm magnification, the periosteal surface is also intact with little surface damage. The angular deposits lower left and right are sediment remains attached to the surface. Fracture damage (upper left) appears to be recent, as the edges are fresh, sharp and rough and at right angles to the periosteal surface.

Indet. bird (Fig.6f)

BMNHmau2. Section taken from the mid shaft, on the caudal surface of the tibiotarsus (see Table 3).

On the periosteal surface at 1 mm magnification, deep pitting is evident, which appears to be a result of possible bioerosion. This has expanded the vascular canals deep within the periosteal layer; otherwise the surface area appears intact. At 10 µm magnification, some damage to the periosteal surface has occurred but is erratically distributed. The damaged surface has exposed the lamellar cortical layer and almost reaches the endosteal surface within. These damaged areas comprise some sharp, rough edges at right angles to the periosteal surface and also rounded thinned edges with no sharp right angles, which indicates that their origins are both mechanical and bioerosional. The periosteal surface, when intact, is without pitting or indentation.

Solitaire *Pezophaps solitaria* (Fig.6b)

BMNHrod1. Distal end of tibiotarsus. Section taken from the caudal surface on the proximal end (see Table 3).

On the periosteal surface at 10 µm magnification, the periosteal surface is almost intact, but where mechanical damage occurs (middle center), the edges are rounded and thinned with no sharp edges indicating natural erosion. No pitting or indentation is visible, but a thin irregular coating of $CaCO_3$ has covered the periosteal surface. The surface is also irregularly covered with sediment particles. At 100 µm magnification, the periosteal surface is comparatively intact, with $CaCO_3$ and sediment particles adhered to the surface. There is no evidence of bioerosional activities.

Hare *Lepus* sp.(Fig.6c)

BMNHre1. Proximal end of right femur. Section taken from the mid-shaft on the dorsal surface (see Table 3).

Species	Associated material	Unassociated material (undamaged)	Unassociated material (damaged). Includes eroded proximal and distal ends of post cranial and cranial elements	Percentage of total fossil material per taxon collected from Mauritius fossil localities by Thirioux
Raphus cucullatus	1 complete/ 1 partial skeleton	1 carpus and metacarpals		10%
Aphanapteryx bonasia	1 complete skeleton, 1h, r, u	1 c; 2 h; 1 ra; 1 u; 16 ow; 2 p; 20 ol; 35 v	1 r; 1 m; 1 s; 6 h; 2 u; 4 ow; 2 p; 6 f; 6 t; 8 ta; 20 ol; 15 v	95.8%
Dryolimnas c. cuvieri		2 h		16%
Mascarenotus sauzieri	1 h, ra, u	2 h; 6 u; 2 ow; 3 f; 1 p; 3 t; 4 ta; 10 ol; 8 v	1 c; 3 r; 4 m; 4 h; 4 u; 2 ow; 1 f; 1 p; 5 t; 4 ta; 2 v	89%
Anas sp		1 ow		6%
Circus maillardi		1 s; 1 ta; 1 ol	1 h; 3 u; 3 ow; 1f; 1 t; 2 ta	70%
Lophopsittacus mauritianus		2 u; 1 ta	5 s; 1 ta	11.6%
Psittacula echo	1 h, ra, u, s	1 r; 8 h; 8 u; 10 ow; 8 f; 6 t; 7 ta; 10 ol; 10 v	5 m; 4 h; 2 u; 10 ow; 2 f; 6 t; 23 ta; 10 ol; 20 v	100%
Psittacula bensoni		3 h; 1 ow; 3 ta	1 r; 2 m; 2 h; 4 ow; 8 ta	100%
Streptopelia picturata?		1 h; 2 ow; 1 ta	1 p	100%
Alectroenas nitidissima		1 h		100%
Columba mayeri		8 h; 1 u; 2 f; 2 t		100%
Passerines		200+ including all elements	300+ including all elements	100%

Table 2. Material collected by Etienne Thirioux and deposited in the MI, MNHN, NHM, and UMZC. The importance of his collection can easily be appreciated, particularly concerning the smaller bird species. Key: c=cranium; r=rostrum, m=mandible, s=sternum, h=humerus; u=ulna; ra=radius; ow=other wing elements; p=pelvis; f=femur; t=tibiotarsus; ta=tarsometatarsus; ol=other leg elements; v=vertebra.

Taula 2. *Material recol·lectat per Etienne Thirioux i dipositat a les col·leccions MNHN, NHM, i UMZC. Es pot apreciar fàcilment la importància d'aquesta col·lecció, particularment pel que fa els ocells passerins petits. Clau: c=crani; r=rostre, m=mandíbula, s=esternó, h=húmer; u=ulna; ra=radi; ow=altres elements de les ales; p=pelvis; f=fèmur; t=tibiotarse; ta=tarsometatarse; ol=altres elements de les potes; v=vèrtebres.*

At 100 µm magnification, almost the entire periosteal surface exhibits surface damage. In particular, the numerous pits and furrows appear to be the result of invertebrate radulae. The lamellar cortical layer has been exposed and vascular canals have become visible through the periosteal surface. Also at 100 µm magnification, a number of comparatively large rod-shaped structures (middle center) appear to be invertebrate frass or possibly invertebrate egg cases. They are too large to represent bacteria. At 1 µm magnification, the vascular canals have been infiltrated with fungal mycelia creating severe destruction of the surface. The segmented hyphae can be seen on the surface and entering the pores. Some of the hyphae can be seen with secondary growth and very fine filaments attesting to fungal damage.

Indet. bird (Fig.6d)

BMNHre2. Section taken from the mid-shaft of the caudal surface of tibiotarsus (see Table 3).

At 1 µm magnification, the periosteal surface is generally intact, but complex fracturing has taken place in some areas forming hexagonal fracture zones and has exposed the lamellar cortical layer below. The edges of the damage are not sharp and at right angles to the periosteal surface and appear to represent non-mechanical destruction as compared to direct mechanical damage. Where the periosteal surface is undamaged, little pitting or indentation is visible. At 100 µm magnification, severe damage has occurred on large areas of the periosteal surface, resulting in exposure of the lamellar cortical layer. Some sediment has also infilled the damaged area. Where visible, the edges of the damaged areas are rounded and not at right angles to the periosteal surface suggesting that bioerosional or chemical degradation has taken place.

***Puffinus* sp.** (Fig. 6e)

BMNHre3. Proximal end of ulna. Section taken from the ventral surface of shaft, distal end (see Table 3).

At 100µm, the periosteal surface is intact and exhibits no pitting, cracking or large-scale damage. Some gentle indentation can be seen top right and this may be a result of chemical or bioerosional damage. The specimen is cracked with sharp edges at right angles to the periosteal surface from the proximal to the distal end, indicating that this may be a post-collection artifact. A deep groove running diagonally from left to right can be seen in the center, and appears to be the result of a tool mark or a knife mark, suggesting this particular specimen had been consumed by man.

Remarks

The SEM and microscopy data suggests that fossil material is subject to a number of destructive agencies that include mechanical, chemical and bioerosional means. Mechanical and bioerosional destruction to fossil bone is more prevalent in marsh deposit fossils, which are subject to periodic fluvial activity, greater exposure to weathering and increased scavenging. Rapid burial, although important to marsh material, is evidently not a prerequisite for good bone preservation within cave systems, since many of the cave fossil specimens were found on or near the surface and are in excellent condition. The cave localities seemingly prevent much of the scavenging agencies removing and disarticulating material but in certain conditions, possible chemical and certainly bioerosional agencies can rapidly destroy fossil material. Chemical agencies are much harder to ascertain and it is not within the scope of this paper to cover this aspect in any great detail.

Species and number	Locality colouration	Element	Locality
Raphus cucullatus NHMmau1	Characterised by a light tan, deep chocolate or almost black colouration exhibiting root marks where the background colour is light tan. Very rarely, <2% of the material is bleached white.	Proximal end of right humerus	Mare aux Songes, Mauritius
Indet bird NHMmau2	Characterised by a light tan, often with darker speckling.	Midshaft of ulna fragment	Le Pouce, Mauritius
Pezophaps solitaria NHMrod1	Characterised by a light cream to almost white colouration.	Left distal ulna	Caverne Gastonia, Plaine Corail, Rodrigues
Lepus sp. NHMre1	Characterised by dark cream, light tan to almost white.	Proximal end of right femur	Caverne de la Tortue, Réunion
Indet bird NHMre2	Characterised by a light tan, with some darker speckling	Midshaft of ulna fragment	Marais L'Ermitage, Réunion
Puffinus sp. NHMre3	Characterised by a light to dark tan with some visible root marks	Midshaft of ulna fragment	Grotte aux Sable, Réunion

Table 3. List of specimens used in diagnosis.

Taula 3. Llista dels espècimens emprats a l'estudi.

pH

All of the sediments collected from the Mascarenes are alkaline, a result of weathering from alkalinic basaltic rocks. This suggests that a low CO_3 content, coupled with high humidity of the Caverne de la Tortue may be the primary factor in rapid deterioration of bone in this locality. The neutral/alkaline composition of the marsh sediments on Réunion and Mauritius may act as a buffering agent to chemical degradation and protect the material from bioerosion. Unlike an acidic marsh environment, e.g. skin and nail but no bone preservation of the bog people (Shipman, 1981), only bone has survived in the marsh deposits of Mauritius and Réunion suggesting a more neutral/alkaline environment. Marsh environments usually have a low pH (Martin, 1999), therefore, the neutral-alkaline chemistry of the sediments (see Table 4) may be conducive to bone preservation. Although bioerosion is not significant on fossil material collected from marsh localities, minor damage due to fluvial agencies, however, is common to many of the elements and compared to cave deposits, rapid burial appears to be an important factor for preservation in the marsh deposits due to the abundance of scavengers (see below).

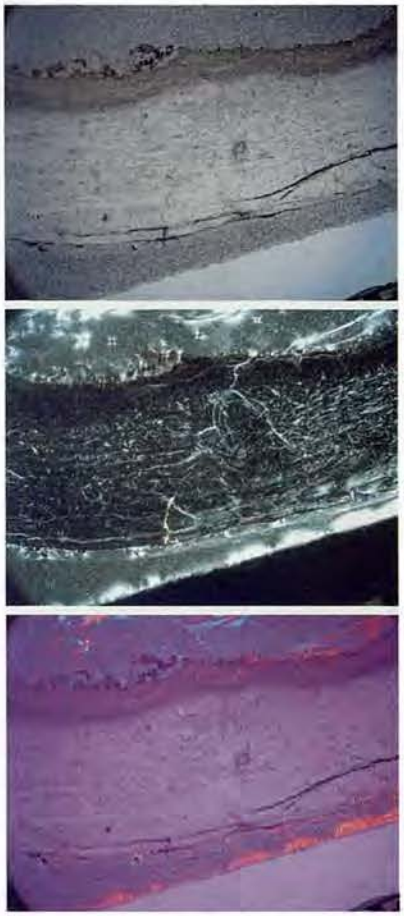


Fig. 5a. Thin section PPL (top); XPL (center); tint PPL (bottom). Dodo *Raphus cucullatus* BMNHmau1. Proximal end of right humerus with transverse section taken proximal to mid shaft. Scale bar = 1mm. In tint PPL, arrows indicate endosteal layer; bioerosion reaching the lamellar cortical layer; osteocyte lucanae; fractures within the upper lamellar cortical layer; periosteal layer. For full description see thin section results.

Fig. 5a. *Secció prima PPL (a dalt); XPL (centre); PPL tenyit (a sota). Dodó,* Raphus cucullatus, *BMNHmau1. Extrem proximal d'húmer dret amb secció transversa presa a la part proximal d'enmig de la canya. Escala = 1mm. A la secció PPL tenyida, les fletxes indiquen la capa endòstia; la bioerosió assoleix la capa cortical lamellar; osteocyte lucanae; fractures dintre la capa cortical lamellar superior; periosti. Per a una descripció completa, vegeu la secció de resultants de les seccions primes.*

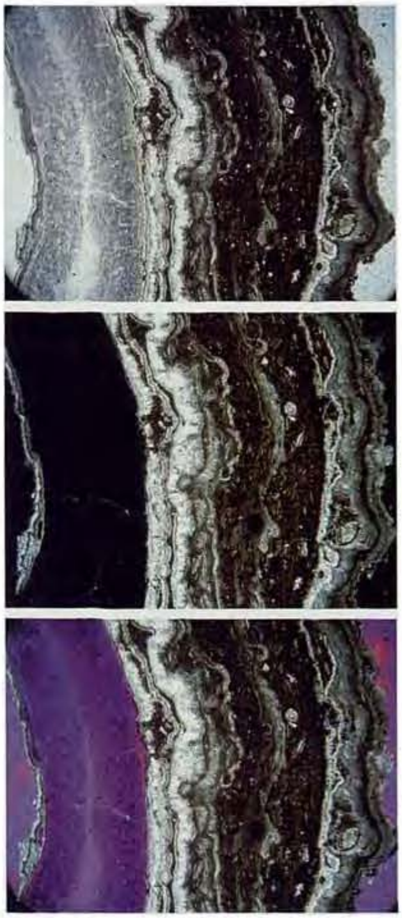


Fig. 5b. Thin section PPL (top); XPL (center); tint PPL (bottom). Solitaire *Pezophaps solitaria* BMNHrod1. Distal end of left ulna with transverse section taken proximal to distal end. Scale bar = 2mm. In tint PPL, arrows represent a different mineralising event. For full description see thin section results.

Fig. 5b. *Secció prima PPL (a dalt); XPL (centre); PPL tenyida (a sota). Solitari* Pezophaps solitaria *BMNHrod1. Part distal d'ulna esquerra amb secció transversa presa a la part proximal de l'extrem distal. Escala = 2mm. A la PPL tenyida, les fletxes representen un esdeveniment mineralitzador diferent. Per a una descripció completa, vegeu la secció de resultants de les seccions primes.*

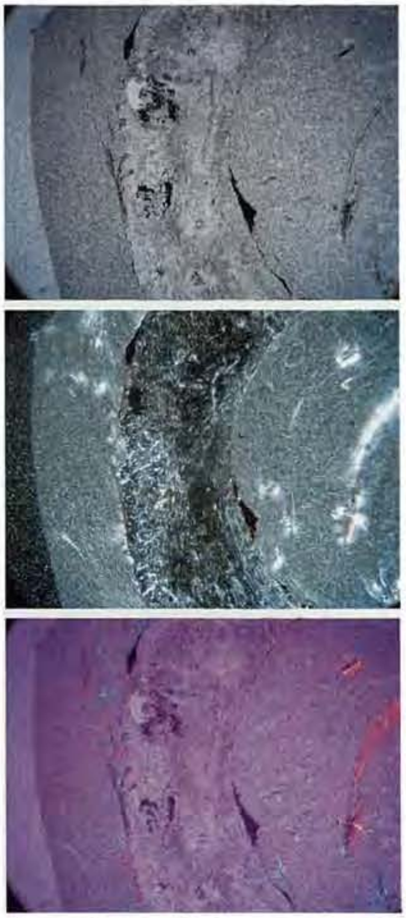


Fig. 5c. Thin section PPL (top); XPL (center); tint PPL (bottom). Hare *Lepus* sp. BMNHre1. Proximal end of right femur with transverse section taken distal to mid shaft. Scale bar = 1mm. In tint PPL, arrows indicate damage to the periosteal surface; upper lamellar cortical layer; sediment infill; endosteal layer; sediment adhesion to the endosteal layer. For full description see thin section results.

Fig. 5c. *Secció prima PPL (a dalt); XPL (centre); PPL tenyida (a sota). Llebre* Lepus *sp. BMNHre1. Extrem proximal de fèmur dret amb una secció transversa presa a la part distal de mig de la canya. Escala = 1mm. A la PPL tenyida, les fletxes indiquen danys a la superfície del periosti; capa cortical lamellar superior; reompliments de sediment; capa endòstia; adhesió de sedimenta la capa endòstia. Per a una descripció completa, veure els resultats de les seccions primes.*

SCAVENGING

Scavenging plays an extremely important role in any natural ecosystem. Carrion is broken down and minerals/nutrients become re-absorbed into several trophic levels via scavenger waste products, burial and dispersal (Shipman, 1981). On the pre-human Mascarenes, it is assumed that a number of species acted as scavengers on the islands, including terrestrial invertebrates, e.g. dipterid flies, molluscs, land crabs, and terrestrial vertebrates such as giant tortoises, scincid lizards and birds. With the extinction of many vertebrate species and a serious reduction in the numbers of invertebrate species after the arrival of man to the islands, scavenging by introduced rats, mice, pigs, cats, dogs, tenrecs, and monkeys presumably now play a significant part in the break down and removal of carrion.

Little attention has been given to the prodigious numbers of land crabs that formerly inhabited the Mascarenes, and in the coastal regions at least it can be envisaged that a scenario not too dissimilar to that on Christmas Island today once occurred there. In particular, Francois Leguat (1708) noted the vast numbers of crabs that were originally present on the mainland of Rodrigues:

"*The Land-Crabs were our next Enemy* [after rats]. *'Tis impossible to destroy them, there's being a prodigious quantity of them in the Grounds., and 'tis very difficult to get them out of their Holes. Their Burrows are very broad, and have several Entrances……, They tore up ourPlants in our Gardens day and Night, and if we shut up the Plants in a sort of Cage, in hopes of saving them ; if they were not far off, they wou'd dig under ground from their Burroughs to get to the plants, and tear them up under the cage.*"

He further describes the breeding season:

"*A little before and after the Full-Moons in July and August, these Crabs march by Millions, from all parts of the Island to the sea. We never met with one but what was laden with eggs : We might then have destroy'd great quantities of them with ease, for they go in Prodigious Troops, and being far from their Burroughs, have no place of Retreat. We'd sometimes kill'd three Thousand in one Evening with Sticks, yet we cou'd not perceive the next day, that their Number was anyway Diminish'd.*"

Large crabs, although somewhat scarce, can still be seen on some of the larger offshore islets of Rodrigues today (pers.obs) and their burrowing activities reflects the impact they would have had as major scavengers on the mainland.

Terrestrial crabs play a major part in excavating the ground and removing, disarticulating and burying all edible objects (Alexander, 1979). Most land crabs, i.e. crabs that predominantly or temporarily inhabit dry habitats, have been exterminated from Mauritius and Rodrigues, but in pre-human times there would have been a great diversity of species. On Rodrigues, the large carnivorous and scavenging species *Geograpsus grayi, Ocypoda cordimana*, and the hermit crab *Coenobita rugosa* were originally found in woods, and some distance from the shore (Miers, 1879). *Ocypoda* sp. is a scavenger but also an adept hunter of sea turtle eggs and hatchlings (Alexander, 1979) and, no doubt, preyed on terrestrial giant tortoise eggs and young as well. True carnivorous crabs, e.g. *Birgus, Geograptus*, and *Coenobita*, feed on other crabs, tortoise and turtle young and scavenge any dead carcasses they encounter (Alexander, 1979; Bourn & Coe, 1979). A very large species, the coconut crab, *Birgus latro*, has been hunted to extinction over most of its range including the Mascarene Islands (Cheke, 1987). On Aldabra, where it is still relatively common, it is a dominant nocturnal scavenger of large and small carcasses, particularly giant tortoises, *Aldabrachelys gigantea* (Bourn & Coe, 1979). According to Bourn and Coe, the coconut crab easily shears off large chunks of decaying flesh, dragging away limb bones and entrails. Up to 14 were observed together at one time on the carcasses of giant tortoises on Aldabra; an entire juvenile tortoise of 38.5 cm curved carapace length was also taken by the crabs. Assumedly, small vertebrate carcasses would, therefore, have needed to have been rapidly buried on the Mascarenes and to some depth in order not to have been removed and disarticulated by land crabs. Such are the scavenging depredations of land crabs, when present in large concentrations, they have been cited as the main reason why so few carrion-breeding flies occur on Aldabra (Alexander, 1979) and they can also seriously influence stratigraphical interpretation by inverting fossil remains due to burrowing (Worthy and Wragg, 2003). On Rodrigues, crab remains of *Geograpsus* and *Ocypoda* are extremely numerous within the caves of the Plaine Corail, which gives an indication of their former abundance and extent of their inland excursions. Unfortunately, little research has been undertaken concerning the techniques crabs use to dispatch carcasses and the resultant damage to bone. For example, claw marks and/or distinctive bone fractures caused by crab scavenging are unrecorded. The virtual extinction of land crabs on the Mascarenes and, as a consequence, the lack of recent crab-scavenged bone material, has made any comparative interpretations concerning the fossil material impossible.

MASS MORTALITY OR TIME AVERAGING

On oceanic islands, many agencies can potentially cause mass mortalities. In the Mascarenes, these agencies include severe cyclones, drought and disease. Shipman (1981), although referring to mammals, suggested the following natural mortality factors: predation, disease, senility (old age), accident and starvation/dehydration, all of which could provide a continual supply of potential carcasses for deposition. However, faunal non-attritional mass mortalities are often difficult to detect in mixed and disarticulated fossil assemblages. Large numbers of disarticulated skeletal elements of a single species may provide evidence for mass mortality or conversely, a slow accumulation of specimens over many centuries. Austin & Arnold (2001) provided carbon isotope ratio dates ranging from 1700-400 BP for the giant tortoise *Cylindraspis* sp., collected from the Mare aux Songes, and 1000 BP for a specimen of *Cylindraspis* from l'Ermitage (Mourer-Chauviré *et al.*, 1999). These results indicate that the deposition of specimens has been going on for at least one millennium at both localities and thus a slow natural accumulation may well have taken place. These accumulations are, therefore, concluded to be a consequence of time-averaging.

Fig. 4a. Terrestrial birds and the fossil record: Mare aux Songes, Mauritius. All material collected from the Mare aux Songes. The data set is based on the collections held at the UMZC; BMNH; MI; MHNH; and UCB. The fossil elements of the dodo *Raphus cucullatus* constitute 75% of the total fossil elements, whilst passerines have not been preserved.

Fig. 4a. *Ocells terrestres i registre fòssil: Mare aux Songes, Mauritius. Tot el material recol·lectat a la Mare aux Songes. El conjunt de dades es basa a les col·leccions hostatjades als UMZC, BMNH, MI, MHNH i UCB. Els elements fòssils de dodó,* Raphus cucullatus, *constitueixen el 75% del total d'elements fòssils, mentre que els passerins no es troben ben representats.*

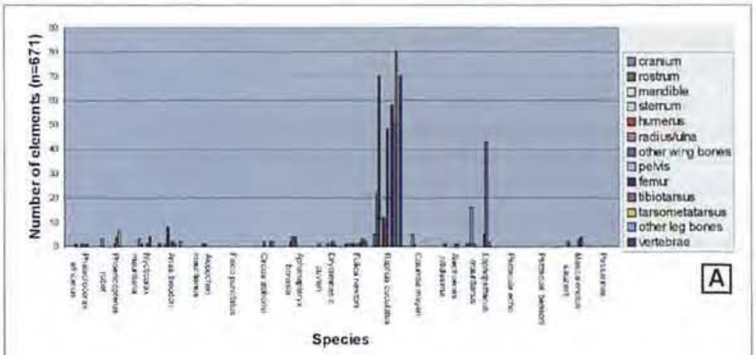


Fig. 4b. Terrestrial birds and the fossil record: Le Pouce, Mauritius. All material collected from caves on Le Pouce and adjacent areas. The data set is based on the collections held at the UMZC; BMNH; MI; MHNH; and UCB. The red rail *Aphanapteryx bonasia* represents 16% (constituting only 1.4% from the Mare aux Songes); echo Parakeet *Psittacula echo* 16% (no specimens have been recovered from the Mare aux Songes); and dodo *Raphus cucullatus* 11% of the total fossil elements represented. Passerines constitute 42% of the total fossil elements, which is in direct contrast with the marsh deposit of the Mare aux Songes.

Fig. 4b. *Ocells terrestres i registre fòssil: Le Pouce, Mauritius. Tot el material recol·lectat a coves de Le Pouce i àrees adjacents. El conjunt de dades es basa a les col·leccions hostatjades als UMZC, BMNH, MI, MHNH i UCB. El rascló roig* Aphanapteryx bonasia *representa el 16% (fa només l',4% a Mare aux Songes);* Psittacula echo *16% (no s'han recuperat exemplars a Mare aux Songes), i el dodó* Raphus cucullatus, *l'11% del total d'elements fòssils representats. Els Passerines fan el 42% del total d'elements fòssils, cosa que contrasta molt amb el dipòsit de l'aiguamoll de Mare aux Songes.*

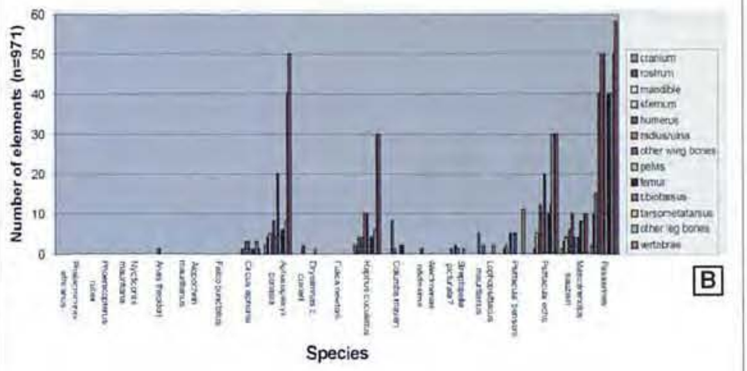


Fig. 4c. Terrestrial birds and the fossil record: Marais de l'Ermitage, Réunion. Data from Mourer-Chauviré *et al* (1999). Understandably, water and marsh birds, e.g. flamingo *Phoenicopterus ruber*, solitaire (ibis) *Threskiornis solitarius*, night heron *Nycticorax duboisi* and the anseriformes genera *Anas*, *Aythya*, and *Alopochen* comprise 87% of the total fossil elements discovered. This marsh locality is situated 0.7km from the coast in a low lying sedimentary basin.

Fig. 4c. *Ocells terrestres i registre fòssil: Marais de l'Ermitage, Réunion. Dades de Mourer-Chauviré et al (1999). Comprensiblement, els ocells aquàtics i limícoles, com, per exemple, el flamenc* Phoenicopterus ruber, *el solitari (un ibis)* Threskiornis solitarius, *l'orval* Nycticorax duboisi *i les Anseriformes dels gèneres* Anas, Aythya *i* Alopochen *comprenen el 87% del total dels elements fòssils obtinguts. Aquest aiguamoll està situat a 0,7 km de la costa en una conca sedimentària baixa.*

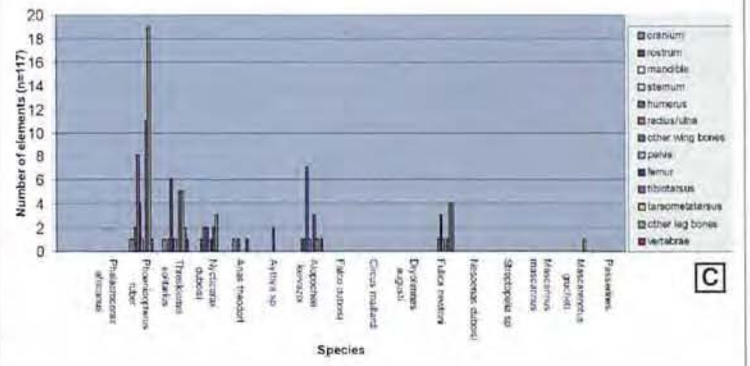


Fig. 4d. Terrestrial birds and the fossil record: Grotte des Premiers Francais; Grotte de l'Autel; Caverne de la Tortue, Réunion. Data from Mourer-Chauviré *et al* (1999). The lack of passerine material within these three cave systems suggests that they have not being preserved in the deposits. Mourer-Chauviré *et al* (1999) mention the absence of passerines from all of the Réunion fossil localities, despite fine-sieving much of the sediments.

Fig. 4d. *Ocells terrestres i registre fòssil: Grotte des Premiers Francais; Grotte de l'Autel; Caverne de la Tortue, Réunion. Dades de Mourer-Chauviré et al. (1999). La manca de materials de passerins a aquests tres sistemes cavernícoles suggereix que no es conserven be a aquests depòsits. Mourer-Chauviré et al. (1999) esmenta l'absència de passerins a tots els depòsits de la Réunion, malgrat que molts dels sediments es varen porgar amb cedasos de malla fina.*

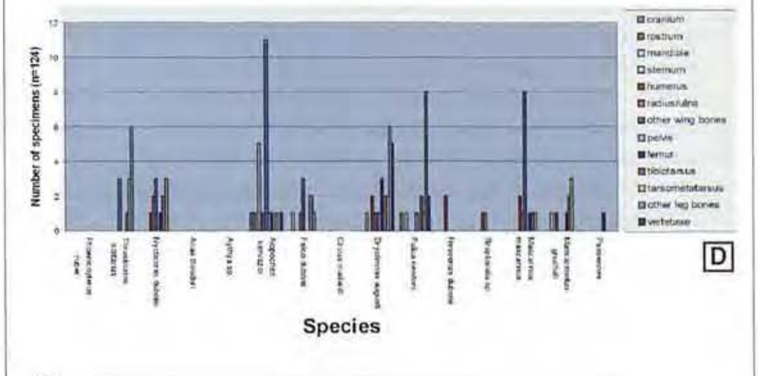
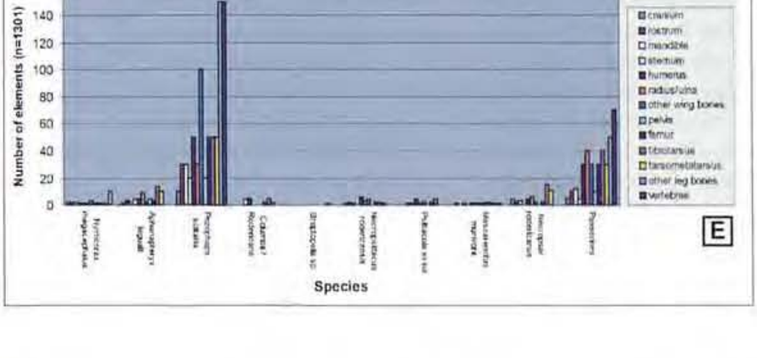


Fig. 4e. Terrestrial birds and the fossil record: Plaine Corail, Rodrigues. The data set is based on the collections held at the UMZC; BMNH; MI; MHNH; and UCB. Due to the large number of specimens of the solitaire *Pezophaps solitaria*, only unnassociated material was counted and constitutes 56% of the total fossil elements. Many complete associated skeletons have also been discovered. Passerines are also well represented comprising 28% of the total. Conversely, owls (0.7% of the total) and parrots (2.8% of the total) are extremely rare.

Fig. 4e. *Ocells terrestres i registre fòssil: Plaine Corail, Rodrigues. El conjunt de dades es basa a les col·leccions hostatjades als UMZC, BMNH, MI, MHNH i UCB. Degut al gran nombre d'especímens de solitari,* Pezophaps solitaria, *només es va contabilitzar el material no associat, que constitueix el 56% del total d'elements fòssils. També s'han descobert molts d'esquelets associats complets. Els Passerines també es troben ben representats, comprenent el 28% del total. Contràriament, les òlibes i mussols (0.7% del total) i els lloros (2.8% of the total) són extremadament rars.*



In addition, it has been suggested that the large accumulation of articulated and associated remains of the solitaire, *Pezophaps solitaria*, in the caverns of the Plaine Corail was due to the last survivors taking refuge from severe cyclonic events or the forest burning by tortoise hunters (Slater, 1879a; Cowles, 1987). As no carbon dating of the material has been attempted, it is premature to suggest that a mass mortality has occurred and again it is more likely to represent a slow, periodic build up of individuals.

THE LACK OF SMALL VERTEBRATE REMAINS, E.G. PASSERINES

Certain Mascarene Island fossil localities including the Mare aux Songes are depauperate in small vertebrate remains, i.e. species weighing <10g or elements <5cm. However, many hundreds of small elements have been collected in cave localities where sieving has taken place (Figs. 4a and 4e). Passerines are known from historical accounts and occasionally approached plague proportions, e.g. the endemic Fody *Foudia* sp., on Réunion (Dubois, 1674). Therefore, certain conditions must exclude small vertebrate remains such as those of passerines from the fossil record of the marsh and Réunion cave localities. The possible reasons for the absence of small vertebrate taxa in the fossil record may be due to:

a) Small taxa evolved/arrived after formation of the fossil locality – unlikely due to the young age of the fossil localities
b) Collection failure – particularly relevant when sediments not sieved
c) Taxa absent due to taphonomic processes – small, lightweight carcasses more likely to be washed away and/or completely removed by scavengers from marsh deposit; bioerosional and chemical degradation within cave deposits
d) Taxa absent due to restricted distribution – unknown as there is extremely limited knowledge about former distribution of passerines on the Mascarenes. Presumably, volant passerines could have inhabited all of the available land space but some species, e.g. Réunion cuckoo-shrike *Coracina newtoni* are extremely restricted in range (Probst 1997), and appear to have always been so
e) Taxa extant but absent in area due to localised extinction or unsuitability of habitat – unknown as there is extremely limited knowledge about former distribution of passerines on the Mascarenes

Assessing fossil diversity can be confused by variation in the durability of skeletal remains present. Some bone may be unidentified in an assemblage because processes such as fluvial activity, predation and scavenging, bioerosion and dissolution may all render small or delicate bones unrecognisable or remove them completely from the fossil record. There is a bias towards the preservation of large bone (>10cm) compared to small bone in the marshy deposits, but not elsewhere, e.g. the cave deposits on Mauritius and Rodrigues. After sieving, Sauzier collected proportionally very few small fossil elements of larger vertebrate species from the Mare aux Songes (Newton & Gadow, 1893)(Fig.4a), and intense sieving in the marsh of L'Ermitage, Réunion, produced very few small vertebrate fossil elements (Mourer-Chauviré *et al.*, 1999) (Fig.4c). Lava tunnel deposits are subject to intense bioerosional and chemical activities, which can completely destroy fossil remains in a comparatively short time, e.g. the hare *Lepus* sp., a species introduced no earlier than c. 1850 (Cheke, 1987). Human bias can also skew faunal composition based on the fossil record. It is much more difficult to identify small, often homogenous skeletal material than larger vertebrate remains and thus the smaller elements are often ignored even when collections are available. Further difficulties arise from historical accounts and the passerine fossil record. Passerines were barely mentioned in the early literature unless they were of an edible size, e.g. *Hypsipetes* bulbuls (Cheke, 1987), and only one of the larger passerine species has been described from the fossil record (Figs.3b and Fig.3c); all other passerines were described from skin specimens held in collections. Determining the diversity of small birds from the historical record is thus problematical.

CONCLUSION

Is the fossil record of the Macarenes representative of the prehuman biota? It is crucial that mode of formation of the fossil assembly is recognised and also that the nature of any taphonomic biases that have affected a particular fossil assemblage be determined. Fossil localities can contain distorted proportions of taxa or skeletal elements. They are assumed to be strongly biased assemblages and therefore are unrepresentative of the original diversity that was available to be fossilised at the time of formation. Furthermore, unscientific collecting and description of specimens can result in further bias (Figs.3b and 3c). For example, seabirds form only a small proportion of museum fossil remains from the Mascarenes (Fig.3d), yet comprise (or comprised) a large component of the ecology (Cheke 1987). This bias has important implications for their use in palaeodiversity estimates and palaeoecological reconstruction. Unfortunately, for most fossil assemblages the true diversity of preservable taxa that were available for inclusion can never be known.

Mascarene fossil assemblages are the result of a complex interaction of biological, chemical and sedimentologi-

Locality	pH value	Sediment status
Mare aux Songe, Mauritius	6.9	Neutral-Alkaline
Marais l'Ermitage, Réunion	7.4	Alkaline
Caverne de la Tortue, Réunion	8.0	Alkaline
Plaine Corail, Rodrigues	7.4	Alkaline
Standard	6.5	Neutral-Alkaline

Table 4. pH results of samples taken from selected Mascarene fossil localities. The poorest preservation of fossil material and the highest alkalinity was found in the Caverne de la Tortue, Réunion.

Taula 4. *Resultats de pH de les mostres preses a diferents localitats fòssilíferes mascarenyes seleccionades. La pitjor preservació i la major alcalinitat es va trobar a la Caverne de la Tortue, Réunion.*

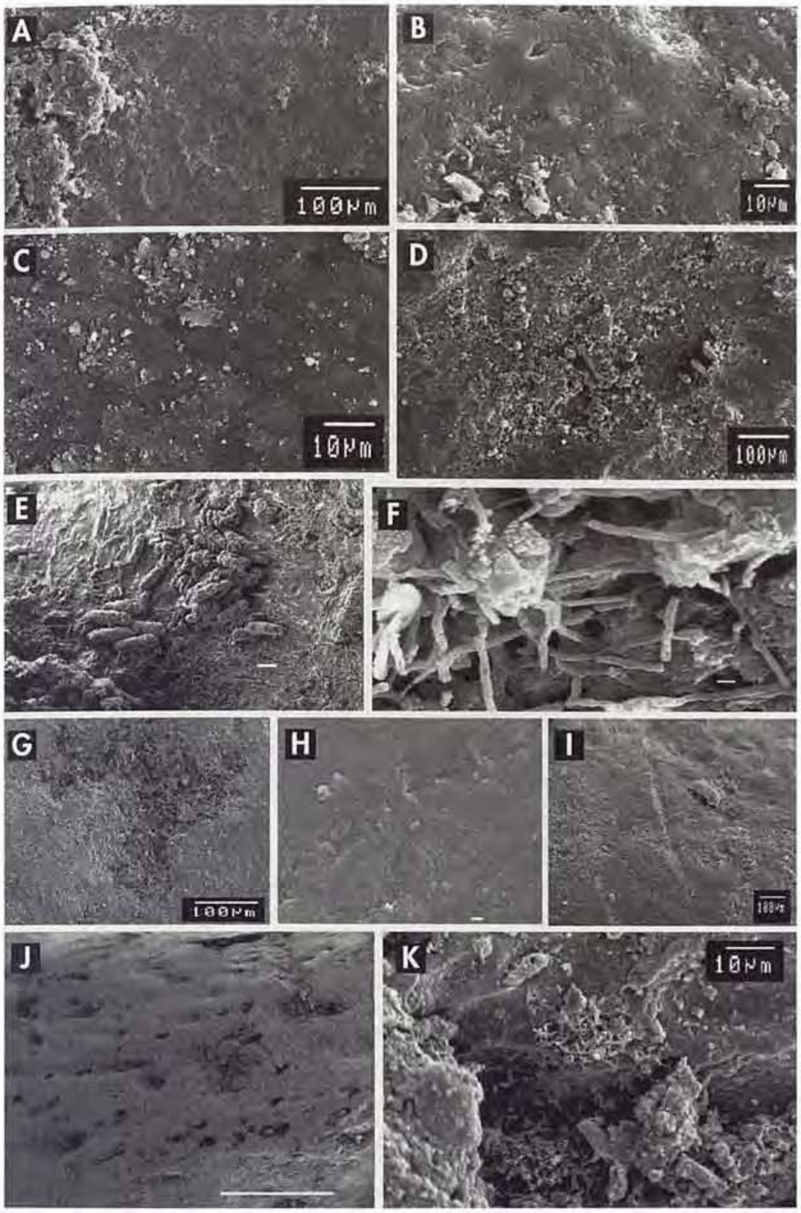


Fig. 6. SEM. **Dodo *Raphus cucullatus*** **BMNHmau1**. Proximal end of right humerus with transverse section taken proximal to mid shaft. Scale = 100μm (A) and 10μm (B). **Solitaire *Pezophaps solitaria*** **BMNHrod1**. Distal end of left ulna with transverse section taken proximal to distal end. Scale = 10μm (C) and 100μm (D). **Hare *Lepus* sp. BMNHre1**. Proximal end of right femur with transverse section taken distal to mid shaft. Scale bar =100μm (E), 1μm (F) and 100μm (G). **Indet bird BMNHre2**. Section taken from the mid-shaft of the caudal surface of tibiotarsus. Scale bar = 1μm (H). ***Puffinus*** **sp. BMNHre3.** Proximal end of ulna with section taken from the ventral surface of shaft, distal end. Scale bar = 100μm (I). **Indet. bird BMNHmau2**. Section taken from the mid shaft, on the caudal surface of the tibiotarsus. Scale bars = 1μm (J) and 10μm (K).

Fig. 6. SEM. ***Dodó,*** **Raphus cucullatus,** *BMNHmau1. Extrem distal d'húmer dret amb una secció transversa presa a la part proximal de la canya central. Escales = 100μm (A) i 10μm (B).* ***Solitari,*** **Pezophaps solitaria,** *BMNHrod1. Extrem distal d'ulna esquerra amb una secció transversa presa a la part proximal de l'extrem distal. Escales = 10μm (C) i 100μm (D).* ***Llebre*** **Lepus** *sp. BMNHre1. Extrem proximal d'húmer dret amb secció transversa presa a la part distal de la canya central. Escales = 100μm (E), 1μm (F) i 100μm (G).* ***Indet ocell BMNHre2.*** *Secció presa a la meitat de la canya de la superfície caudal del tibiotars. Escala = 1μm (H).* **Puffinus** *sp. BMNHre3. Extrem proximal d'ulna amb una secció presa a la superfície ventral de la canya, a l'extrem distal. Escala = 100μm (I).* ***Ocell indeterminat, BMNHmau2.*** *Secció presa a la meitat de la canya, a la superfície caudal del tibiotars. Escala = 1μm (J) i 10μm la (K).*

cal processes. Hydrological processes are also important but all of these processes do not explain all depositional criteria. There is a fundamental lack of knowledge concerning other taphonomic processes operating during the formation and deposition of fossil material from marsh and cave environments. As with many palaeontological studies, interpretation of data is often difficult to resolve and many factors have to be taken into consideration when attempting to reconstruct palaeoenvironments, particularly on dynamic oceanic islands.

Sadly, further data from the Masacarenes may not be obtainable in the foreseeable future. It is ironic that recent high profile ecological research and conservation on a group of islands, which famously contain so many endangered species, has failed to notice that the most endangered areas today are the fossil localities themselves. On Mauritius, the collecting areas of Thirioux are now impenetrable and completely overgrown with dense exotic scrub. The Mare aux Songes has witnessed a hundred years of neglect and is presently scheduled to become part of a golf course. The largest and almost unique limestone locality at Bel Ombre has also been extensively quarried. On Réunion, the Kervazo cave site has now been removed for construction purposes and in early 2003, a road was built right through l'Ermitage marsh completely destroying the locality (Mourer-Chauviré pers. comm). On Rodrigues, a recent extension of the airport threatens some very important caverns on the Plaine Corail and roof collapse has already occurred (pers. obs). It is, therefore, imperative that as much information is obtained from seemingly well-known or new fossil localities while the opportunities still exist.

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MITOCHONDRIAL AND NUCLEAR GENES FROM THE EXTINCT BALEARIC BOVID *MYOTRAGUS BALEARICUS*

Carles LALUEZA-FOX, Lourdes SAMPIETRO, Tomàs MARQUÈS, Josep Antoni ALCOVER & Jaume BERTRANPETIT

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Resum

Myotragus balearicus és un bòvid extingit de les Illes Balears Orientals o Gimnèsies (Mallorca, Menorca i illots que les envolten). *Myotragus* presenta nombroses novetats evolutives que enfosqueixen el seu emplaçament taxonòmic dintre dels Caprinae. A un projecte desenvolupat els darrers anys hem analitzat diferents mostres d'ossos de *Myotragus* i hem recuperat el gen cytb mtDNA complet, una seqüència del gen 12S mtDNA, una seqüència de la regió D-loop, i una seqüència d'un gen nuclear multi-còpia (el rDNA 28 S), emprant tècniques de DNA antic. Diferents controls experimentals, incloent-hi un laboratori dedicat, obtenció independent de rèpliques, solapament de fragments, extraccions múltiples i clonatge de productes PCR, donen suport a l'autenticitat de les seqüències. Els arbres filogenètics nous situen consistentment *Myotragus* a una posició basal al clade *Ovis+Budorcas*. Emperò, alguns gèneres de Caprinae, tals com *Oreamnos* i *Ammotragus*, presenten posicions inestables a tots els arbres. La branca llarga observada a *Myotragus* correspon a una taxa evolutiva elevada a aquesta línia que podria estar associada a la seva petita mida corporal. A més, la recuperació de gens nuclears per primera vegada d'una espècie extingida de la Mediterrània obre noves possibilitats de recerca sobre els trets genòmics i fenotípics.

Paraules clau: *Myotragus balearicus*, DNA antic, Caprinae, DNA mitocondrial, DNA nuclear, filogènia.

Abstract

Myotragus balearicus was an extinct endemic bovid from some of the Balearic Islands (Mallorca and Menorca). *Myotragus* had many evolutionary novelties that obscure its phylogenetic placement among the extant Caprinae. In a project developed during the last years, we have analyzed several *Myotragus* fossil bones, and have retrieved the complete mtDNA cyt b gene (1143 bp in length), a sequence from the mtDNA 12S gene, a sequence from the D-loop region, and a sequence from a multi-copy nuclear gene (the 28 S rDNA), using ancient DNA techniques. Different experimental controls, including a dedicated laboratory, independent replication, overlapping fragments, multiple extractions and cloning of PCR products, support the authenticity of the sequences. The new phylogenetic trees consistently place *Myotragus* in a position basal to the *Ovis+Budorcas* clade. However, some Caprinae species, such as *Oreamnos* and *Ammotragus*, show unstable positions in all trees, attributable to a quick initial radiation of the Caprinae lineages. Moreover, the retrieval of nuclear genes for first time from an extinct species from the Mediterranean area opens new possibilities of research on comparative genomics and genetic bases of phenotypic traits.

Key words: *Myotragus balearicus*, ancient DNA, Caprinae, mitochondrial DNA, nuclear DNA, phylogeny.

INTRODUCTION

DNA sequences have been retrieved from extinct species in the last two decades (see Hofreiter *et al.*, 2001). Almost all the ancient DNA studies, including the first complete extinct genome (Cooper *et al.*, 2001) have been based on the analysis of mitochondrial DNA (mtDNA), the genome of the organelles that provide energy to the cells. The reason of this identification between ancient DNA and mtDNA is due to the fact that the DNA is chemically degraded; since there are thousands of mtDNA copies in each cell, it is much more easier to retrieve mitochondrial than nuclear DNA. To date, only few studies have been able to soundly demonstrate the retrieval of sequences from nuclear DNA genes from Siberian mammoths, the ground sloth and the cave bear (Greenwood *et al.*, 1999; Orlando *et al.*, 2002; Poinar *et al.*, 2003).

In this study, we have retrieved mitochondrial and nuclear DNA sequences from the extinct *Myotragus balearicus*, a bovid that evolved in isolation in the Balearic Islands (Bate, 1909). *Myotragus* is a extremely modified Caprinae, characterized by a series of unusual morphological traits developed throughout more than three million years of evolution (Alcover *et al.*, 1981; Bover & Alcover 1999a; 1999b; Alcover *et al.*, 1999a; 1999b), that became extinct between 3,640 and 2,135 years cal BC (Ramis & Alcover, 2001), probably after the arrival of first humans to these islands. The morphological peculiarities of *Myotragus*, including extreme size reduction, a single evergrowing lower incisor, modified limb bones and frontal eyes (Alcover *et al.*, 1981), makes it difficult to clarify its taxonomic position.

In previous studies (Lalueza-Fox *et al.*, 2000; 2002), we obtained bits of the mtDNA cytochrome *b* (cyt *b*) gene from two different *Myotragus* bone specimens from Mallorca island, one found in Cova Estreta (Pollença) and the other found in Cova des Gorgs (Escorca). The cyt *b* sequences indicated that *Myotragus* seems to be genetically close to the Takin (*Budorcas*) and the Sheep (*Ovis*). Moreover, the quick radiation of all the Caprinae, roughly 20 Mya (Vrba, 1985) and the short cyt *b* fragment retrieved made the previous analysis unable to fully resolve the phylogeny of this group. To try to fully resolve its phylogeny, we decided to retrieve the complete cyt *b* gene and some other genetic markers of *Myotragus*; to do this, we selected a third *Myotragus* sample, excavated in 2002 from Cova des Gorgs, that looked macroscopically very well preserved; we have designed different sets of overlapping primers for retrieving the complete cyt *b* gene, as well as a fragment from another mtDNA gene, the 12 S, and a fragment from the mtDNA HVR I. In addition, we retrieved a nuclear gene from the same extract, 28 S rDNA (located in the 10 chromosome), taking advantage to the fact that there are some hundreds of copies of this gene in the vertebrate genome (Laudien Gonzalez *et al.*, 1985). Our future aims are to try to retrieve single copy nuclear genes from this species.

MATERIALS AND METHODS

A left tibiae (MNIB 60176) bone from *Myotragus balearicus* from Cova des Gorgs (Escorca, Mallorca), dated to 6,010-5,830 cal BC 2s (Beta-177239) was chosen for DNA analysis because of its excellent external preservation.

DNA was extracted following standard procedures described elsewhere (Lalueza-Fox *et al.*, 2002). The sample was demineralized overnight, incubated overnight with a lysis solution, extracted with phenol-chloroform and concentrated and desalinized with centricon columns. Several fragments of mtDNA cyt *b* gene were successfully amplified and sequenced until complete the whole gene (Table 1).

The cyt *b* sequences matched the sequence previously retrieved from another *Myotragus* bone from the

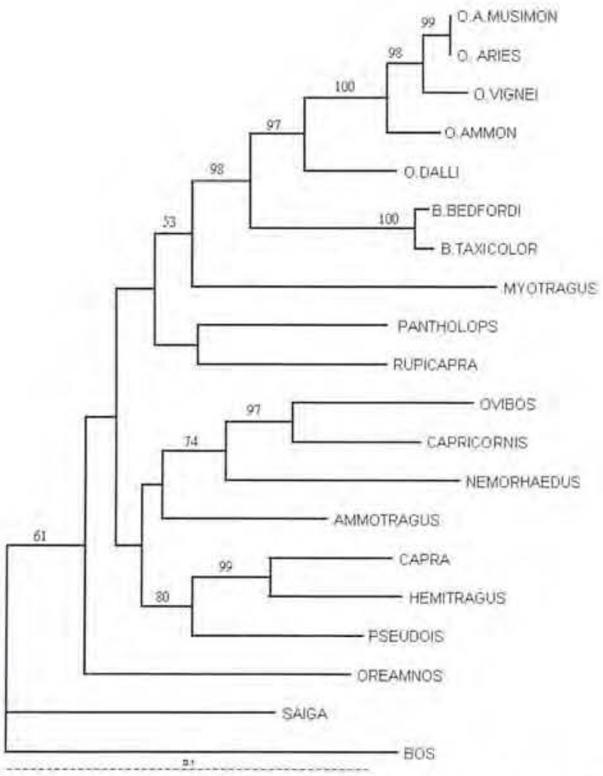

Fig. 1. Maximum likelihood tree of the entire cyt *b* (1143 bp) of all Caprinae species in databases. Nodes with bootstrap support greater than 50% are depicted.

Fig. 1. Arbre de màxima probabilitat del cyt b (1143 parells de bases) de totes les espècies de Caprinae. S'indiquen els nodes amb un suport de bootstrap superior al 50%.

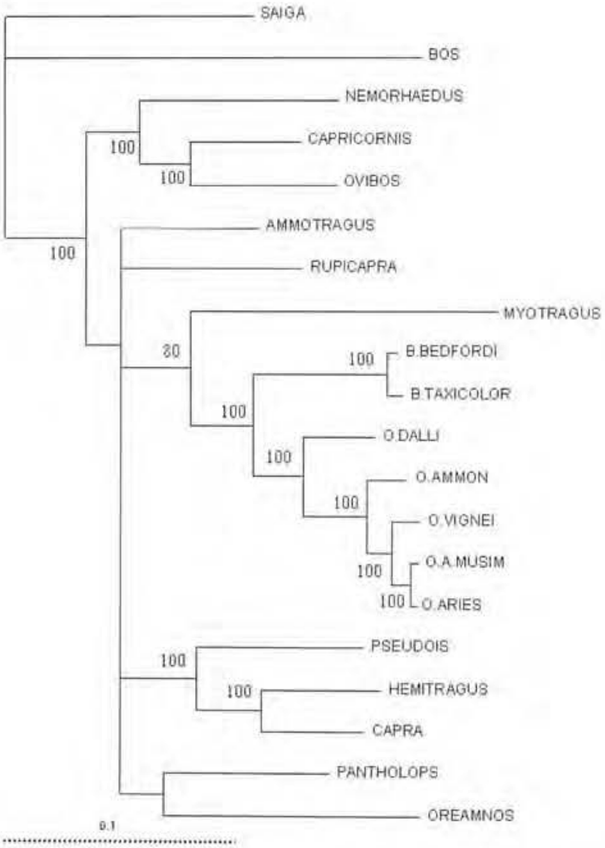

Fig. 2. Bayesian tree of the entire cyt *b* (1143 bp) of all Caprinae species. Nodes with bootstrap support greater than 50% are depicted.

Fig. 2. Arbre Bayesià del cyt b (1143 parells de bases) de totes les espècies de Caprinae. S'indiquen els nodes amb un suport de bootstrap superior al 50%.

same site (Lalueza-Fox *et al.*, 2000); multiple controls, such as independent replication of the results in two different laboratories and cloning of different, overlapping PCR products, contributed to the authentication of the sequences. All the work was carried out in a dedicated ancient DNA laboratory, with UV lights, air-positive pressure and regular bleaching of the working surfaces. No signs of contamination with exogenous DNA were observed along the study. For the 12 S gene, some primers were designed to match the previous Caprinae sequences published by Gatesy *et al.* (1997).

Due to the exceptional quality of this extract, a pilot project was launched for trying to retrieve a fragment of a nuclear gene. The 28 S rDNA was chosen because it is present in some hundreds of copies in the genome. The primers used to amplify the 28 S rDNA were those designed by Greenwood *et al.* (1999) to be vertebrate-specific (Table 1). 5 μl of extract were added to 20 μl PCR reactions, containing 1x reaction buffer, 1 unit of taq DNA polymerase, 2.5 mM of MgCl2, 25 pmol of each primer. Forty cycles of 1 min at 94°C, 1 min at 50°C and 1 min at 72°C were performed. PCR products were resolved in 1% low-melting agarose gels in a TA buffer; bands were excised from the gel and subjected to a second 30 cycles of PCR with limiting reagents. PCR product was cloned with the SureClone Ligation Kit (Pharmacia, Upsala, Sweden) following supplier's intructions. Inserts were sequenced with 3100 Gene Analyzer (Applied Biosystems).

Several phylogenetic analyses were performed with the *Myotragus* sequences; the whole cyt *b* of all Caprinae genera (including subspecies of *Ovis* and *Budorcas*), were obtained from the GenBank, and a maximum likelihood analysis (ML) was performed using PHYLIP v3.6 (Felsenstein, 1993) package. The analysis considered *Bos* as outgroup, although it could be observed that *Saiga* behaved also as a perfect outgroup. To test the robusticity of the tree clades, a 1,000 bootstrap repeats were performed. A maximum parsimony (MP) and NJ tree from a distance matrix (using Kimura two parameters model) were also generated for the cyt b using PHYLIP v3.6. A Bayesian inference of phylogeny was also performed with MrBayes v.2.01 programme (Huelsenbeck & Ronquist, 2001), using general time reversible (GTR) model, partition defined for each base position within codons, sites specific rates estimated for each partition and estimated proportion of base types from the data. 500,000 trees were generated, with burning completed by the 5,000th tree; thus, the first 5,000 trees were discarded.

RESULTS

The complete cyt *b* gene (Table 2) was retrieved in 11 overlapping fragments (see Table 1), including the 338 section already retrieved in Lalueza-Fox *et al.* (2002). All cyt *b* fragments were routinely cloned (not shown), although very few heteroplasmies were detected in the direct sequencing, attributable to both the exceptional preservation of the sample and the short lengths of the fragments; consequently, the error rates (number of substitutions/1,000 bp) are very low (<2).

The 12 S gene sequence (Table 4) was retrieved in three overlapping fragments (Table 1), and the short HVRI sequence (Table 3) in a single amplification (Table 1). The 12 S sequence displays a substitution diagnostic of all Caprinae, a G in np 732 of the *Ovis* mtDNA genome (Gatesy *et al.*, 1997). There are fewer sequences available for the 12 S and HVRI region than for the cyt *b* gene; therefore, we focused the analysis mainly in the latter gene.

The PCR of the 28 S nuclear gene yielded a very faint band around 140 bp and was subsequently cloned and sequenced (Table 1). The 96 bp sequence obtained from *Myotragus* is similar to that found in other Caprinae (Table 5), and clearly different to the human one. Moreover, no other bovids, extinct or living, had been analyzed in the same laboratory; therefore, the 28 S sequence seems to be endogenous of *Myotragus*. The

Cyt *b*	12 S
L14136 5´-GCTTGATATGAAAAACCATCGTTG-3´	L599 5'-CTCAAAGGACTTGGCGGTGC-3'
H14313 5´-TGTGTCGGATGTATAGTGTATTG-3´	H673 5´-GAAGATGGCGGTATATAGAC-3´
L14310 5´-ATCCTAACAGGCCTATTCCT-3´	L671 5´-TCACCAATCCTTGCTAATAC-3´
H14481 5´-CCGATGTTTCATGTTTCTAGGA-3´	H805 5'-AATGGCTTTCGTATTAAATT-3'
L14475 5´-CGAGGCCTGTACTACGGATC-3´	L733 5'-AACAAGAGTAAGCTCAATCA-3'
H14650 5´-AACTGAGAATCCGCCTCAG-3´	H891 5'-CGGTGTGTGCGTGCTTCATG-3'
L14631 5´-GCTATCCCATACATTGGAAC-3´	
H14813 5´-GTATARTARGGGTGAAATGG-3´	HVRI
L14792 5´-TCCAACAACCCCTCAGGAATTC-3´	L16,125 5'-CCTTCTTCTCGCTCCGGGCC-3'
H14987 5´-TTGATCGTARGATTGCGTATGC-3´	H16,227 5'-AATTAGTCCATCGAGATGTC-3'
L14973 5´-CCTCACATCAAACCCGAATG-3´	
H15159 5´-TCCTCCAATTCATGTGAGTG-3´	28 S
L15152 5´TTCTGAATCCTAGTAGCCGACC-3´	L28S 5´-GGTCGTCCGACCTGGGTATA-3´
H15327 5´-TGCAGTCATCTCCGGTTTACAAGAC-3´	H28S 5´-TCTAATCATTCGCTTTACCGGAT-3´

Table 1. Primer sequences used in this study for different mtDNA and nuclear genes; L and H refer to light and heavy strand, respectively. and numbers refers to the 3' position of the *Ovis* mtDNA sequence.

Taula 1. *Seqüències de cebadors emprades a aquest estudi per a diferents gens de DNA mitocondrial i nuclear; L i H es refereixen a filaments lleugers i pesats, i els nombres es refereixen a la posició 3' de la seqüència de DNA mitocondrial d'*Ovis.

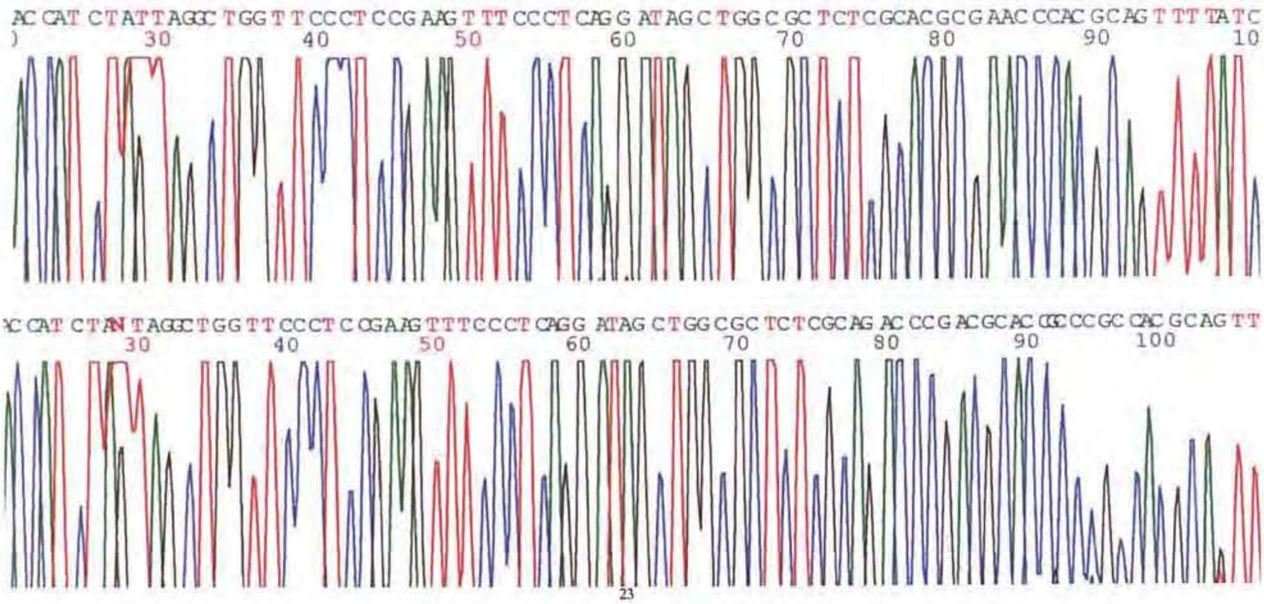

Fig. 3. Sequence chromatogram of the diagnostic fragment of the *Myotragus* 28 S nuclear gene (top), as compared to human (bottom).

Fig. 3. Cromatograma de la seqüència del fragment diagnòstic del gen nuclear 28 S de Myotragus *(a dalt) comparat amb l'humà (a sota).*

cloning of the 28 S PCR product showed that two of the sequences (about 20% of the clones) are human contaminants; this accounts for the noise observed in the direct sequencing of the PCR product. Most likely, the human DNA comes from handling of the *Myotragus* bones during its excavation and posterior morphological study.

The cyt *b* ML tree (Fig. 1) shows a topology roughly similar to that found in previous studies on Caprinae phylogeny (e.g., Hassanin & Douzery, 1999; Lalueza-Fox *et al.*, 2002); some of the clades, that were already supported by high bootstrap figures, are present, specially *Capricornis+Ovibos+Nemorhaedus* (74,3%) and *Hemitragus+Pseudois+Capra* (79,8%). Some species show unstable positions in the trees, especially *Ammotragus, Pantholops, Rupicapra* and *Oreamnos* (with *Saiga* in a basal position and likely to be not a Caprinae); again, the problematic position of these taxa have been already reported (e.g., Groves & Shields, 1996; Hassanin & Douzery, 1999). However, our tree has been finally able to resolve the phylogenetic position of *Myotragus*, which it is now basal to the *Budorcas+Ovis* clade; the bootstrap value for the *Myotragus+Budorcas+Ovis* grouping is 53,1%. The MP and NJ trees produced an identical tree topology for *Myotragus, Budorcas* and *Ovis*, although the already mentioned unstable species differ in their placement among different trees. In the Bayesian tree (Fig. 2), the three stable Caprinae clades (*Capricornis+Ovibos+Nemorhaedus, Hemitragus +Pseudois+Capra* and *Ovis+Budorcas*) have bootstrap values of 100; the position of *Myotragus* basal to the latter species is supported by a lower bootstrap figure of 80.

The ML tree with the 12 S fragment produced a slightly different topology (not shown); the *Capricornis+Ovibos+Nemorhaedus* and *Hemitragus+Pseudois +Capra* clades are well supported by bootstrap analysis (85.4% and 70.8%, respectively), while *Myotragus* tend to cluster basal to the *Capricornis+ Ovibos+Nemorhaedus* clade instead of with *Ovis*. This discrepancy most likely can be attributed to its basal placement in the *Budorcas+Ovis* clade in the cyt *b* tree, which cause unstability in the *Myotragus* placement when fewer species and shorter DNA sequences are consider, as it is the case with the 12 S gene. In the HVR1 sequence (not shown), *Myotragus* shows the highest homology with *Budorcas* (85%).

DISCUSSION

Different genetic trees support the phylogenetic position of *Myotragus* as closely related to *Ovis* and *Budorcas*. From its basal position at the *Ovis+Budorcas* clade, it can be deduced that both taxa diverged after the divergence of the *Myotragus* lineage, likely to have occurred around 5.35 million years ago, when the *Myotragus* ancestors became isolated in the emerging Balearic Islands. However, the complete resolution of the Caprinae phylogeny cannot be achieved with the cyt *b* gene alone, as some species of the subfamily (specially *Oreamnos*) still have an unstable position. This is likely to be due to the initial evolutionary radiation of the Caprinae.

A fairly long genetic branch of *Myotragus* in the ML and NJ trees was previously detected in the short cyt *b* fragment (Lalueza-Fox *et al.*, 2002) and was attributed to a faster substitution rate in this species with respect to other Caprinae. This different rate was initially explained by a putative early age of first reproduction and a shorter generation time in *Myotragus* than in other Bovids (Lalueza-Fox *et al.*, 2002). In mammals, the generation and gestation time are usually related to the body size (see, for instance, Martin & MacLarnon, 1985).

Myotragus is the smallest Caprine known; some adult specimens reached only 22 cm in height. The ratio of neonate to adult *Myotragus* weight has been estimated, from recently found neonate bone remains, to be only 2%, again the smallest ratio ever described in Bovids (Bover & Alcover, 1999a). Although the reproductive strategy and gestation time in *Myotragus* are currently unknown, it seems clear that the extreme reduction in body size affected both biological processes. From the correlation between generation time and body size recorded in mammals (Martin & MacLarnon, 1985) a reduction both in the age of the first reproduction and in the generation time would seem to be the expected result of such a dwarfism process. The long-term isolated evolution towards dwarfism not only occurred in the Balearic Islands, but also in other Mediterranean Islands, where endemic mammals like dwarf deers, dwarf hippos and dwarf elephants were present until the arrival of humans (Burness *et al.*, 2001). Therefore, this an evolutionary hypothesis that could be tested with the retrieval of DNA from other dwarf endemics and the comparison of evolutionary rates of related extant species. However, several tests we applied with the complete cyt *b* data, based on the ratio of synonymous (Ks parameter) and non synonymous substitutions (Ka parameter) between *Myotragus* and related Caprinae (*Budorcas* and *Ovis*), failed to find statistically significant differences in the *Myotragus* branch length.

An alternative explanation for the long branch of *Myotragus* is that the sub-structuring of its evolutionary lineage is missing; in this sense, there were other Caprinae endemics in Europe and in other Mediterranean islands (e.g. *Nesogoral* and *Gallogoral*) that could be closely related to *Myotragus*. The inclusion of genetic data from these lineages, if technically possible, might significantly alter the *Myotragus* branch pattern we found.

Finally, this study is one of the few instances where ancient nuclear DNA has been recovered, and the first one in which nuclear DNA has been retrieved from an extinct species from the Mediterranean area. The possibility of retrieving nuclear sequences, with a wide range of genetic markers available, could finally allow to clarify the phylogenetic position of *Myotragus* as well as the extant Caprinae with a problematic position. Also, our research demonstrates the potential interest of this approach in comparative genomics; our future goals are to retrieve single copy nuclear genes that can be informative of phenotypic aspects of *Myotragus*.

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Capricornis	ATG	ATT	AAC	ATT	CGA	AAA	ACT	CAC	CCA	CTA	ATA	AAA	ATT	GTA	AAT	AAT	GCA	TTT	ATT	GAT
Nemorhaedus	...	.CC	...	..C	...	...	...	...	...	...	...	...	..C	...	...	...	...	...	...	..C
Oreamnos	...	.CC	...	..C	...	...	..C	...	...	...	...	...	...	...	..C	..C	...	...	...	..C
Rupicapra	...	.CC	..T	...	...	...	...	...	...	...	...	...	...	...	..C	..C	...	..C	...	...
Ammotragus	...	..C	...	..C	...	...	..C	...	...	...	...	...	...	...	..C	..C	...	...	...	..C
Budorcas	...	..C	...	..C	...	...	...	...	...	...	...	...	..C	...	..C	..C	...	C.C	...	..C
Ovibos	...	.CC	..T	..C	...	...	...	...	...	...	...	...	...	...	...	..C	..G	...	...	..C
Pseudois	...	.CC	...	..C	...	..G	..C	...	...	...	...	...	...	...	..C	..C	...	..C	...	..C
Hemitragus	...	.CC	...	..C	...	...	..C	...	...	...	...	...	...	...	..C	..C	...	...	...	..C
Capra	...	.CC	...	..C	...	..G	..C	...	...	T..	...	...	...	...	..C	..C	...	...	...	..C
Ovis	...	..C	...	..C	...	...	..C	...	...	...	...	...	...	...	..C	..C	...	..C	...	...
Pantholops	...	.CC	...	...	...	...	...	...	...	...	...	...	...	...	..C	..C	...	..C	G..	..C
Saiga	...	..C	...	..C	...	...	..C	...	...	..T	...	...	..C	...	...	..C	...	...	...	...
MYOTRAGUS	...	.CC	...	T.C	...	...	..C	A..	...	...	...	...	...	...	..C	..C	...	..C	...	..C

Capricornis	CTC	CCA	ACC	CCA	TCA	AAC	ATC	TCA	TCA	TGA	TGA	AAC	TTC	GGC	TCC	CTC	CTG	GGC	ATC	TGC
Nemorhaedus	...	...	...	...	C..	...	...	...	.TG	..G	...	...	...	...	...	...	..A	...	...	...
Oreamnos	...	...	..T	...	...	...	...	...	...	...	...	..T	..T	...	..T	...	T.A	..T	...	...
Rupicapra	...	...	G.T	..G	...	...	...	...	...	...	...	...	..T	...	...	...	..A	...	...	...
Ammotragus	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	..A	...	...	...
Budorcas	...	...	..T	...	...	...	...	...	...	...	...	...	..T	..A	...	...	..A	...	.CT	...
Ovibos	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..A	..T	...	...
Pseudois	...	...	G.T	...	...	...	...	...	...	...	...	...	..T	..A	...	...	..A	...	...	...
Hemitragus	..T	...	...	...	...	...	...	...	...	...	...	...	..T	..A	...	...	..A	...	..T	...
Capra	...	...	...	...	...	...	...	...	...	...	...	...	..T	..A	...	...	..A	..A	..T	..G
Ovis	...	...	G.T	...	...	..T	..T	...	...	...	...	...	..T	...	..T	...	..A	...	..T	...
Pantholops	...	...	G..	...	...	...	...	...	...	...	...	...	..T	...	...	...	..A	...	..T	...
Saiga	...	...	G..	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
MYOTRAGUS	...	...	G..	...	...	...	...	...	...	...	...	...	...	...	...	...	..A	...	G..	...

Capricornis	CTA	ATT	CTA	CAA	ATC	CTA	ACA	GGC	CTA	TTC	CTA	GCA	ATA	CAC	TAC	ACA	TCC	GAT	ACA	ACG
Nemorhaedus	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	T..	...	..C	...	..A
Oreamnos	T..	...	T..	...	..T	...	...	...	...	...	...	...	...	...	...	...	...	..C	...	..A
Rupicapra	T..	...	T..	..G	...	...	..G	...	...	...	...	...	...	...	...	...	...	...	...	G.A
Ammotragus	...	...	T..	...	...	T..	...	...	...	..T	...	...	...	...	...	...	...	..C	...	.TA
Budorcas	T..	GC.	...	...	...	T..	...	...	...	...	...	...	...	...	...	...	...	...	...	..A
Ovibos	...	...	...	...	...	T..	...	...	...	..T	...	...	...	...	...	...	...	..C	...	..A
Pseudois	T..	.C.	...	...	...	...	..G	...	...	...	...	...	...	...	..T	...	...	..C	...	.TA
Hemitragus	..G	...	T..	..G	...	...	...	...	..G	...	...	...	...	...	...	...	...	..C	...	.TA
Capra	...	..C	T..	...	...	..G	...	...	...	...	...	...	...	...	..T	...	...	..C	...	.TA
Ovis	T..	...	T..	..G	..T	...	...	...	...	...	...	...	...	...	..T	...	C..	..C	...	..A
Pantholops	T.G	G..	T..	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	...	...	..A
Saiga	...	..C	...	...	..T	...	...	...	...	...	...	...	...	...	...	...	G.T	..C	...	G.A
MYOTRAGUS	T..	..C	T..	...	...	...	...	...	...	...	...	...	...	...	..T	...	...	..C	...	..A

Capricornis	ACA	GCA	TGT	TCT	TCT	GTA	ACA	CAC	ATT	TGC	CGA	GAC	GTA	AAC	TAC	GGC	TGA	ATT	ATC	CGA
Nemorhaedus	...	...	...	...	...	...	...	...	..C	...	...	...	...	...	..T	..T	...	...	...	...
Oreamnos	...	...	..C	..C	...	...	...	...	..C	..T	...	...	...	...	..T	...	...	...	...	...
Rupicapra	...	...	..C	..C	...	...	..C	...	...	...	...	..T	...	...	...	...	...	..C	...	...
Ammotragus	...	...	.TC	..C	...	...	G.C	...	..C	...	...	...	...	...	...	...	...	...	...	...
Budorcas	.T.	...	..C	..C	...	...	G.C	...	...	..T	...	...	...	...	..T	...	...	..C	...	...
Ovibos	...	...	.TC	...	...	...	...	...	...	...	..G	..T	...	...	...	...	...	..C	..T	...
Pseudois	...	...	.TC	..C	...	..G	..T	...	..C	...	..G	..T	..C	...	..T	...	...	...	...	...
Hemitragus	...	...	.TC	...	...	...	..C	...	...	...	...	..T	...	..T	..T	...	...	..C	...	...
Capra	...	...	.T.	..C	...	...	..T	...	...	..T	...	..T	...	..T..T.........C				...	...	
Ovis	...	...	.TC	..C	...	...	..C	...	...	...	...	...	..G	...	..T	...	...	...	...	...
Pantholops	...	...	.TC	...	...	...	..C	...	...	...	...	..T	..T	...	..T	...	...	...	..T	...
Saiga	...	...	.TC	CAC	...	..T	...	...	..C	...	...	...	..C	...	..T	...	...	...	...	...
MYOTRAGUS	...	...	..C	..C	...	..C	G.C	..T	...	...	...	...	...	...	..T	...	...	...	...	...

Capricornis	TAT	ATA	CAC	GCA	AAC	GGA	GCA	TCA	ATA	TTC	TTT	ATC	TGC	CTA	TTC	ATA	CAC	GTA	GGA	CGA
Nemorhaedus	..C	...	...	...	...	...	...	...	...	..T	..C	...	...	...	...	...	...	...	...	...
Oreamnos	...	...	...	...	...	...	..T	..C	...	..T	..C	...	...	...	..T	...	...	...	...	...
Rupicapra	..C	...	..T	...	..T	...	...	...	...	..T	..C	...	...	...	...	...	..T	...	...	...
Ammotragus	...	...	...	...	...	..G	...	...	...	...	...	..T	...	...	...	...	...	...	...	...
Budorcas	...	..G	...	..G	...	...	...	...	...	..T	...	...	...	...	..T	..G	..T	...	...	...
Ovibos	...	...	...	...	...	...	...	...	...	...	..C	...	...	...	...	..G	...	...	...	...
Pseudois	..C	...	...	...	...	...	...	...	...	...	..C	...	...	...	...	...	..T	...	..G	...
Hemitragus	..C	...	...	...	...	...	...	...	...	...	...	...	...	..G	...	...	..T	A.C	...	...
Capra	..C	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	A.C	...	...
Ovis	...	...	...	...	...	..G	...	...	...	..T	...	...	...	...	..T	..G	..T	...	...	...
Pantholops	..C	...	...	...	...	...	...	...	...	..T	...	...	...	...	...	...	...	...	...	...
Saiga	...	...	..T	...	...	...	...	..C	...	...	...	...	...	...	...	...	...	...	...	...
MYOTRAGUS	...	...	..T	...	...	...	...	..C	...	..T	..C	G..	...	...	..T	..G	...	..G	...	..G

Table 2

Capricornis	GGC	CTA	TAC	TAC	GGA	TCG	TAC	ACT	TTC	TTA	GAA	ACA	TGG	AAC	ATC	GGG	GTA	ATT	CTC	CTA
Nemorahedus	...	...	...	...	...	..A	...	...	..T	...	...	...	...	...	...	..A	...	G.C	...	...
Oreamnos	...	...	..T	..T	...	..A	..T	..C	..T	...	...	...	..A	...	..T	..A	...	..C	...	T..
Rupicapra	...	...	..T	...	...	..A	...	...	..T	C..	...	...	..A	...	...	..A	...	..C	...	...
Ammotragus	...	...	..T	...	...	..A	...	...	..T	C..	...	...	..A	..T	G.A	..A	..G	..C	...	...
Budorcas	...	..G	..T	...	...	..A	...	..C	...	...	...	...	..A	...	...	..A	...	...	...	...
Ovibos	...	...	...	...	...	..A	...	...	...	...	...	...	..A	...	..A	...	...	...	..T	...
Pseudois	...	...	..T	...	...	..A	..T	..C	..T	C..	..G	...	..A	...	...	..A	A.C	...	...	...
Hemitragus	...	...	..T	...	...	..A	...	..C	...	C..	...	...	..A	...	..T	..A	...	..C	...	...
Capra	..T	...	..T	..T	...	..A	..T	..C	..T	C..	...	...	..A	...	..T	..A	...	..C	...	..G
Ovis	...	...	..T	..T	...	..A	..T	..C	...	C..	...	...	..A	...	...	..A	...	..C	...	...
Pantholops	..T	...	...	...	...	..A	...	.TC	...	...	..G	...	..A	...	...	...	...	..C	...	...
Saiga	...	..T	..T	...	...	..C	..T	..A	...	C..	...	...	..A	...	..T	..A	..T	...	..T	...
MYOTRAGUS	...	...	...	...	...	..A	...	...	...	C..	...	...	..A	...	...	..A	A..	..C	...	...

Capricornis	CTC	ACA	GCG	ATA	GCC	ACA	GCA	TTC	ATA	GGC	TAT	GTC	CTA	CCA	TGA	GGA	CAA	ATA	TCA	TTC
Nemorhaedus	T.T	G..	A.A	...	...	...	...	...	...	...	...	...	...	...	...	...	..G	...	...	...
Oreamnos	..T	...	A.A	...	...	..G	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Rupicapra	...	...	A.A	...	...	...	..G	..T	..G	...	..C	...	...	...	...	...	..G	...	...	...
Ammotragus	T..	G..	A.A	...	...	...	...	...	...	..A	...	...	..G	...	...	...	..G	...	...	...
Budorcas	T.T	G..	A.A	...	...	...	...	...	...	...	...	...	T..	...	...	...	...	...	...	..T
Ovibos	...	.T.	A.A	...	..T	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Pseudois	T..	G..	A.A	...	...	...	...	...	...	...	..C	...	T.G	...	...	...	...	...	...	..T
Hemitragus	...	...	A.A	...	...	...	...	...	...	...	...	...	T..	...	...	...	..G	...	...	...
Capra	...	G.G	A.A	..G	...	...	...	...	...	...	...	..T	T..	...	...	...	...	...	...	...
Ovis	T.T	G.G	A.A	...	...	...	...	...	...	...	...	...	T..	...	...	...	...	...	...	...
Pantholops	T.T	G..	A.T	...	...	...	...	...	...	...	...	..T	T..	...	...	...	...	...	...	...
Saiga	T..	G..	A.A	...	...	...	...	...	...	..A	...	...	...	...	...	...	...	...	...	...
MYOTRAGUS	T..	...	A.A	...	..T	...	...	...	...	..T	..C	..T	T..	...	...	...	...	...	..T	..T

Capricornis	TGA	GGG	GCT	ACA	GTT	ATT	ACC	AAC	CTC	CTC	TCA	GCA	ATC	CCA	TAC	ATT	GGC	ACA	AAC	CTA
Nemorhaedus	...	...	..A	...	...	...	...	..T	..T	...	...	...	...	...	..T	...	...	...	...	...
Oreamnos	...	..A	...	...	..C	..C	..T	...	...	...	...	...	...	...	...	..C	...	...	...	...
Rupicapra	...	...	..C	...	..C	..C	...	..T	...	...	...	...	...	...	...	..C	...	...	...	...
Ammotragus	...	...	..A	...	..C	..C	...	...	..T	...	...	...	...	...	...	...	...	...	G..	..G
Budorcas	...	..A	..A	...	..C	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Ovibos	...	..A	...	...	..C	..C	..T	...	...	...	...	...	...	...	...	..C	...	...	...	...
Pseudois	...	...	..A	...	..C	..C	...	...	..T	...	...	...	...	..C	..T	...	...	...	..T	...
Hemitragus	...	...	..A	...	..C	..C	...	...	..T	...	...	...	..T	...	..T	..C	...	...	...	...
Capra	...	...	..A	...	..C	..C	..T	..T	..T	...	...	...	...	...	..T	...	...	...	...	...
Ovis	...	..A	..A	...	...	...	...	...	...	..T	...	...	..T	...	..T	...	...	...	...	...
Pantholops	...	..A	..A	...	..A	...	...	...	...	..T	...	...	...	...	...	...	...	...	G..	...
Saiga	...	..A	..A	...	..C	..C	...	..T	...	..T	...	...	...	...	..T	..C	...	...	G..	...
MYOTRAGUS	...	..A	..A	..C	...	..C	...	...	...	...	...	..T	...	...	...	...	..A	..C	..T	..T

Capricornis	GTA	GAA	TGA	ATC	TGA	GGA	GGA	TTC	TCC	GTA	GAC	AAA	GCC	ACC	CTC	ACC	CGA	TTC	TTT	GCC
Nemorhaedus	..C	...	...	...	...	..G	...	...	..A	...	...	...	..T	..T	...	...	...	...	..C	...
Oreamnos	..C	...	...	...	...	..G	..G	...	..A	...	...	...	..T	...	...	...	...	...	..C	...
Rupicapra	..C	..G	...	...	...	..G	..C	...	..G	...	...	...	..T	...	...	...	...	...	...	...
Ammotragus	..C	...	...	...	...	..G	...	...	..A	...	...	...	..T	..T	...	...	...	...	..C	...
Budorcas	..T	..G	...	...	...	...	...	...	..A	...	...	...	..A	T..	...	...	...	...	...	...
Ovibos	..C	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..T	...	..T
Pseudois	..C	...	..G	...	...	..G	...	...	..A	...	...	..G	...	..T	...	...	...	...	..C	...
Hemitragus	..C	...	...	...	...	...	...	...	..A	...	...	...	..T	...	..A	...	...	...	..C	..T
Capra	..C	...	...	...	...	...	...	...	..A	...	...	...	...	..T	...	...	...	...	..C	...
Ovis	..C	...	...	...	..G	...	...	...	..A	...	...	...	..T	...	...	...	...	..T	..C	...
Pantholops	..C	...	...	...	...	..G	...	...	..A	...	...	...	..T	...	..T	...	...	...	...	...
Saiga	...	...	...	...	...	..G	..T	..T	..A	...	..T	...	..A	...	...	...	...	...	..C	...
MYOTRAGUS	...	...	...	...	...	...	...	...	..A	...	...	..G	...	...	...	..A	...	...	..C	..T

Capricornis	TTC	CAT	TTC	ATT	CTC	CCA	TTC	ATC	ATC	ACA	GCC	CTC	GCC	ATA	GTG	CAC	CTA	CTT	TTC	CTC
Nemorhaedus	...	..C	...	..C	...	...	..T	...	..T	...	..T	ACT	..T	...	..C	...	...	...	...	...
Oreamnos	...	..C	...	...	...	...	..T	...	...	G..	...	...	...	...	..C	...	T..	...	...	...
Rupicapra	..T	..C	...	..C	...	...	...	...	..T	G..	...	T.A	...	...	..C	...	...	..C	...	...
Ammotragus	...	..C	...	..C	...	...	..T	G.A	...	G..	...	..A	...	...	..C	...	T..	...	...	...
Budorcas	..T	..C	...	..C	...	...	..T	...	...	G..	...	...	...	...	..C	..T	T..	...	...	...
Ovibos	...	..C	..T	..C	...	...	..T	...	...	GT.	...	...	..T	...	..A	..T	T.G	..C	...	...
Pseudois	...	..C	...	..C	...	...	..T	..T	..T	.T.	...	...	...	...	..C	...	...	...	...	...
Hemitragus	...	..C	...	...	...	...	...	...	..T	G..	...	...	...	...	..C	...	..G	..C	...	...
Capra	...	..C	..T	..C	...	...	...	...	..T	G..	...	...	..T	...	..C	...	..G	..C	...	...
Ovis	..T	..C	..T	...	T..	...	...	...	...	G..	...	...	...	...	..T	...	...	..C	...	...
Pantholops	...	...	...	...	...	...	...	...	...	G..	...	...	...	...	..C	...	...	..C	...	...
Saiga	...	..C	...	..C	...	...	..T	..T	...	G..	..T	...	..T	...	..C	...	...	...	..T	..T
MYOTRAGUS	..T	..C	...	..C	...	...	..T	..T	...	...	...	...	...	...	..C	...	...	..A	...	...

Table 2

Capricornis	CAC	GAA	ACA	GGA	TCC	AAC	AAC	CCC	ACA	GGA	ATC	TCA	TCA	GAC	ACA	GAC	AAA	ATC	CCA	TTC
Nemorhaedus	..T	..G	.T.	...	...	...	...	...	...	..T	...	C..	...	...	.T.	...	...	...	...	..T
Oreamnos	...	...	...	...	..T	..T	...	..A	...	...	..T	.T.	...	...	G..	...	...	..T	...	..A
Rupicapra	..T	...	...	...	..A	...	...	...	...	...	...	C..	...	..T	G.G	..T	...	...	...	..T
Ammotragus	..T	...	..G	...	...	...	...	...	...	...	..T	...	...	...	G..	...	...	...	...	...
Budorcas	...	...	...	...	...	...	...	...	...	...	..T	C.G	...	..T	G..	..T	...	..T	...	..T
Ovibos	...	...	...	...	...	...	...	...	...	...	..T	C..	...	...	..G	...	...	...	...	...
Pseudois	...	...	...	...	..T	...	...	...	...	...	...	C..	...	...	...	...	...	...	...	...
Hemitragus	...	...	...	..G	...	...	...	...	...	..G	..T	C..	...	..T	...	...	...	...	...	..T
Capra	...	...	...	...	...	...	...	...	...	...	..T	C..	...	...	...	...	...	...	...	..T
Ovis	...	...	...	...	...	...	...	...	...	...	..T	C..	..G	...	...	..T	...	..T	..C	...
Pantholops	...	...	...	...	...	...	...	...	...	...	..T	C..	...	..T	G..	...	...	...	...	..T
Saiga	...	...	...	...	..T	...	...	...	...	...	...	C..	...	..T	T..	...	...	...	...	...
MYOTRAGUS	...	...	...	...	...	...	...	...	T..	...	..T	C..	...	...	G..	...	...	...	...	..T

Capricornis	CAC	CCC	TAC	TAC	ACA	ATC	AAA	GAT	ATC	CTA	GGC	ATC	GTG	CTA	CTA	ATC	CTC	ACC	CTC	ATA
Nemorhaedus	...	..T	..T	..T	...	...	...	...	..T	...	...	GCT	A.A	...	...	...	...	...	..T	..T
Oreamnos	...	...	...	..T	..T	..T	...	...	...	...	...	GC.	A.A	...	..C	...	...	...	..T	...
Rupicapra	...	...	...	..T	..C	..T	...	..C	..T	...	...	GC.	.T.	...	...	...	...	...	..T	...
Ammotragus	...	..T	...	...	..C	...	...	...	..T	...	...	GC.	A..	...	...	...	...	...	...	.C.
Budorcas	...	..T	..T	...	..C	..T	...	...	...	...	..A	G..	A.A	...	...	...	...	GT.	...	..G
Ovibos	...	...	...	..T	...	...	...	..C	..T	...	...	GC.	A.A	...	...	...	..T	...	..T	...
Pseudois	...	..T	...	...	..C	..T	...	...	..T	...	...	GCT	.CA	..G	...	...	...	G..	..G	...
Hemitragus	...	..T	...	...	..C	..T	...	...	..T	T..	...	GC.	A.A	...	...	..T	..T	GT.	..A	...
Capra	...	..T	...	...	..C	..T	...	...	...	T..	...	...	A..	...	...	..T	..T	GT.	..A	...
Ovis	...	..T	..T	...	..C	..T	...	..C	...	...	..T	GCT	A.C	...	...	...	...	.T.	...	..G
Pantholops	...	...	...	..T	..C	..T	...	..C	...	...	...	GCT	A.A	...	...	...	..A	.T.	...	...
Saiga	...	...	...	...	..C	..T	...	..C	..T	...	...	GC.	C.A	...	..T	..T	..A	.T.	...	...
MYOTRAGUS	...	...	..T	...	..C	..T	...	..C	...	...	...	..G	A.A	...	...	..T	T.A	.T.	...	..G

Capricornis	CTA	CTA	GTA	CTG	TTC	ACA	CCC	GAC	CTA	CTC	GGA	GAC	CCA	GAC	AAC	TAC	ACT	CCA	GCA	AAC
Nemorhaedus	T..	..G	...	T.A	...	...	..T	...	T..	..T	...	..T	...	...	...	..T	..C	...	...	...
Oreamnos	...	...	...	T.A	...	T..	...	...	T..	...	...	...	...	...	...	...	...	...	...	...
Rupicapra	...	..G	...	..A	..T	...	..T	...	...	...	...	...	...	..T	...	..T	..C	...	..G	...
Ammotragus	...	...	...	..A	..T	...	...	..T	...	...	..G	...	...	...	...	..T	..C	...	...	..T
Budorcas	T.G	...	...	..A	..T	.T.	.TT	...	G..	..T	...	...	...	..T	..T	..T	..C	...	...	..T
Ovibos	...	...	...	T.A	...	...	...	...	...	..T	...	...	...	...	...	..T	..C	...	...	...
Pseudois	T..	...	...	T.A	..T	...	...	...	...	...	...	...	...	...	...	...	..C	...	...	...
Hemitragus	T..	...	...	..A	..T	.T.	...	...	...	..T	...	...	...	...	...	..T	..C	...	...	..T
Capra	T..	...	...	..A	...	...	...	...	...	...	..G	..T	...	...	...	..T	..C	...	...	...
Ovis	...	...	...	..A	...	..G	..T	...	T..	...	...	...	...	...	...	...	..C	...	...	...
Pantholops	T..	...	...	..A	..T	T..	...	...	...	...	...	...	...	...	..T	..T	..C	...	...	...
Saiga	..T	...	..C	..A	..T	T..	..A	...	..G	..T	...	...	...	...	...	...	..R	...	...	...
MYOTRAGUS	...	...	...	..A	...	...	..A	...	...	...	...	...	...	..T	..T	..T	..A	...	..C	...

Capricornis	CCA	CTC	AAC	ACA	CCC	CCT	CAC	ATC	AAG	CCC	GAG	TGA	TAC	TTC	CTA	TTT	GCA	TAC	GCA	ATC
Nemorhaedus	...	...	.G.	...	...	...	...	..T	..A	..T	..A	...	..T	...	...	...	...	..T	...	...
Oreamnos	..G	..A	..T	...	..T	..C	..T	...	...	...	..A	...	...	...	...	...	...	...	...	...
Rupicapra	...	...	...	...	...	...	...	...	..A	...	..A	...	..T	...	T.G	...	...	..T	..G	...
Ammotragus	...	...	...	...	...	...	..T	..T	..A	..T	..A	...	...	...	...	...	...	...	...	...
Budorcas	...	...	...	...	...	...	...	...	..A	..T	..A	...	..T	...	...	...	...	...	...	...
Ovibos	...	...	...	...	...	...	...	..T	..A	..A	...	...	...	...	...	...	...	...	...	...
Pseudois	...	...	...	...	...	...	...	..T	..A	...	...	...	...	...	...	...	...	...	...	...
Hemitragus	...	...	...	...	...	...	...	..T	..A	..T	..A	...	..T	..T	...	...	...	...	..G	...
Capra	...	...	...	...	...	...	...	..T	..A	..T	..G	..G	..T	...	...	...	...	...	...	...
Ovis	...	..T	...	..T	...	...	...	...	..A	..T	..A	...	...	...	...	...	..G	...	...	...
Pantholops	..C	...	...	...	..A	..C	...	..T	..A	..T	..A	..G	...	..T	...	...	...	...	...	...
Saiga	...	..T	...	...	...	..A	..T	..T	..A	...	..A	...	...	...	...	..C	...	...	...	...
MYOTRAGUS	...	...	...	...	...	...	...	...	..A	...	..A	...	...	...	...	..C	...	...	...	..T

Capricornis	CTA	CGA	TCA	ATC	CCC	AAC	AAA	CTA	GGC	GGA	GTT	TTA	GCC	CTA	GTC	CTC	TCA	ATT	CTA	ATC
Nemorhaedus	T..	...	...	...	...	..T	...	...	...	...	..C	C..	...	..G	...	...	...	...	T..	..T
Oreamnos	T..	...	...	...	...	..T	...	...	..A	...	..C	C..	...	...	.C.	...	...	..C	...	G.A
Rupicapra	...	...	...	..T	...	...	...	..T	..A	...	..C	C..	...	...	..A	...	...	..C	...	...
Ammotragus	...	...	...	...	..T	..T	...	..G	..A	..C	..C	C..	..A	...	...	...	...	..C	T..	...
Budorcas	T..	...	...	...	...	...	...	...	..A	...	..C	C.C	...	...	A..	...	...	..C	...	G..
Ovibos	...	...	...	..T	..T	...	...	...	...	...	...	C..	...	...	C..	...	...	...	...	..T
Pseudois	...	...	...	..T	...	...	..G	...	..A	...	..C	C..	...	...	A..	...	...	..C	...	...
Hemitragus	T..	...	...	..T	...	...	...	...	..A	...	..C	C..	...	...	...	...	...	..C	...	...
Capra	...	...	...	..T	...	...	...	...	..A	...	..C	C..	...	...	...	...	...	..C	...	...
Ovis	T..	...	...	...	..T	..T	...	...	..A	...	..C	C.C	...	...	A..	...	...	..C	...	G..
Pantholops	...	...	...	...	...	...	...	...	..A	...	..C	C.G	...	...	...	...	..G	..C	...	..T
Saiga	..C	...	...	..T	..T	..T	...	...	..A	...	..C	C..	...	...	...	..A	...	..C	...	...
MYOTRAGUS	...	...	...	..T	...	..A	...	...	...	...	...	C..	...	...	...	...	...	...	..G	...

Table 2

Capricornis	CTA	GCA	CTC	GTA	CCC	TTC	CTC	CAC	ACA	TCC	AAA	CAA	CGA	AGC	ATA	ATA	TTC	CGA	CCA	ATC
Nemorhaedus	...	...	A.T	...	..T	C..	...	...	...	...	...	...	...	...	..G	...	...	...	...	...
Oreamnos	...	AT.	T.T	...	..T	...	..T	..T	.T.	...	...	...	...	..T	...	..G	...	...	...	..T
Rupicapra	..G	.T.	...	...	...	C..	..T	...	...	...	...	...	...	...	..G	...	...	...	...	...
Ammotragus	...	AT.	...	...	...	...	...	..T	...	...	...	...	..G	...	..G	...	...	...	...	...
Budorcas	...	.T.	A..	A.G	...	C..	...	...	...	..A	..G	...	...	...	...	...	...	...	...	...
Ovibos	...	...	...	...	..T	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Pseudois	...	.T.	..T	A..	...	...	...	...	...	..T	...	...	...	...	...	..G	...	...	...	...
Hemitragus	T..	A..	..T	...	...	...	..T	...	...	...	...	...	...	...	...	...	...	...	...	...
Capra	T..	.T.	..T	...	..T	...	...	...	...	..T	...	...	...	...	...	...	...	..C	...	...
Ovis	...	.T.	A.T	A..	...	C..	...	..T	...	..A	..G	...	..G	...	...	...	...	...	...	...
Pantholops	...	.T.	...	...	...	..T	...	..T	.T.	...	...	...	...	...	..G	...	..T	...	..T	..T
Saiga	...	.TC	...	A..	...	..G	...	...	...	..T	...	...	...	...	...	...	...	..G	...	..T
MYOTRAGUS	...	.TG	..T	A..	...	C..	...	...	.A.	...	...	...	T..	...	...	...	...	.AG	...	..T

Capricornis	AGC	CAA	TGT	ATA	TTC	TGA	ATC	CTA	GTA	GCA	GAT	TTA	CTT	ACA	CTC	ACA	TGA	ATT	GGA	GGA
Nemorhaedus	...	...	..C	T..	...	...	.CT	...	...	...	...	...	..A	G..	...	...	...	...	...	...
Oreamnos	..T	...	..C	G..	...	...	.C.	...	...	...	..C	C..	..A	G..	...	...	...	..C	...	...
Rupicapra	...	...	..C	...	...	...	..T	...	...	...	..C	C..	T.A	...	...	...	...	...	...	...
Ammotragus	...	...	..C	...	...	..G	...	...	...	...	..C	...	..A	...	...	...	...	...	...	...
Budorcas	...	...	..C	...	...	...	..T	...	...	..C	..C	C..	..A	...	...	...	...	...	...	..C
Ovibos	...	...	...	...	...	...	..A	...	...	...	..C	...	..G	...	...	...	...	...	...	...
Pseudois	...	...	..C	...	...	...	...	...	...	...	..C	C..	..A	...	...	...	...	..C	...	...
Hemitragus	...	...	..C	...	...	...	...	...	.C.	..G	..C	...	..G	...	...	...	...	...	...	...
Capra	...	...	..C	G..	...	...	...	...	...	...	...	C..	T.A	...	...	...	...	...	...	...
Ovis	..T	...	...	...	...	...	...	...	...	..C	..C	C..	T.A	...	...	...	...	...	...	...
Pantholops	..T	...	..C	...	...	...	...	...	...	...	..C	C..	T.A	...	..T	...	...	..C	...	...
Saiga	...	...	..C	C..	...	...	G.T	...	...	...	..C	C..	..A	...	...	...	...	...	...	...
MYOTRAGUS	..T	...	...	C..	G..	...	..T	T..	...	...	..C	C..	..A	...	...	...	...	...	...	..C

Capricornis	CAG	CCA	GTC	GAA	CAC	CCC	TAC	ATT	ATT	ATT	GGA	CAA	CTA	GCA	TCC	ATC	ATA	TAC	TTC	CTA
Nemorhaedus	..A	...	...	...	T.T	...	..T	...	..C	...	...	...	..G	..T	...	...	...	..T	...	T.C
Oreamnos	..A	...	..T	...	...	...	...	..A	G.C	...	..C	...	...	...	...	...	..G	...	..T	..C
Rupicapra	...	...	...	...	...	..T	...	...	..C	...	...	...	...	...	...	...	...	..T	...	..C
Ammotragus	..A	...	...	...	A..	...	..T	..A	..C	...	...	...	...	...	..T	...	...	..T	...	..C
Budorcas	...	...	..T	...	...	...	..T	...	...	...	...	...	...	..G	..T	...	...	..T	...	..C
Ovibos	...	..G	...	...	...	..T	..T	..C	...	...	...	...	...	...	...	...	...	...	...	..C
Pseudois	..A	...	...	...	...	...	..T	..C	...	...	...	...	...	...	..T	...	...	...	...	..T
Hemitragus	..A	...	...	...	..T	..T	..T	...	..C	...	...	..G	...	...	...	..T	...	..T	...	..C
Capra	...	...	...	...	..T	...	..T	...	...	...	...	...	...	...	..T	..T	...	...	...	..C
Ovis	...	...	..T	...	...	...	...	..C	...	...	...	...	...	...	..T	..T	...	..T	...	..T
Pantholops	..A	...	...	...	...	..T	..T	..C	...	...	...	...	...	...	...	...	...	...	..T	...
Saiga	..A	...	..T	...	T.T	..A	..T	...	.CA	...	..C	...	...	...	..A	...	...	..T	..T	..T
MYOTRAGUS	...	...	..T	...	...	...	..T	...	...	...	...	..G	...	...	..T	..T	...	..T	...	..T

Capricornis	ATC	ATC	CTA	GTA	CTG	ATG	CCA	GTA	GCT	AGT	ACC	ATC	GAA	AAC	AAC	CTC	CTA	AAA	TGA	AGA	AAA
Nemorhaedus	..T	...	...	...	..A	..A	...	...	...	G.C	...	...	...	...	..T	...	...	...	...	...	...
Oreamnos	...	..T	...	...	A.A	..A	...	...	...	..C	..T	...	...	...	...	...	...	...	...	...	...
Rupicapra	..T	...	...	...	A.A	..A	...	...	...	..C	...	...	...	...	...	...	...	...	...	.A.	T..
Ammotragus	...	..T	...	...	A.A	..A	...	...	...	..C	...	...	..G	..T	...	...	...	...	...	...	T..
Budorcas	...	..T	...	..T	A.A	..A	...	...	...	..C	...	...	...	...	...	..T	...	...	...	...	...
Ovibos	...	...	..G	..G	..A	...	...	A.G	...	..C	..T	...	...	...	...	...	...	...	...	...	...
Pseudois	...	..T	T..	...	A.A	..A	...	...	...	..C	.G.	..T	...	...	.N.	...	...	...	...	...	C..
Hemitragus	..T	..T	...	...	A.A	..A	...	.C.	..C	..C	...	..T	...	...	...	...	...	...	...	..G	C..
Capra	..T	..T	...	...	A.A	..A	...	...	...	..C	...	..T	...	..T	...	...	...	...	...	...	C..
Ovis	...	..T	...	..C	A.A	..A	...	...	...	..C	.T.	...	...	...	...	...	...	...	...	...	C..
Pantholops	..T	...	...	...	T.A	..A	...	...	..C	..C	..T	...	...	...	...	...	...	...	...	...	C..
Saiga	C.T	..T	...	...	..A	..A	...	...	..C	...	..T	..T	...	..T	...	...	...	..G	...	.A.	T..
MYOTRAGUS	...	..T	...	..C	A.A	..A	...	..G	..G	..C	...	...	...	...	...	...	...	...	...	...	C..

Table 2 [pages 0-0]. *Myotragus* sequence of the complete mtDNA cyt *b*, aligned with the sequence of all Caprinae species. Dots indicate sequence identity.

Taula 2 [pàgines 0-0]. *Seqüència completa del mtDNA cyt b de* Myotragus, *alineat amb la seqüència de totes les espècies de Caprinae. Els punts indiquen identitat a la seqüència.*

BOS	CATAAACCGTGGGGGTCGCTATCCAATGAATTTTACCAGGCATCTGGTTCTTTCTTCAGGGCCATCTCACC
CAPRA	...T............A.A...TG......CC...TA..AG.............................T
MYOTRAGUS	...T....T.......A....AAG.G....CCG..TA..A............................G..
OVIS	...T..T.........A.A...TG.......C...TA..AG.............................T
CAPRICORNIS	...T..TT........A.....TT...........T...A...............................
BUDORCAS	...T..T.........A.....TG...........T...................................

BOS	TAAAACAGTCCATTCTTTCCTCTTAAATAA
CAPRA	......C.C.....................
MYOTRAGUS	........C........C..C.........
OVIS	......C.C...........C.........
CAPRICORNIS	.....TC.C...CA......C.........
BUDORCAS	......C.C...........C.........

Table 3. *Myotragus* sequence of a mtDNA HVRI fragment, aligned with sequences found in GenBank of other Caprinae (including *Bos* for comparison).

Taula 3. *Seqüència d'un fragment del gen mtDNA HVRI de* Myotragus, *alineada amb les seqüències d'altres Caprinae trobades al Banc de Gens (incloent-hi* Bos *per comparació).*

BOS	TTTATATCCTTCTAGAGGAGCCTGTTCTA-TAATCGATAAACCCCGATAAACCTCACCAATTCTTGCTAATACAG
PANTHOLOPS	....C.C..C...................-.............................G.C......G......
OVIBOS	......C......................-...............................C.........T...
NEMORHAEDUS	......C..AC.................G-...............................C.........T...
OREAMNOS	......C..C...................-..................T............C.............
CAPRA	......C......................-...............................C.............
PSEUDOIS	..C...C......................-...............................C.............
MYOTRAGUS	..C...C.....................G-...............................C.........T...
OVIS ARIES	......C......................-...............................C.............
AMMOTRAGUS	......C.....................GA...............................C....G....T...
O.DALLI	......C......................-...............................C.............
O.CANADENSIS	......C......................-...............................C.............
CAPRICORNIS	.........AC..................-...............................C.........T...
HEMITRAGUS	......C......................-...............................C.............

BOS	TCTATATACCGCCATCTTC-AGCAAACCCTAAAAA--GGAAAAAAAGTAAGCGTAATTATGATACATAAAAACGT
PANTHOLOPS	...................-..........G....--...............TC...C..C.........G....
OVIBOS	...................-...............--....T..........TC...C..AT.G......G....
NEMORHAEDUS	.................C.-.....G.........--....C.....C....TC...C..AT........G....
OREAMNOS	.T.................-...............--....C..........TC...C...C........G....
CAPRA	...................-...............--....C..........TC...C.CA.C.......G....
PSEUDOIS	...................-...............--....C..........TC...C.CAGC.......G....
MYOTRAGUS	...................-...............--....C..G.......TC...C.CATC.......G....
OVIS ARIES	...................-...............A-..G.C..........TC...A..A.C.......G....
AMMOTRAGUS	...................C...............GG....C..........TC...C..AGC.......G....
O.DALLI	...................-...............--....C..........TC...A..A.........G....
O.CANADENSIS	...................-...............--....C..........TC...A..A.........G....
CAPRICORNIS	...................-...............--....T..........T....C..AT........G....
HEMITRAGUS	...................-...............--....C..........TC...C.CA.C.......G....

BOS	TAGGTCAAGGTGTAACCTATGAAATGGGAAGAAATGGGCTACATTCTCTACACCAAGAGAATCAA-GCACGAAAG
PANTHOLOPS	.....................G.......................T.....CT.....A...TT.-AT.......
OVIBOS	.....................G.G.....................T....TC..T...A...TT.CAT.......
NEMORHAEDUS	.................A...G.......................T....TTT.T...A...TT.TAT.......
OREAMNOS	.....................G.......................T.....C.A.-..AT..TT.-AT.......
CAPRA	.................C...G.......................T.....CTT....A...T-.-AT.......
PSEUDOIS	.................C...G.G.....................T.....CT.....A...TT.-A........
MYOTRAGUS	.....................G.......................T.....CTT....A...TC.-A........
OVIS ARIES	.....................G.G.....................T.....C.A.-..A...TT.-AT.......
AMMOTRAGUS	.....................G.......................T.....CT.....A...TC.-AT.......
O.DALLI	.....................G..........................T.....C.A.-..A
O.CANADENSIS	.....................G..........................T.....T.A.-..A
CAPRICORNIS	.....................G..........................T....TCT.T...A
HEMITRAGUS	.................C...G..........................T.....TT.....A

BOS	TTATTATGAAACCAATAACCAAAGGAGGATTTAGCAGTAAACTAAGAATAGAGTGCTTAGTT-GAATTAGGC
PANTHOLOPS	CC.........TT....G..-....C....
OVIBOS	CC..........T...GG..-....C....
NEMORHAEDUS	CC..........T...GG.T................C.........................-.........
OREAMNOS	CC..........T...GG..T....C....
CAPRA	CC.........TT...G.................T...........................-.........
PSEUDOIS	.C.........TT...G.................T............G..............-...C.....
MYOTRAGUS	CC..........T...GG.T..-.........
OVIS ARIES	CC.........TT....G..-....C....
AMMOTRAGUS	CC.........TT...GG................T...........................-...CC....

Table 4. *Myotragus* sequence of a mtDNA12 S fragment, aligned with sequences found in GenBank of other Caprinae (including *Bos* for comparison). Sequences of *O.dalli, O. canadensis, Capricornis* and *Hemitragus* are not available for the whole fragment considered.

Taula 4. Seqüència d'un fragment del gen mtDNA12 S de Myotragus, *alineada amb les seqüències d'altres Caprinae trobades al Banc de Gens (incloent-hi* Bos *per comparació). No es disposa de les seqüències de* O.dalli, O. canadensis, Capricornis *i* Hemitragus *per a tot el fragment considerat.*

BOS	GGGGCGAAAGACTAATCGAACCATCTAGTAGCTGGTTCCCTCCGAAGTTTCCC
CAPRA	....
MYOTRAGUS	....
OVIS	....
RUPICAPRA	....

BOS	TCAGGATAGCTGGCGCTCTCGCA-AACGC-ACAG-ACCC-----ACGCAGTTTT
CAPRA	.......................-...C-------....-----..........
MYOTRAGUS	.......................---...G----A....-----..........
OVIS	.......................------------....-----..........
RUPICAPRA	.......................G.-..-G...AG....-----..........

Table 5. *Myotragus* sequence of the nuclear gene 28 S rDNA, aligned with sequences of *Capra, Ovis* and *Rupicapra* obtained in this study (including *Bos* for comparison).

Taula 5. Seqüència del gen nuclear 28 S rDNA de Myotragus, *alineada amb les seqüències de* Capra, Ovis *i* Rupicapra *obtingudes a aquest estudi (incloent-hi* Bos *per comparació).*

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INTEGRATING THE FOSSIL RECORD IN THE STUDY OF INSULAR BODY SIZE EVOLUTION: EXAMPLE OF OWLS (AVES, STRIGIFORMES)

Antoine LOUCHART

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Resum

Les òlibes i els mussols (Aves, Strigiformes) constitueixen un dels millors elements per fer estudis sobre la mida corporal i diferents característiques al·lomètriques, que contemplin espècies vivents i fòssils d'ocells insulars, incloses algunes espècies recentment extingides. Al present estudi s'inclou, com a registre d'espècies vivents, devers 150 taxa insulars, distribuïts sobre 230 illes o arxipèlags. S'inclouen devers 350 taxa continentals com a comparació. El registre de taxa extingits està constituït per 35 òlibes o mussols endèmics, un terç dels quals s'inclouen dintre del gènere *Tyto*. A l'anàlisi del registre actual es consideren diferents variables, incloent-hi característiques físiques i biològiques insulars. Per als taxa vivents i extingits s'han registrat variables amb característiques intrínseques de qualsevol taxon insular. Aquestes són l'evolució de la talla corporal, la classe de talla corporal, l'evolució d'al·lometries, el rang taxonòmic i l'hàbitat. Els resultats revelen alguns patrons d'evolució insular. Aquests patrons difereixen considerablement quan es considera només el registre actual o el registre fòssil. Entre d'altres, el registre actual tendeix a estar empobrit en taxa insulars grans, degut a impactes antropogènics selectius. A més, la via més freqüent d'evolució insular deduïda a partir de l'anàlisi del registre actual sembla ser una suau tendència a la minva de mida, mentre que la tendència oposada es pot deduir a partir del registre fòssil, amb alguns casos extrems únics. Una altra volta aquestes diferències es deuen a extincions selectives. Quan s'integren conjuntament, els dos registres no indiquen cap tendència a l'evolució de la talla corporal d'òlibes i mussols a les illes.

No hi ha cap "llei insular" per a aquest grup. Aquestes dues observacions es poden estendre a ocells en general, però fa falta un estudi integrat de gran abast. S'observen tendències al·lomètriques a les cames i a les ales, que són les mateixes que es poden observar al conjunt dels ocells. També s'observa una tendència cap a peus i urpes més grans al les òlibes insulars. Els mecanismes que afecten els exemples típicament insulars d'evolució de la talla corporal i d'evolució al·lomètrica constitueixen un altre tòpic complex i difícil. No obstant, s'assenyalen alguns factors i algunes perspectives per a investigar. Es mostra en quina via l'evolució de les òlibes/mussols a Còrsega és original. Els impactes antròpics són els factors principals per explicar les diferències entre el registre vivent i el fòssil. S'han extingit preferentment els taxa més grans, i els taxa endèmics que són resultat d'una evolució extrema. Te poc sentit considerar només el registre fòssil, talment com considerar només les faunes actuals. Com se sap pel que fa la diversitat taxonòmica i la riquesa específica, les faunes insulars vivents estan molt esbiaixades considerant la talla corporal a una comunitat. Les dades sobre els registres vivents i fòssils es complementen en molts d'aspectes. Es recomana una integració dels dos registres, quan sigui possible, abans d'emetre interpretacions. S'indiquen alguns suggeriments per al reconeixement de tipus biològics d'illes, els quals també requereixen tenir en compte l'extens registre fòssil.

Paraules clau: al·lometria, extincions antròpiques, ocells, mida corporal, illes, Strigiformes.

Abstract

Owls (Aves, Strigiformes) constitute one of the best samples for studies including both living and fossil insular bird taxa, including recently extinct, focusing on body size and some allometrical characteristics. For the extant record, around 150 endemic insular taxa, distributed on 230 islands or archipelagoes, were included in the present analysis. Around 350 continental taxa were included for comparisons. The record of extinct taxa is constituted of 35 insular endemic owls, with one third in the genus *Tyto*. Several variables were considered for the extant record, including physical and biological insular characteristics. Variables for characteristics intrinsic to every insular taxon were recorded for extant and extinct records. These are the evolution of body size, body size class, evolution of allometries, taxonomic rank, and habitat. The results provide some patterns of insular evolution. These patterns differ considerably when one considers only the extant or the extinct record. Among others, the extant record tends to be impoverished in larger insular taxa, this being due to selective anthropogenic impacts. In addition, the most frequent way of insular body size evolution seems to be slightly in favour of decreases in the extant record, while the extinct record shows the opposite trend, with some unique extreme cases. Again, these differences are due to the selective extinctions. When integrated together, the two records indicate no general trend for owls in the evolution of size on islands.

There is no 'island rule' either for this group. These two observations might be extended to birds in general, but a comprehensive, integrated study is needed. Allometrical trends are observed on legs and wings that are the same as in birds as a whole. A trend toward larger feet and claws in insular owls is observed as well. The mechanisms underlying the typically insular cases of body size evolution and allometrical evolution are another, complex and difficult topic. However, some factors, and some perspectives for investigations, are emphasized. It is shown in what way the evolution of owls in Corsica is original. Anthropogenic impacts are the main factors to account for the differences between the extant and the extinct record. They made extinct preferentially the larger taxa, and the endemic taxa resulting from evolutions of extreme amplitude. It is meaningless to consider only the fossil record, as well as to trust only the extant record. As was known for the richness and taxonomic diversity, extant insular avifaunas are also heavily biased considering body size in a community. Data on living and fossil records are complementary on many grounds. A quantitative integration of these records is recommended, whenever it is possible, before interpretations. Some suggestions for the recognition of biological types of islands are drawn, which also necessitate taking into account the extensive recent fossil record.

Keywords: allometry, anthropogenic extinctions, birds, body size, islands, Strigiformes.

INTRODUCTION

What is the insular trend for body size in birds, if there is any: increase, decrease, or a more complex trend? The answer is unclear, as it is for other Tetrapods. Frequently, the examples cited deal with giantism associated with a reduction or loss of flight ability. The studies were rare or restricted to certain groups until recently. Mayr & Vaurie (1948, in Grant, 1965b) and Amadon (1953, in Grant, 1965b) were the first to detect in some groups today or on some islands a trend to an increase in size, considered from then to be rather general. Grant (1965b) reported individual studies showing the opposite trend, always on living groups, and at low taxonomic levels of divergence (generally subspecies). Grant (1965a) noticed that the living Passeriformes on the Tres Marías Islands (Mexico) show a clear trend to a decrease in weight. Again these are low taxonomic levels divergences, and of low amplitude. Then a growing consensus emerged that there is no simple general insular body size trend (increase or decrease) for birds (Grant, 1968, Carlquist, 1974; Case, 1978; Gaston & Blackburn, 1995; Blondel, 2000; and some restricted surveys cited by these authors). Blondel (2000) recalled the cases of giantism in vegetarian species (e.g. *Aepyornis, Dinornis, Sylviornis, Pezophaps, Raphus*...), and of dwarfism in many Passeriformes. The cases of giantism are numerous, often linked to a reduced or loss of flight ability. Others seem clearly linked to the size of preys (e.g. *Harpagornis moorei;* see Alcover & McMinn, 1994). Actually, the diversity and complexity of examples are great. Some examples of dwarfism exist in diverse groups, of various sizes: many Rallidae (e.g. Ryan *et al.*, 1989); two species of emus (genus *Dromaius*, Casuariiformes – Australian islands up to the recent Holocene; Parker, 1984); a cassowary (*Casuarius lydekkeri*, Casuariiformes – New Guinea; Rich *et al.*, 1988). Conversely, giantism is reported in extinct Passeriformes (e.g. *Emberiza alcoveri* – Canary Islands; Rando *et al.*, 1999), or a Caprimulgiformes (genus *Megaegotheles* – New Zealand; Rich & Scarlett, 1977). The latter cases are associated with strong reductions in flight ability (and tarsus lengthening for *E. alcoveri*). Thus, there is no evidence for a general trend toward either an increase or a decrease in size in insular birds, which seems confirmed by two recent studies (Clegg & Owens, 2002; Cassey & Blackburn, 2004).

Recently a study proposed evidence for the 'island rule' in birds (Clegg & Owens, 2002), but some remarks may be opposed to this view. The 'island rule' was established for mammals where large species tend to decrease and small ones to increase in size on islands (e.g. van Valen, 1973; Lomolino, 1985; see Meiri *et al.*, 2004 for some exceptions). The sample analyzed by Clegg & Owens (2002) was small and suffered from several important biases, some of the most problematical being the absence of data from the recent fossil record (dating from before the anthropogenic extinctions and extirpations on islands) and the exclusion of all the flightless taxa. The island/mainland differences observed in this extant sample were generally small and rarely reached the 5 % minimal value proposed by Lomolino (1985). Then, the trends observed were of very low magnitude (essentially less than 1 or 2 % in body weight on average), and cannot compare with the well marked island rule in mammals (with up to 50% differences in some groups). This will not be developed here, yet it is better at present to consider as unknown whether the 'island rule' applies to birds or not.

To summarize, there are only more or less striking individual examples of insular dwarfism or giantism in birds, but yet no trend appears, either with extant or with extinct forms. A necessary step is now to start integrating both records. As suggested by Case (1978), given the great disparity of patterns seen in birds, both living and extinct, it may be useful to examine bird orders separately for example, and to integrate both living and recently extinct taxa. Most of these recent extinctions or local extirpations on islands were due to anthropogenic impacts. In most cases, these impacts were Holocene in age, repeated, and indirect, such as introduction of diseases, continental predators or competitors, modification of landscape, but sometimes also direct over-hunting by humans (Olson & James, 1982; James & Olson, 1991; Olson & James, 1991; Milberg & Tyrberg, 1993; Steadman, 1995; Mourer-Chauviré *et al.*, 1999; Sadler, 1999; Duncan *et al.*, 2002; Blackburn *et al.*, 2004). The absence of such taxa in the avifaunas of today is therefore unnatural, and the only way to approximate the natural communities and complete taxon lists is to integrate both the living impoverished faunas and the recently extinct taxa. Hitherto very few analyses based on such an integrated insular record for birds have been made, a recent example being the study of an integrated Holocene bird record of New Zealand (Cassey & Blackburn, 2004). The objective of the present work is to present preliminary conclusions arising from analyses made on an integrated native insular record of the Strigiformes (owls) of the world.

The order Strigiformes is particularly well-adapted for this study, because (1) extant insular owls are widespread and frequently exhibit size and allometrical modifications; (2) recently extinct owls are well represented in the fossil record of islands, they also often exhibit these kinds of modifications - and they are relatively easy to identify osteologically. Their intermediate flight abilities can explain this. They are sedentary enough to undergo insular evolution, without too much gene flow from the continent (or other islands). Meanwhile, they sometimes cross important distances over the sea, which allows them to colonize islands up to 3500 km apart from any other land.

A study of body size and allometrical evolutions in both the recent fossil and extant records of insular owls was carried out. Some preliminary results will be exposed, as well as conclusions about the method, and perspectives to improve the pertinence of such analyses.

METHODS

The body size is expressed as a semi-quantitative variable, given the necessary approximations from the literature on extant taxa, as well as from the data on extinct forms. The allometries studied here are the relative size of the beak, the wings, the legs, the pedal digits and claws. These data are also expressed as semi-quantitative variables.

A very recurrent problem is to avoid apparently insular taxa, which actually have a relictual distribution, for anthropogenic or natural reasons, the island(s) having played the role of a refugium. Therefore, some apparently insular characteristics can well be not insular at all. The Laughing Owl *Sceloglaux albifacies* (G.R. Gray), probably extinct, was known only in New Zealand, but there are some doubts arising from the possibility of a recent wider distribution (e.g. König *et al.*, 1999). A similar case could be that of the Papuan Hawk Owl *Uroglaux dimorpha* (Salvadori), which presents today a disjunct insular distribution (Holt *et al.*, 1999; König *et al.*, 1999). According to Case (1978), many insular giant reptiles actually display a relictual distribution compared with recent Pleistocene times, like the giant monitor lizard of Komodo.

An even more widespread problem is the identification, as precise as possible, of the direct ancestor of an insular form (on the continent or on adjacent islands). It is the only way to evaluate the direction and amplitude of the insular modifications. The living Giant Scops Owl *Mimizuku gurneyi* (Tweeddale), of the Philippine Islands, was until recently often considered a dwarf eagle owl (close to the genus *Bubo*). However, recent DNA analyses by Miranda *et al.* (1997) demonstrated that it is closer to the smaller scops owls of the genus *Otus*, therefore making it a giant insular owl. This is an extreme case, with the inversion of the interpretation of body size evolution, but smaller uncertainties exist for many other taxa.

In all the cases where these kinds of doubt exist, the taxon implied was not included in the list of in situ evolved insular owls. For example, the extinct *Tyto balearica* as a species, of Western Mediterranean Islands, was not included because its closest continental relative is not known, and it is not clear at which taxonomic level it can be considered an insular owl (Louchart, 2002). *Sceloglaux albifacies*, despite typical insular-looking characteristics (long legs, short wings, terrestrial habits), is not included in the body size analyses because of its possibly relictual distribution, and its unknown ancestry (König *et al.*, 1999).

All the non-indigenous owls on islands (introduced by man) were excluded from all the analyses.

A nomenclatural, but important issue is that of the terms « dwarf » and « giant », which imply that strong modifications are involved. Actually, it is obvious at a first glance that most of the insular size modifications are slight. Proportionate dwarfism and proportionate giantism were defined as heterochronies with isometrical conservation of proportions (Gould, 1977), but no limit was quantified to define dwarfism or giantism as opposed to slight decrease or increase in size. Other categories of heterochronies imply allometrical modifications joined to the dwarfism or giantism. Many cases of heterochrony with allometries are known in flightless insular birds (e.g. Livezey, 1989; 1990; 1993; 1995), but in most cases with Strigiformes, it remains to be tested whether the allometries implied are correlated with a trend in body size modification. With this in mind, the data on size and allometries are considered separately here. The modifications were arbitrarily considered here as slight (moderate) between 5 % and 10-15 % of change in mass, and important (strong) over this value. In the latter case, the terms dwarfism and giantism are also used.

The minimal value of 5 % of difference in mean weight (or an equivalent cubed linear measurement) between an insular taxon and its mainland counterpart to record it as a size modification follows Lomolino (1985) who defined this value as the minimum statistically reliable and applied it to mammals.

Throughout the text unless the context indicates otherwise, the term "island" refers to either an island or an archipelago.

BODY SIZE - EXTANT STRIGIFORMES

The data

A database was constituted with two main tables. In the first one, the individuals are the endemic insular taxa. In the second one, the individuals are the islands.

The variables were defined as follows.

Intrinsic variables: variables relative to the endemic insular taxa

The individuals are the endemic insular taxa (n=148) on the world: from the sub-species to the genus.

Description of the variables:

- In situ body size evolution of the taxon

The insular taxonomic unit can display the following states for this variable:

-2: important decrease (dwarfism)
-1: slight decrease
0: no change
1: slight increase
2: important increase (giantism)
?: unknown

The cases where insular endemic subspecies show invariance in size compared with the closest continental subspecies were taken into account for all the subspecies in the genus *Tyto*. For five species of Strigidae (three of *Otus* and two of *Ninox*), all the subspecies invariant in size or allometry between themselves were considered a unique insular (endemic or not) subspecific taxon called « other subspecies » for the intrinsic variables (in each of the five cases). This choice is justified by the slight differentiation observed on other characters, and because they would have disequilibrated the information too much with poorly differentiated taxa, the focus of the study being on the evolutionary changes. These choices will always be taken in consideration when the data are compared and interpreted: the cases of invariance will not be quantitatively interpreted. On the other hand, these subspecies have of course been taken in account for the variables relative to the insular communities of owls associated with every studied taxon (see below).

- Taxonomic rank of insular in situ differentiation

The insular endemic taxon was considered as a taxonomic category, ranging from the subspecies to the genus. If a polytypic species is insular, it was taken into account as such, and its different subspecies as well. Other example: if a monotypic species is insular at the genus level, it was taken in account once at the genus level. The states for this variable are:

1: subspecies
2: species
3: group of close species, superspecies, or genus

- Size class (category of weight) of the insular taxon

Five categories are defined:

1: < or = 150 g
2: 151 – 250 g
3: 251 – 500 g
4: 501 – 1000 g
5: > 1000 g

In the cases where the weight is not known, and no allometrical difference is reported, the weight was inferred from other measurements, and using close taxa for which these and the weight were both known.

N.B.: The taxa having undergone a size modification were classified in the category corresponding to their present size, *i.e.* after the size evolution. This choice is justified by uncertainties as regards a « precise » estimation of the weight of the ancestral taxon. In addition, it appears that a taxon would generally be only very rarely classified in a different size class if considered before rather than after size evolution. The consequences of the possible bias, minimized by the use of rather wide size classes, will be taken into account in the section Results (see below).

- The type of vegetation frequented by the insular taxon

Six categories are defined:

1: forested
2: semi-forested
3: forested to semi-open
4: semi-open
5: open to semi-open
6: open
i: indifferent (as regards the characteristics of density and height of vegetal cover considered here)

Extrinsic variables: variables relative to the island context

The individuals are the islands (n=230).

Description of the variables:

Physical extrinsic variables

- The latitude

The variable is the latitude of the island (for an archipelago, the mean of the latitudes of the different islands), distributed in three classes:

1: 0° - 19°
2: 20° - 39°
3: 40° - 59°

There is no case at higher latitudes.

The values combine northern and southern latitudes together in the same categories.

- The surface

The variable corresponds to the surface of the island (for an archipelago, the sum of all the surfaces of the individual islands) in km^2; the surfaces are classified in five categories:

1: 1 – 100 km^2
2: 101 – 1000 km^2
3: 1001 – 10 000 km^2
4: 10 001 – 100 000 km^2
5: 100 000 km≈ - 1000 000 km^2

The four largest islands included here are by decreasing order of surface: Madagascar (787 000 km^2), New Guinea (771 900 km^2), Borneo (730 000 km^2), and Sumatra (473 606 km^2).

- The distance

This is the distance from the island (for an archipelago, the smallest one) to the closest continent or larger island where the parent-taxon lived most probably. It is classified in four categories:

1: 10 – 50 km
2: 51 – 500 km
3: 501 – 1000 km
4: 1001 – 2000 km
?: case where the area of distribution of the parent-taxon is unknown

- The situation of the island relative to the continental plateau deep of less than 200 m

Categories:

0: beyond the limits of the continental plateau
1: within the limits of the continental plateau (relative to the geographical unit from which the distance was measured)

Extrinsic variables related to the community of owls present on the island

Some characteristics of the communities of Strigiformes were recorded for every island. These characteristics are only approximately pertinent because some recent changes in distributions can affect the community which was originally contemporaneous with the evolutionary changes on the insular taxa. These changes are generally unknown. As far as possible, only sympatric taxa were considered in every community.

- The total number of taxa on the island having undergone an evolution in size in situ

All the different taxa were taken in account (insular as well as non-endemic insular), avoiding any redundancy (only the taxa considered at the lowest taxonomic rank being recorded).

The value taken by the variable is the number of taxa for each island.

The following five variables represent the total number of taxa on an island included in every of the size classes:

- Number in size class 1 (< or = 150 g)
- Number in size class 2 (151 – 250 g)
- Number in size class 3 (251 – 500 g)
- Number in size class 4 (501 – 1000 g)
- Number in size class 5 (> 1000 g)

Similarly, the following five variables represent the proportions of taxa in the different size categories relative to the total number of taxa on the island:

- Proportion in size class 1 (< or = 150 g)
- Proportion in size class 2 (151 – 250 g)
- Proportion in size class 3 (251 – 500 g)
- Proportion in size class 4 (501 – 1000 g)
- Proportion in size class 5 (> 1000 g)

Remaining variables:

- The number of endemic insular taxa on the island

• The total number of taxa of Strigiformes on the island

• The proportion of taxa having undergone an evolution in size relative to the total number of taxa on the island

This ratio is expressed in the following categories:
1: 0.01 – 0.20
2: 0.21 – 0.40
3: 0.41 – 0.60
4: 0.61 – 0.80
5: 0.81 – 1
?: unknown

• The proportion of endemic insular taxa relative to the total number of taxa on the island

This ratio is expressed in the following categories:
1: 0.01 – 0.20
2: 0.21 – 0.40
3: 0.41 – 0.60
4: 0.61 – 0.80
5: 0.81 – 1
?: unknown

• The total number of different genera on the island

• The proportion of genera relative to the total number of taxa on the island

This ratio is expressed in the following categories:
1: 0 – 0.20
2: 0.21 – 0.40
3: 0.41 – 0.60
4: 0.61 – 0.80
5: 0.81 – 1
?: unknown

• The total number of taxa divided by the decimal logarithm of the surface of the island

This value is expressed in the following categories:
1: 0 – 0.33
2: 0.34 – 0.67
3: 0.68 – 1
4: 1.01 – 1.33
5: 1.34 – 1.67
6: 1.68 – 2
7: 2.01 – 2.33
?: indeterminate

The two tables –insular taxa table and islands table– are linked by the co-occurrences, *i.e.* every occurrence of a different taxon on a different island.

The sources used to establish this database (with *Access*™) are (in chronological order):

Olson (1978, 1995); Bunn *et al.* (1982); Talbot Kelly (1982); Pyle & Engbring (1985); Buden (1987); Fry *et al.* (1988); Louette (1988); Langrand (1990); Burton (1992); Sargeant (1992); Dunning (1993); Taylor (1994); Castro & Phillips (1996); Cramp (1998); Del Hoyo *et al.* (1999); Bruce (1999); Holt *et al.* (1999); Marks *et al.* (1999); Doughty *et al.* (1999); and different geographical atlases for the physical characteristics of islands.

A total of 343 taxa were considered, among which 148 are endemic insular.

230 islands were included in the analysis. They are islands of more than 1 km^2.

The map on Fig. 1 indicates the location of these islands.

N.B.: The analyses and interpretations were processed considering the Strigiformes as a whole, independently of the taxonomy, because this group is judged ecologically and morphologically rather homogeneous. Qualitatively, the trends appear well shared between the Tytonidae and the Strigidae.

Bivariate analyses

Some analyses using the Kendall's coefficient of rank correlation were processed (using *Statistica*™). The variables are semi-quantitative (discrete categories established from quantitative data, discrete or continuous) and ordered. Therefore this type of analysis is particularly well suited. The degree of correlation obtained between the variables two by two is Kendall's tau (τ). It was calculated by the formula (Kendall, 1938, in Sprent, 1992):

$$\tau = (n_c - n_d) \,/\, (^1/_2\, n\, (n-1))$$

with n_c the number of pairs of concordant observations and n_d the number of discordant observations between variables two by two; n is the total number of observations. The analyzed data can be summarized in a series of tables of contingency, expressing the cross numbers between all the states of the variables two by two. The fact that several variables were frequently affected by a question mark is considered carefully for the interpretations. All the bivariate tests were processed, and those indicating correlations at least significant ($p<0.05$) were retained. The value of t≈ indicates the degree of correlation ($0<\tau^2<1$), and can be expressed in %.

For the correlations among extrinsic variables, the individuals are the 220 islands. For the correlations among intrinsic and extrinsic variables considered altogether, the individuals are the 148 endemic insular taxa (from the subspecies to the genera).

Results

It is difficult to interpret correlations for two isolated variables, because it is not clear whether and how the causal relations are distributed. Nevertheless, the following observations are noteworthy.

Correlations among extrinsic variables

Many variables are very significantly correlated positively ($p<0.01$). Many of these correlations just reflect some obvious common components of the variables (like number of insular taxa – their proportion to the total, etc.) but have no insular meaning. The remaining ones, when showing values of t≈ greater than 10%, are shown in the Table 1. These correlation values remain of low magnitude, however: only two exceed 26%.

It seems that the more endemic the community is, the more frequent is the phenomenon of size evolution (proportion of cases): 51.9% correlation. Under conditions of endemism, it seems that owls « frequently » undergo size modifications.

The proportion of different genera relatively to the total number of taxa tends to be higher when the richness in endemic insular taxa is lower (40.4% correlation). A possible explanation is that an island with a low specific richness is likely to have a relatively high number of different genera. A corollary is that many different genera can reach an island, even small or remote, probably in a short time geologically. Then, a relatively lower competition is likely to occur between different genera than between species of the same genus, all other things being equal, allowing preferentially different genera to cohabit longer together. This is well known generally in animals.

Incidentally, the distance to a continent (or a larger island), is negatively correlated with the presence of a continental platform, but only rather slightly (23.8% correlation). Actually, the correlations show that the presence or absence of the platform seems at least as important as the distance regarding the insular characteristics of the communities. For typically sedentary birds like many owls, a continental bridge during low sea level periods was certainly necessary for some of the colonizations, at least for the weaker flyers.

Correlations among intrinsic and extrinsic variables considered altogether

The correlations are generally of far lower magnitude than in the case of the extrinsic variables alone. Even if highly significant, few exceed a value of 5%. Only four exceed a value of 10%, with a maximum of 26.5%, all but one being without insular signification (see above). There is only a weak trend (12.3% correlation) for larger insular endemic taxa to frequent more open habitats. This may however apply to mainland taxa as well. A future study including all continental owls will provide some clues to answer this question.

The absence of correlation between the surface of the island and any other variable is noticeable. The latitude is correlated, positively and weakly, only with the vegetation type frequented by taxa. Apparently, forested habitats are more frequented on lower latitude islands. This could be simply due to the predominance of such habitats on tropical islands. The distance is therefore the only geographical characteristic affecting communities and size evolution in this analysis. It is possible that this is affected by anthropogenic selective extinctions and extirpations, which will be developed in the section Discussion.

Finally, a negative correlation, significant but of very low magnitude (τ^2= 2.59%) appears between the direction of the evolution of size and size class of the taxa. It is apparent on Fig. 7. The smaller taxa would tend very slightly to increase in size, the larger to decrease, but this is no more apparent when fossils are integrated (Fig. 8; and see below).

Remark

A co-occurrence today in real sympatry (and in the same environments) of two species of one genus on one island is not rare (e.g. several islands of Indonesia for the genus *Tyto*). Even three species of *Tyto* occur together in SE New Guinea: *T. alba meeki*, *T. longimembris* and *T. tenebricosa*, but the latter lives in cloudy rain forest, whereas the two others occur in open habitats (König *et al.*, 1999). Generally, the two sympatric species are of different size in *Tyto*. However, at least in two cases (Timor and Solomon Islands), the two species are of the same size: here *T. alba delicatula* and *T. longimembris*; they also live in the same habitats (König *et al.*, 1999). This is partly in contradiction with a widespread idea (see Grant, 1965b) that two species of the same genus rarely co-exist on an island, due to interspecific competition. It appears that some traits – probably behavioural - other than size alone, can allow such a sympatry within one genus. In the fossil record, at least three species of the genus *Tyto* certainly co-existed in the Mio-Pliocene of the palaeo-« island » of Gargano (Ballmann, 1973, 1976; Pavia, pers. com.). Two species of *Tyto* lived together during part of the Pleistocene in Corsica (Louchart, 2002), and three in the Pleistocene of Cuba (*T. alba*, *T. noeli*, *T. riveroi*; Arredondo, 1982). In each of these fossil examples, however, the co-existing species were of different body size (Table 2).

	Distance	Continental plateau	Number of insular endemic taxa	Proportion of different genera genera to the total number of taxa
Continental plateau	*23.8*			
Proportion of different genera to the total number of taxa			*40.4*	
Number of taxa showing size evolution			51.9	
Number of taxa in the size class 1		11.4		
Number of taxa in the size class 2				*17.2*
Number of taxa in the size class 5		12.1		
Ratio richness / surface		10.1		*26.0*

Table 1. Correlation values τ^2 higher than 10%, between extrinsic insular variables, after Kendall's rank correlation test. All these values are expressed in %, and correspond to highly significant correlations (p<0.01). In normal police: positive correlations. In italics: negative correlations. Here are shown only the correlations with a signification for insularity (see the text).

Taula 1. *τ^2 valors de correlació superiors al 10%, entre variables insulars extrínsiques, segons el test de correlació re rangs de Kendall. Tots aquests valors s'expressen en % i corresponen a correlacions altament significatives (p<0.01). En lletres rodones, correlacions positives. En cursives, correlacions negatives. Es mostren només les correlacions amb un significat per a l'anàlisi de la insularitat (veure text).*

Species	Island/Archipelago	Known age	Putative ancestor	Size evolution	Allometrical evolution of tarsus	Allometrical evolution of wing	Size class	Taxonomic rank of divergence
Tyto balearica cyrneichnusae	Corsica, Sardinia	Middle Pleistocene	*Tyto* sp.	?	?	0	4	1
Tyto cavatica	Puerto Rico	Pleistocene	*Tyto glaucops/ insularis/bargei*	0			3	2
Tyto gigantea	Gargano	Mio-Pliocene	*Tyto* sp.	2	L?		5	2
Tyto neddi	Barbade (Lesser Antillean Is.)	Quaternary	*Tyto* sp.	1			4	2
Tyto noeli	Cuba	Pleistocene	*Tyto alba*	1			4	2
Tyto ostologa	Hispaniola	Pleistocene	*Tyto alba*	1			4	2
Tyto pollens	Great Exuma, New Providence (Bahamas)	Pleistocene	*Tyto alba*	1	-L		5	2
Tyto riveroi	Cuba	Pleistocene	*Tyto alba*	2			5	2
Tyto robusta	Gargano	Mio-Pliocene	*Tyto* sp.	2	LL		4	2
Tyto nov. sp.	Sicily	Middle Pleistocene	*Tyto* sp.	1 or 2			4	2
Tyto sp.	Gargano	Mio-Pliocene	*Tyto* sp.	?			4	
Tyto sp.	Madeira	Pleistocene	*Tyto* sp.	-1?			2 or 3	2?
Tyto? letocarti	N.-Caledonia	Holocene	?	?			3	
Mascarenotus grucheti	Réunion	Holocene	*Otus* sp.	2(?)	LL	-1	3	3
Mascarenotus murivorus	Rodrigue	Holocene	*Mascarenotus* sp.	0			3	2
Mascarenotus sauzieri	Mauritius	Holocene	*Mascarenotus* sp.	0			3	2
aff. *Otus scops*	Madeira	Quaternary	*Otus* sp.	?			1	
Gymnoglaux sp.	Cuba	Pleistocene	?	0			1	2
Bubo (Strix ?) perpasta	Gargano	Mio-Pliocene	*Bubo* sp. (?)	-1?			4	?
Bubo insularis	Corsica, Sardinia	Pleistocene	*Bubo (bubo)*	-2(?)	L(?)	-1	4	2
Bubo osvaldoi	Cuba	Pleistocene	*Bubo* sp.	1?		-1	5	2
Grallistrix auceps	Kauai (Hawaii)	Holocene	*Grallistrix* sp.	0			3	2
Grallistrix erdmani	Maui (Hawaii)	Holocene	*Grallistrix* sp.	-1?			3	2
Grallistrix geleches	Molokai (Hawaii)	Holocene	*Strix*	?	LL	-1	3	3
Grallistrix orion	Oahu (Hawaii)	Holocene	*Grallistrix* sp.	-1?			3	2
Ornimegalonyx oteroi	Cuba	Pleistocene	*Strix/Ciccaba*	2	L	-2	6 (=5)	3
Ornimegalonyx sp. 2	Cuba	Pleistocene	*Strix/Ciccaba* ?	?	?	?	?	?
Athene angelis	Corsica	Pleistocene	*Athene noctua*	2	-L	-1	3	2
Athene cretensis	Crete, Armathia	Pleistocene	*Athene noctua*	1	L		3	2
Athene sp.	Eubea	Holocene ?	*Athene noctua*	1			2	2
Athene trinacriae	Sicily	Middle Pleistocene	*Athene noctua*	0	L		2	2
Athene nov. sp.	Puerto Rico	Pleistocene	*Athene (cunicularia)*	-1?			2	2
Athene sp.	Cova na Reia - Eivissa (Balearic Is.)	Pliocene	*Athene* sp.	-1??			2	2
Athene (cunicularia)	New Providence (Bahamas)	Pleistocene	*Athene (cunicularia)*	-1			2	1?
Pulstarix arredondoi	Cuba	Pleistocene	*Pulsatrix perspicillata*	1	-L		4	2

Table 2. Extinct endemic insular Strigiformes in the world. The four species of *Grallistrix* are very homogeneous in terms of size and allometries, as well as the three species of *Mascarenotus*. For each of these genera, only one of the species is chosen for the size and allometrical modifications, the other species being considered as showing little change inside the genus. In *Grallistrix*, the type species *G. geleches* of Molokai, is arbitrarily considered here as representative of the basal level of evolution of the genus. In *Mascarenotus*, the species of the largest island (Réunion) *M. grucheti* is similarly considered as such. In the genus *Ornimegalonyx*, four species have been described, but it is now considered most likely that only two are valid (W. Suarez and O. Jiménez, pers. com.). *Ornimegalonyx oteroi* – the type species - and *Ornimegalonyx* sp. 2 are retained here. The references used are cited in the text.

Taula 2. Strigiformes endèmics insulars extingits del món. Les quatre espècies de Grallistrix *són molt homogènies en termes de mida i al·lometries, igual que ho són les tres espècies de* Mascarenotus. *Per a cadascun d'aquests gèneres només s'ha triat una espècie per analitzar les modificacions de talla i al·lomètriques, considerant-se que hi hauria pocs canvis dintre del gènere. A* Grallistrix, *es considera* G. geleches, *l'espècie tipus de Molokai, com a representativa del nivell basal d'evolució del gènere. A* Mascarenotus, *es considera com a tal l'espècie de l'illa més gran (La Réunion),* M. grucheti. *Al gènere* Ornimegalonyx *s'han descrit quatre espècies, però actualment sembla que el més probable es que només n'hi hagi dues de vàlides (W. Suarez and O. Jiménez, pers. com.). Es retenen aquí* Ornimegalonyx oteroi *– l'espècie tipus – i* Ornimegalonyx *sp. 2. Les referències emprades es citen al text.*

INTEGRATION OF THE RECORD OF EXTINCT INSULAR STRIGIFORMES

The intrinsic characteristics of the 35 extinct insular endemic Strigiformes recorded here were evaluated (Table 2). 13 taxa belong to the genus *Tyto*, and 22 are Strigidae. They are distributed over the world (Fig. 1). The body size class was recorded for each extinct taxon using the relationships established for predatorial birds by Campbell & Marcus (1992) between the least circumference of the femur and tibiotarsus and the body weight.

The islands which have a most significant fossil record of Quaternary owls are generally not the same as those where live today the largest numbers of endemic owls (with the noticeable exception of the Greater Antilles). This is a geographical effect of the extinctions discussed in this paper. The two records are thus complementary geographically.

The sources used to establish the synthetic Table 2 are (in chronological order):

Wetmore (1920, 1937); Brodkorb (1959, 1969); Ballmann (1973); Arredondo (1972, 1975, 1976, 1982); Olson (1978, 1984, 1985); Olson & Hilgartner (1982); Rich & van Tets (1982); Weesie (1982, 1988); Pieper (1985); Mourer-Chauviré & Weesie (1986); Steadman (1986); Balouet & Olson (1989); Mourer-Chauviré & Sanchez Marco (1988); Olson & James (1991); Alcover *et al.* (1992) ; Burton (1992), Cheneval & Adrover (1993); Alcover & McMinn (1994); Arredondo & Olson (1994); Mourer-Chauviré *et al.* (1994, pers. com.); Mourer-Chauviré *et al.* (1997); Mourer-Chauviré *et al.* (2001); Mlikovsky (1998a; 1998b); Tyrberg (1998); Pieper *fide* Jaume *et al.* (1993, in Tyrberg, 1998); Steadman & Hilgartner (1999); Pavia (2000); Louchart (2001; 2002); Pavia & Mourer-Chauviré (2002), O. Jiménez (pers. com.), M. Pavia (pers. com.), W. Suárez (pers. com.).

Extrinsic variables are often not well documented for the extinct taxa. Therefore, only intrinsic variables give semi-quantified results for the extinct record.

Size: observations and interpretations

The data allow a qualitative comparison between extinct and extant insular taxa, as regards the univariate trends shown by the analysis of the intrinsic variables. Every of the following intrinsic variable was considered separately: direction and amplitude of size evolution, size class, taxonomic rank of divergence. The vegetation type of the habitat being unknown for most of the extinct taxa, this variable was not included in this comparison.

Any bias toward an under-representation of the smaller taxa in the fossil record can be excluded, because the fossils of owls are easily identifiable, and the smallest owls are still « small to medium sized » birds, very unlikely to be overlooked by avian palaeontologists. This confidently allows the following interpretations.

Trends in the evolution of size in situ (Figs. 2- 4)

The indeterminate cases (« ? ») were excluded from this analysis.

The extant taxa showing insular evolution of size display a trend to decreases in size: there are almost twice as many decreases as increases in size (Fig. 2). Among the cases of important size modifications, six are decreases (dwarfisms), while only one is an increase (giantism: *Mimizuku* (*Otus*) *gurneyi* (Tweeddale), of the Philippine Islands).

The extinct taxa, on the other hand, show other trends (Fig. 3). Their disparities in comparison with the

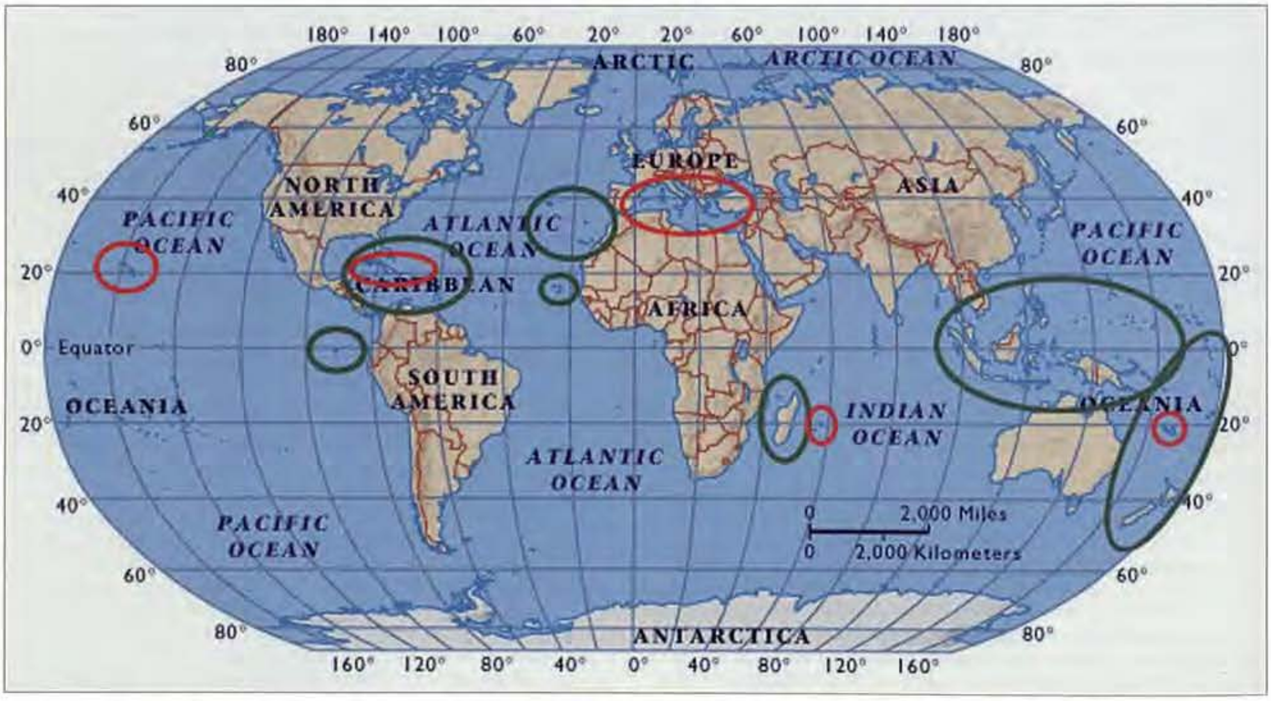

Fig. 1. Map showing the distribution of the principal islands or archipelagos where endemic extinct (in red) and living (in green) Strigiformes are recorded.

Fig. 1. Mapa que mostra la distribució de les illes principals on s'han documentat Strigiformes endèmics extingits (en vermell) i vivents (en verd).

extant record are in that:

- they include a larger proportion of moderate increases in size;
- they include a considerably larger proportion of important increases in size;
- the fossil record concentrates almost all the cases of giantism;
- dwarfism is very rare: only the case of *Bubo insularis* (Pleistocene-Holocene of Corsica and Sardinia) is well supported (Louchart, 2002).

Most of the decreases in size are uncertain. There is a need for a more precise account of the evolutionary relationships.

The deficit in cases of giantism in living owls is clearly the effect of differential extinctions and extirpations, for the same reasons as with the size classes. This will be developed in the section Discussion. When the extant and extinct taxa are considered altogether, there is no remaining trend in the evolution of size: there are symmetrically almost as many increases as decreases (Fig. 4). In the extant record, island by island, there is no exclusion between the cases of decreases and those of increases in size: the higher the number of all cases of size modification on an island, the higher the number in both the directions. Therefore even at the scale of individual islands there is no insular trend in the evolution of size.

Size classes (Fig. 5)

The extant taxa in the two classes of smallest size (less than 250 g) are not well represented among the taxa that are present both on islands and on the continents. These size classes are better represented among insular endemic taxa. This is probably due to the higher proportion of allopatric species in certain genera in these size classes (e.g. *Otus, Ninox*), compared with classes of larger body size. In both these extant records the intermediate size class (3) is the best represented as is the case in most systematic groups of animals.

In extinct insular taxa, the large sizes (more than 500 g) are relatively better represented than in extant ones, endemic as well as non-endemic. A special size class (n° 6) may even be created for the extinct Pleistocene *Ornimegalonyx oteroi*, the giant owl of Cuba, which measured around one meter high; however it is retained in the size class 5. The amplitude of the evolution of size in situ for this genus is unknown, because its continental ancestor is not identified, but it is provisionally placed in the category « +2 ». Globally the taxa of large size are under-represented in the extant insular record. Such a difference in size representations reflects the selective recent extinctions and extirpations, mainly anthropogenic (see section Discussion).

The taxonomic ranks of divergence (Fig. 6)

The quasi-absence of cases of differentiation at a subspecific rank in the extinct record is due to difficulties in osteological discrimination of fossils at these very low degrees of divergence (see also Brodkorb, 1959; about possible subspecific ranks for extinct *Tyto* in the Caribbean Islands).

Size classes and evolution of size (Figs. 7-8)

The slight trend noticed for extant taxa alone is per-

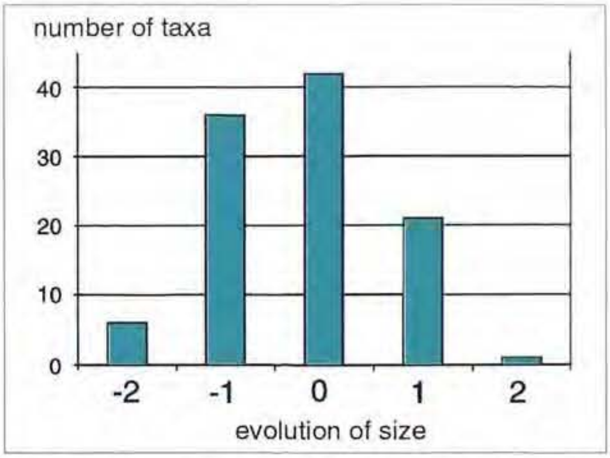

Fig. 2. Distribution of the extant endemic insular taxa of Strigiformes according to the categories of size evolution.

Fig. 2. Distrbució dels taxa d'estrigiformes insulars endèmics vivents d'acord amb les categories d'evolució de talla.

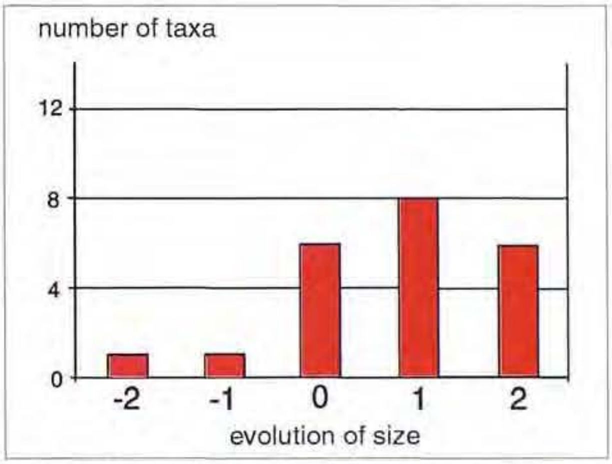

Fig. 3. Distribution of the extinct endemic insular taxa of Strigiformes according to the categories of size evolution.

Fig. 3. Distrbució dels taxa d'estrigiformes insulars endèmics extingits d'acord amb les categories d'evolució de talla.

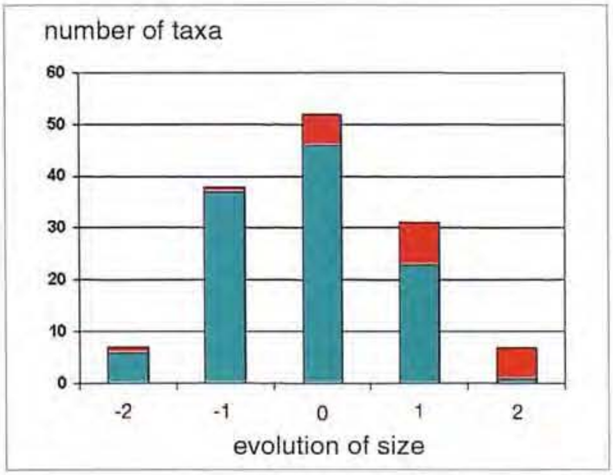

Fig. 4. Quantitative integration of the two endemic insular records: extant (in turquoise) and extinct (in red) taxa. Distribution of the taxa of Strigiformes according to the categories of size evolution.

Fig. 4. Integració quantitativa dels dos registres insulars endèmics: taxa vivents (en turquesa) i extingits (en vermell). Distribució dels taxa d'estrigiformes d'acord amb les categories d'evolució de la mida.

ceptible on the Fig. 7: smaller extant taxa show more increases in size, and larger ones show more decreases.

For extinct taxa alone, however, the pattern is different. Most of the moderate increases revealed by extinct taxa concern those which were already large before isolation (classes 4 and 5), and the giantism essentially concerns large taxa too. The smallest taxa which evolved toward giantism, extinct and extant records altogether, led to *Athene angelis*, from the Pleistocene of Corsica (Louchart, 2002), and *Mimizuku (Otus) gurneyi*, living in the Philippine Islands, as well as probably the first differentiated species of *Mascarenotus*, ancestral to the others, all in the Mascarene Islands.

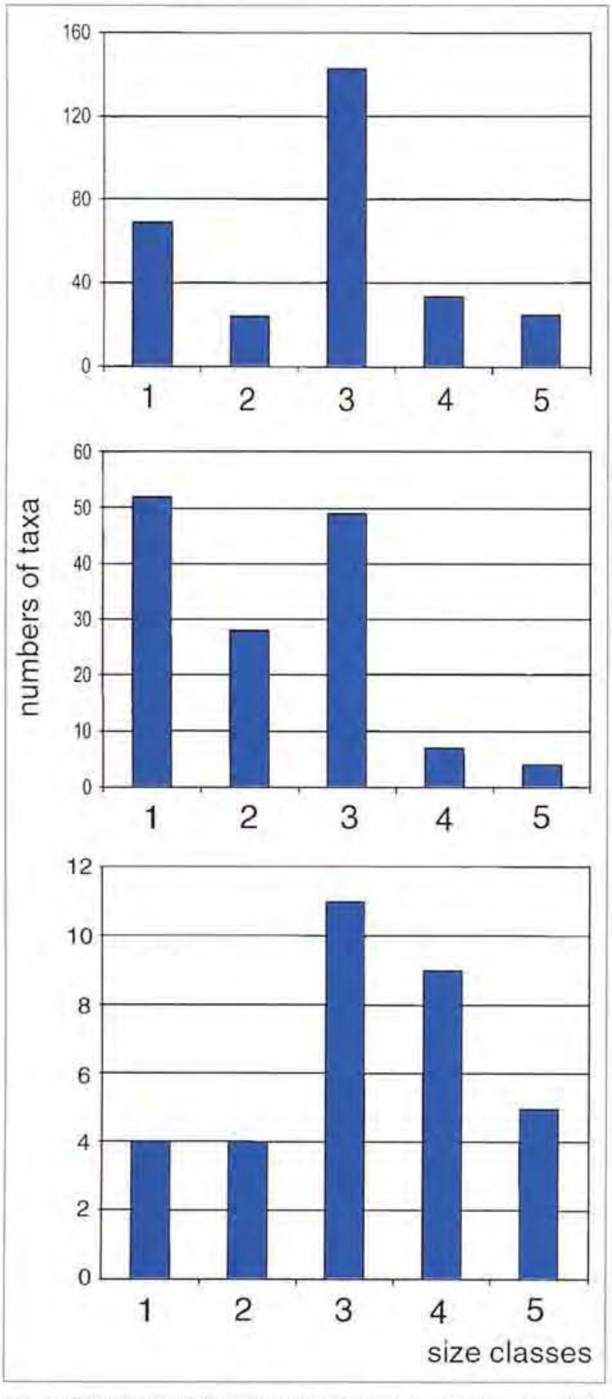

Fig. 5. Distribution of the taxa of Strigiformes according to the different size classes. Top: Extant taxa present simultaneously on islands and on the mainland. Middle: extant endemic insular taxa. Bottom: extinct endemic insular taxa.

Fig. 5. *Distribució dels taxa d'estrigiformes segons les diferents classes de talla. A dalt: taxa vivents presents simultàniament a illes i continents. En mig: taxa insulars endèmics vivents. A sota: taxa insulars endèmics extingits.*

When the extinct and extant data are put together, there is no more correlation between the size category and the direction of size evolution (Fig. 8).

Therefore, there is no 'island rule' for owls: the smaller ones do not tend to increase in size (14 decreases and 15 increases), while the larger ones only slightly tend to decrease (31 decreases and 24 increases).

Another way to confirm the absence of 'island rule' in owls is to consider other groupings of size classes. If the size class 3 is considered the medium one, then it is useful to look at the trends in the classes of smaller size than 3 vs. the ones of larger size than 3. In addition this allows to avoid the possible bias induced by the necessary choice to assign the size class of a taxon after in situ evolution (see section Methods). This bias would affect the proportion of taxa showing an increase vs. a decrease in size only in the intermediate class (3). If a category of larger taxa is defined as separated from the category of smaller taxa by the equivalent of the class 3, then no taxon can be erroneously put in a wrong category from being classified after in situ evolution, because no case has been recorded that would cross two limits of size class in the course of its insular size modification. The best marked cases cross only one size class limit and are rare (14 cases over 84). Thus, examining the proportions of decreases and increases for taxa included in disjunct "extreme" size classes makes it possible to eliminate this possible bias (which would act against the island rule). The Table 3 confirms that the absence of island rule is not an artifact: the smaller classes (1 or 1+2) comprise similar numbers of decreases and increases, while the larger classes (4+5 or 5) comprise even slightly more increases than decreases.

		Decrease	Increase
smaller	Size class 1	11 (2)	10 (2)
	Size classes 1+2	14 (3)	16 (2)
larger	Size classes 4+5	8 (1)	11 (4)
	Size class 5	3 (0)	4 (3)

Table 3. Distribution of the cases of insular body size modification of the smallest and the largest Strigiformes (living + extinct) in the categories 'decrease' (categories -1 and -2 lumped) and 'increase' (categories 1 and 2 lumped) according to the size of the taxa. First row: size class 1 only; second row: size classes 1 and 2; third row : size classes 4 and 5; fourth row: size class 5 only. The 'medium' size class 3 is excluded. In parentheses after every total is indicated the number of best marked modifications (categories '-2' and '2').

Taula 3. *Distribució dels casos de modificació de la mida corporal de les estrigiformes més petites i més grans (vivents i extingides) a les categories de "minva" (categories – 1 i -2 juntes) i "increment" (categories 1 i 2 juntes) d'acord amb la mida dels taxa. Primera filera, només la classe de mida 1; segona filera, classes de mida 1 i 2; tercera filera, classes de mida 4 i 5; quarta filera, només la classe de mida 5. S'ha exclós la classe de mida "mitjana" 3. Darrera cada total, entre parèntesi, s'indica el nombre de modificacions més marcades (categories "-2" i "2").*

	Strong negative allometry (-2)	Moderate negative allometry (-1)	Moderate positive allometry (1)	Strong positive allometry (2)	Moderate shortening (-L)	Moderate lengthening (L)	Strong lengthening (LL)
Beak	1: *Otus pauliani*	3: *Tyto alba gracilirostris*; *T. a. meeki*; *Phodilus badius parvus*	2: *Tyto alba sumbaensis*; *T. a. crassirostris*	1: *Nesasio solomonensis*			
Wing	1: *Ornimegalonyx* sp. †	8: *Tyto alba bargei*; *Mascarenotus grucheti* †; *Bubo insularis* †; *B. osvaldoi* †; *Grallistrix* sp. †; *Athene angelis* †; *Sceloglaux albifacies* (†); *Asio otus canariensis*	1: *Tyto novaehollandiae calabyi*				
Tarsus			3: *Tyto alba gracilirostris*; *T. a. schmitzi*; *T. novaehollandiae calabyi*	1: *Nesasio solomonensis*	4: *Tyto pollens* †; *Athene angelis* †; *Pulsatrix arredondoi* †; *Nesasio solomonensis*	8: *Tyto alba ernesti*; *T. a. detorta*; *Otus insularis*; *Pyrroglaux podarginus*; *Ornimegalonyx* sp. †; *Athene cretensis* †; *A. trinacriae* †; *Sceloglaux albifacies* (†)	5: *Tyto robusta* †; *Otus nudipes*; *Gymnoglaux lawrencii*; *Mascarenotus* sp. †; *Grallistrix* sp. †
Foot digits and claws		3: *Phodilus badius parvus*; *Otus alfredi*; *O. collari*	7: *Tyto alba ernesti*; *T. a. detorta*; *T. a. gracilirostris*; *T. a. schmitzi*; *T. a. crassirostris*; *T. novaehollandiae calabyi*; *Otus alius*	2: *Athene angelis* †; *Nesasio solomonensis*			

Table 4. Allometrical evolution in endemic island owls, living and extinct altogether. Only the instances where a change occurred are taken in account here. The values correspond to the number of taxa falling in every category. †: extinct taxon.

Taula 4. *Evolució al·lomètrica als mussols i òlibes insulars, vivents i extingits, tots junts. Només es tenen en compte els exemples en els quals s'han detectat canvis. Els valors corresponen als nombres de taxa que cauen dins cada categoria. †: taxon extingit.*

Allometrical insular evolution

Allometrical trends in insular birds are well known: on the beak, wing or tarsus, in living or extinct Passeriformes (Grant, 1965a,b; 1966; Rando *et al.*, 1999; Segui, 1998); on the wing or the tarsus in Falconiformes (e.g. Suarez & Olson, 2001), in Psittaciformes (*Necropsar rothschildi*, J.P. Hume, pers. com.), in Strigiformes (references in this study); on the wing in the numerous examples of reduction or loss of flight ability in insular (mainly extinct) taxa, known in at least 14 orders of birds (references in Louchart, 2001). The trends, when present, are in an increase of the relative size of the beak and the relative length of the tarsus, and a decrease in the relative size or length of the wing. All these are likely to be observed on fossil bones.

Allometries were recorded for extant, as well as extinct owls, when the information was available or interpretable. These data were analyzed to evaluate the place of Strigiformes in this context. The sources used to complete the database were the same as for body size.

The data for extant, and moreover for extinct taxa are not abundant. Only a qualitative comparison of the two records can be made. It reveals that the trends displayed are basically the same for both, but are more extreme in the extinct taxa.

Data and observations

Description of the variables

When a modification occurs in the length of limbs in birds, the most distal elements are affected at most and first (Rando *et al.*, 1999). It is judged pertinent to interpret osteological data of the tarsometatarsus length in terms of hindlimb length, and the recent data of length in the ornithological literature either on the « tarsus » or on the whole limb as representative of the changes in hindlimb length as well.

- Beak

Five categories are defined:
-2: strong negative allometry
-1: moderate negative allometry
0: isometry
1: moderate positive allometry
2: strong positive allometry

- Wing

Four categories are defined:
-2: strong negative allometry
-1: moderate negative allometry
0: isometry
1: moderate positive allometry

- Tarsometatarsus / « tarsus »

Six categories are defined:
-L: moderate shortening
0: isometry
1: moderate positive allometry (in all its dimensions)
2: strong positive allometry (in all its dimensions)
L: moderate lengthening
LL: strong lengthening

- Pedal digits and claws

Four categories are defined:
-1: moderate negative allometry
0: isometry
1: moderate positive allometry
2: strong positive allometry

Univariate trends (Table 4)

Data relative to the pedal digits and claws and to the beak are available almost only in the extant record. One case is however included here (Table 4): the extinct *Athene angelis* exhibits a positive allometry on pedal digits and claws (Louchart, 2001; 2002). This information is not listed in the Table 2.

Uncertain cases are excluded in the present analysis. Isometries are widely predominant, and they are not included in the Tables 2 and 4.

Some trends appear for pedal digits and claws, the tarsus and the wing (Table 4):

- The pedal digits and claws tend to get stronger. This is a newly observed insular trend.
- The tarsus tends essentially to get longer.
- The wing tends to get reduced.

Correlations between variables

These allometrical evolutions do not tend to show clear correlations with any other variable in this study, which is probably due in part to the small size of the sample.

Between each other, the observed trends seem to

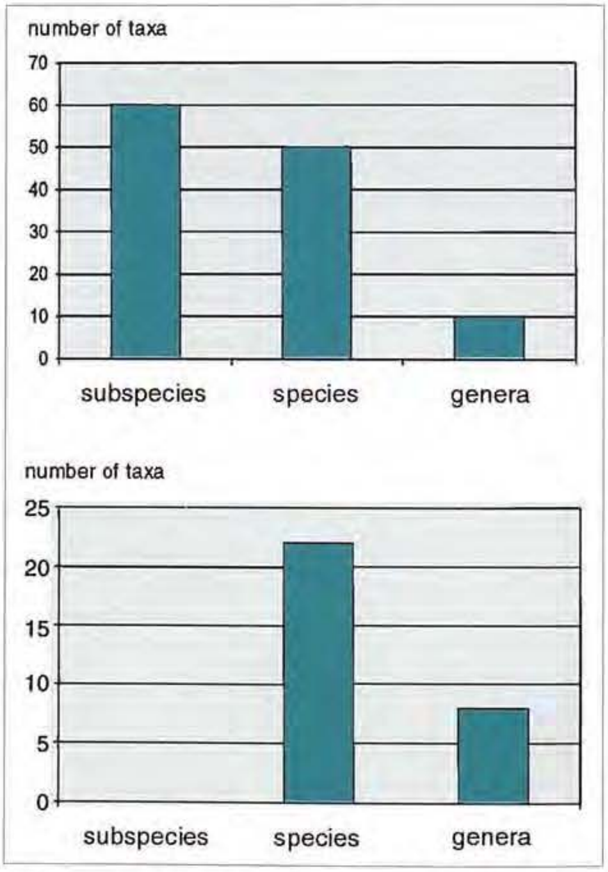

Fig. 6. Distribution of the taxa of Strigiformes according to the three categories of taxonomic rank of divergence. Top: extant endemic insular taxa. Bottom: extinct endemic insular taxa.

Fig. 6. Distribució dels taxa d'estrigiformes d'acord amb les tres categories de rang taxonòmic de divergència. A dalt: taxa insulars endèmics vivents. A sota: taxa insulars endèmics extingits.

show some dependence, qualitatively, given the characteristics of the taxa concerned:

- the positive allometrical evolution of pedal digits and claws seems positively correlated with that of the tarsus;

- the allometrical evolution of the beak seems positively slightly correlated with the two preceding, but there is however no clear resulting univariate trend for the beak.

DISCUSSION

Grant (1965a,b) observed that in passerines, the evolutions of body size and allometries are independent. This seems to apply also to the Strigiformes, but the small sample regarding the allometries does not allow to test it statistically. Allometries and size are treated separately here.

Evolution of size

No general trend for increase or decrease in size appears for insular Strigiformes. This tends to confirm the absence of such a general trend for birds.

Secondly, no 'island rule' applies to insular Strigiformes, when extinct and extant are integrated, despite a rather important range of body sizes (spanning more than two orders of weight): there is no relation between the size of a taxon and the direction of its insular size evolution. No analogy can be drawn with the island rule known in both living (e.g. Lomolino, 1985) and extinct mammals (e.g. Mein, 1983; Guérin, 1997). This tends to support the absence of such a reliable rule observed hitherto in birds, despite the questionable statement of Clegg & Owens (2002). There is no evidence either for the 'island rule' from the Holocene native bird record of New Zealand (Cassey & Blackburn, 2004).

Considering the anthropogenic impacts that will be developed later (see below), the interpretations of the bivariate analyses on the extant database must be very cautious.

A threshold effect seems to appear between the moderate increase in size, and the giantism. The value of this threshold is difficult to precise, but the effect is clear: beyond this value, the influence of the size of preys is markedly expressed, especially for giantism, in every individual case. Giantism can generally be explained by the adaptation of the owl to indigenous and/or endemic larger mean size of preys than on mainland.

Under the threshold value, every case considered separately, no pattern related to the size of prey can be detected. Precise data on the diet of insular owls are often missing, but this observation is consistent with a lack of influence of disparate sizes of prey on the size of living *Tyto alba* (Fig. 9; Taylor, 1994).

Considering the marked decreases in size, the relatively small size of prey can be influential sometimes, but other factors certainly play a role. They are not identified yet, but sometimes a noticeably insectivore diet is reported, for example, showing the possible role of the nature of prey, not only its size.

As part of an « island syndrome », islands typically display a release of some constraints (interspecific competition, predation...), and a strengthening of some others (confinement, limitation of some resources, intraspecific competition) (e.g. Adler & Levins, 1994; Blondel, 2000). Some of these factors have been variously proposed to shape the body size trends observed in diverse Amniotes. These can be roughly summarized:

- optimal body size (Damuth, 1993; Brown, 1995) - sometimes with a reference to Cope's rule (e.g. Damuth, 1993); this concept and the value of the possible optimal body size in mammals are however disputed (e.g. Meiri *et al.*, 2004),
- release of predation by medium sized Carnivores (Thaler, 1973; van Valen, 1973; Sondaar, 1977; partly inspired by Valverde, 1964),
- change in demographic strategy (Melton, 1982),
- territoriality associated with sexual size dimorphism (Louchart, 2001),
- (near) absence of large predators (Case, 1978),
- increase in intraspecific competition, due to higher density (Robinson-Wolrath & Owens, 2003),
- increase in density of some prey; relative abundance of prey (Case, 1978),
- release in interspecific competition (Case, 1978; Lomolino, 1985; Angerbjörn, 1986, in Grant, 1998; Millien, 1999),
- increase of the ratio food resource / food requirement, associated with territoriality (Case, 1978),
- different size of prey compared with mainland (Case, 1978; Alcover *et al.*, 1992); only over a threshold value (Louchart, 2001),
- Bergmann's rule and insular climate types (Foster, 1964); incidentally this ecographic rule applies well to continental owls generally (e.g. Del Hoyo *et al.*, 1999),
- Limited surface area of islands (e.g. Grant, 1998),
- Limitation in vegetal food resources (Sondaar, 1977; Azzaroli, 1982, Lawlor, 1982; Ryan *et al.*, 1989),
- Increased sedentarity in some birds (see e.g. Louchart, 2001).

Some of these factors were proposed together in conjunction (e.g. Case, 1978). Many were dismissed recently, depending on the taxonomic group and the trend considered, but the interactions between them are so complex, and the contexts so intricate, that no synthetic satisfying explanation of the real trends emerges yet.

Considering the Strigiformes alone, there is no general insular trend to be explained, but giantism and dwarfism seem to correspond to typically insular conditions (e.g. presence of giant mammalian prey...). It seems that some explanations for size changes could be searched in the optimal size theory (especially for some decreases in size), in the prey density/availability (especially for dwarfism), in the size of prey available (over a threshold value, at least for giantism), and in the territoriality of the owl taxon (Louchart, 2001).

Allometries

The predatory nature of owls obviously has consequences on the observed allometries of the pedal digits and claws, and a priori possibly also those of the tarsus.

The trend for pedal digits and claws to get stronger in insular owls was hitherto never reported. This special adaptation is likely to be found even more regularly as more precise data become available for extant as well as extinct taxa. The Fearful Owl *Nesasio solomonensis* (Solomon Islands) feeds on unusually large prey for an owl of this size, somehow "replacing" absent *Ninox* (Burton, 1992; Doughty *et al.*, 1999; Del Hoyo *et al.*, 1999; König *et al.*, 1999). Its relatively very strong feet and claws (and strong beak and large and stout tarsus) are probably related to this habit, and in some continental owls they are associated to similarly unusually large prey (Bruce, 1999; Marks *et al.*, 1999). The case of the extinct *Athene angelis*, similarly exhibiting strong feet and claws, may be interpreted in the same manner (Louchart, 2002). It is very likely that many extant cases of strong feet and claws on insular owls (e.g. *Tyto*) can be interpreted this way as well. For both extant and extinct taxa, the data are missing on the often overlooked phalanxes, but it will be most interesting to investigate them.

A special adaptation to ornithophagy might also give rise to relatively strong feet and claws, as suggested by examples on extant Falconiformes (M. Pavia, pers. com.). This possibility deserves attention.

The other allometrical trends observed may have a large part in common with birds as a whole. Considering the reduction of the wing and the lengthening of the tarsus, the diverse explanations that have been proposed are:

- more terrestrial habits than on mainland (Arredondo, 1975; Weesie, 1982; Rando *et al.* 1999),
- ornithophagy in forested habitat (Olson & James, 1991), due to absence of mammals,
- forested habitat and specialized predation on repti-

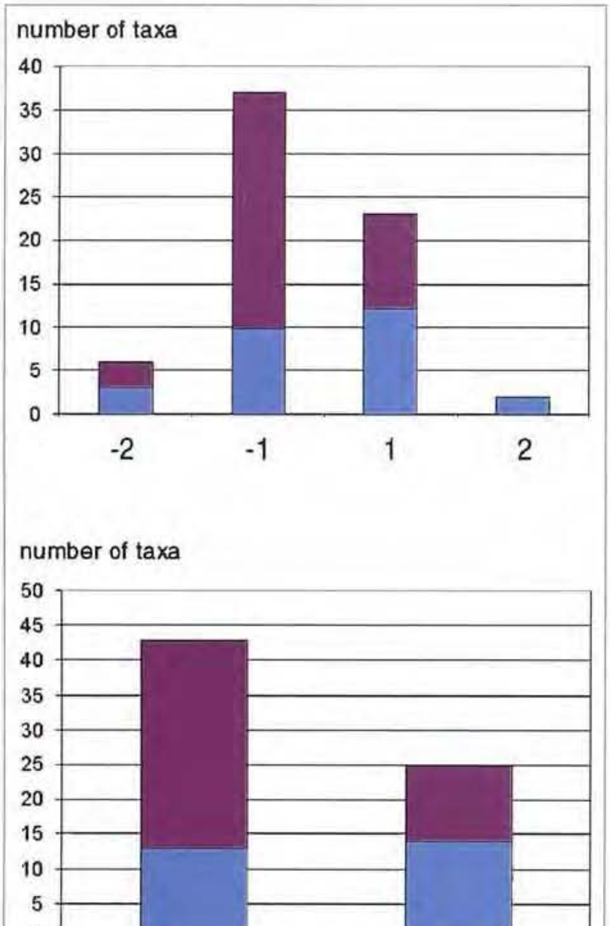

Fig. 7. Distribution of the different size classes of the extant endemic insular taxa of Strigiformes according to the categories of size evolution. In light blue: smaller taxa (size classes 1 and 2). In violet: larger taxa (size classes 3 to 5). Top: detailed categories of size evolution. Bottom: categories grouped in decreases and increases.

Fig. 7. *Distribució de les diferents classes de talla als taxa d'estrigiformes endèmics insulars vivents, segons les categories d'evolució de la talla. Blau clar: taxa més petits (classes de talla 1 i 2). Violeta: taxa més grans (classes de talla 3 a 5). A dalt: categories detallades d'evolució de la talla. A sota: categories agrupades en increments i minves.*

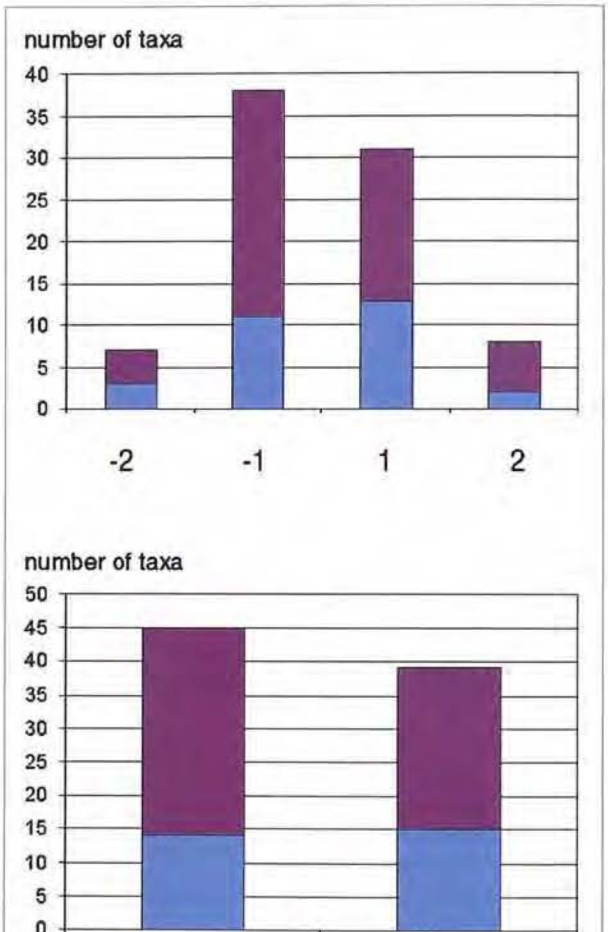

Fig. 8. Integrated distribution of the different size classes of all the endemic insular taxa of Strigiformes (living + extinct) according to the categories of size evolution. In light blue: smaller taxa (size classes 1 and 2). In violet: larger taxa (size classes 3 to 5). Top: detailed categories of size evolution. Bottom: categories grouped in decreases and increases.

Fig. 8. *Distribució integrada de les diferents classes de talla de tots els taxa d'estrigiformes endèmics insulars (vivents + extingits) segons les categories d'evolució de talla. Blau clar: taxa més petits (classes de talla 1 i 2). Violeta: taxa més grans (classes de talla 3 a 5). A dalt: categories detallades d'evolució de la talla. A sota: categories agrupades en increments i minves.*

les on vertical surfaces (J.P. Hume, pers. com.; example of some historically known *Mascarenotus*),

- terrestriality and insectivory (Suarez & Olson, 2001),
- oriented extension of some dimensions of habitat niche, due to the release of interspecific competition (Blondel, 2000), like:
  - for the tarsus: firmer perches on average – including the ground (Grant, 1965a,b; 1966),
  - for the beak: more types of foods, including larger particles (Grant, 1965a,b; 1968; 1998),
- character displacement (Grant, 1998),
- increased sedentarity (Grant, 1998),
- Allen's rule and insular climate types (discussed e.g. in Grant, 1965b).

The factors that are likely to explain the most general insular trends observed in birds are an increased terrestriality linked with a reduced predation pressure, a special diet sometimes devoid of non-flying mammals (for predatory birds), and an increased sedentarity.

For the Strigiformes, all of these three groups of factors clearly apply, more or less independently, to account for the trends. Shorter wings are in general a consequence of sedentarity and release of predation. Longer legs can be linked with terrestriality (staying or moving on the ground, e.g. probably *Gymnoglaux lauwrencii* and *Otus nudipes* – Greater Antilles, *Otus insularis* – Seychelle Islands, or the extinct *Athene cretensis, Ornimegalonyx oteroi*...), or with a special diet (e.g. possibly the extinct *Grallistrix* spp., *Mascarenotus* spp...). A marked insectivore diet is shared by *G. lawrencii*, *Otus nudipes* and *Pyrroglaux podarginus* (the latter of the Palau Islands, Micronesia), all three having lengthened hindlimbs (and partly unfeathered). Thus, such a diet could also favor this allometrical change, as in the falcon *Falco kurochkini* (Suarez & Olson, 2001). All these factors are not exclusive of each other.

There is no evidence for an insular climatic influence on either body size or allometries in owls or more generally in birds. A particular climate on average on islands has not been firmly established yet, some authors having even opposite opinions on this issue (cooler, or warmer than on the mainland at the same latitudes). Actually a warmer and moister climate is likely on most oceanic islands compared with mainland, which needs to be quantified, but the evidence is missing for continental islands.

The special diets (enhanced or exclusive ornithophagy, herpetophagy, insectivory) are consequences of the lack of indigenous non-flying mammals on oceanic islands. These terrestrial mammals are the main diet of a very large proportion of owl species on the continents.

The allometries of feet and claws seen above may sometimes « replace » the expected change in body size of the predator to follow the size of indigenous prey.

The predatory ecology of the Strigiformes appears influential in case of giantism. The obvious examples of extinct giant owls reveal more of the pattern. Generally, the islands standing far from a continent are free of Carnivores. Alcover & McMinn (1994) indicated that the Viverridae colonized islands up to 300 km from the continent (Ethiopian and Oriental regions). In most cases, among the Carnivores, only some otters colonize farther than 30 km. The distance is therefore indirectly influential in this particular way. On these islands the Strigiformes take a predominant role of predator, as strong and complementary to that of the diurnal raptors treated by Alcover & McMinn (1994). On several islands, the largest predator before the anthropogenic impacts was an owl (Burness *et al.*, 2001).

What can be considered as parallelism was noticed by Arredondo (1976) and Olson (1978), between the evolution of the different species of *Tyto* on the palaeo-archipelago of Gargano (Mio-Pliocene), and that of the species of *Tyto* on the Greater Antillean Islands (Pleistocene): in both cases the body size of the three species are spaced out at the same values approximately. These two archipelagoes had in common the absence of Carnivores (otters excepted), and the presence, probably abundant, of often giant mammalian prey (Rodents, Insectivores, and others; Arredondo, 1976). These common traits are in part due to moderate (intermediate) distances to the respective continents. As another striking parallelism, on each one of the Galapagos and Canary Archipelagoes (the latter partly) lives a small and dark endemic species of *Tyto*: respectively *Tyto* (*alba*) *punctatissima* and *T. alba gracilirostris*. Among the other similarities between these

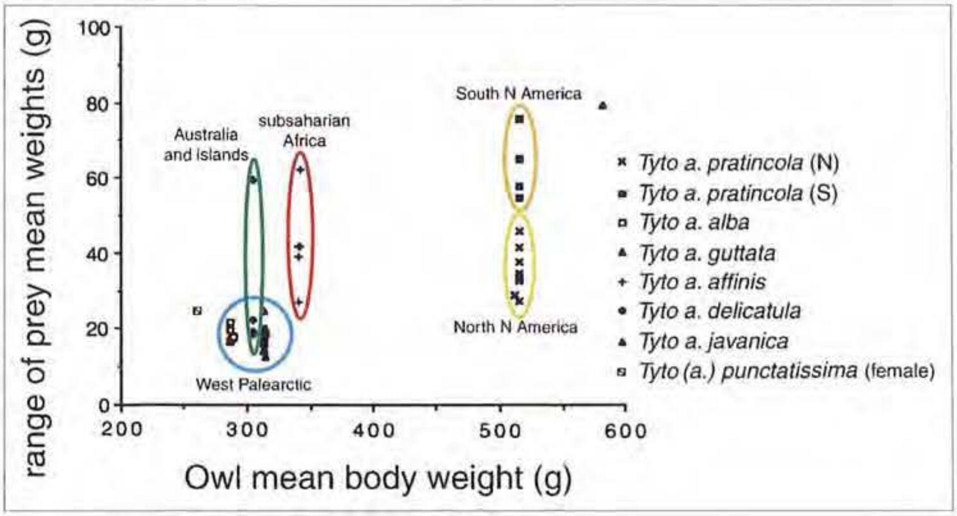

Fig. 9. Relation between the mean size of different populations of *Tyto alba* and the mean size of some samples of their preys. Modified after Taylor (1994).

Fig. 9. *Relació entre la mida mitjana de diferents poblacions de* Tyto alba *i la mida mitjana de diverses mostres de les seves preses. Modificat a partir de Taylor (1994).*

two archipelagoes, Rando *et al.* (1999) cited the presence of an endemic buzzard (*Buteo*), of lava mice, and of giant rats. These two archipelagoes have in common physical (volcanic origin) and geographical (east side of an ocean, intertropical) characteristics. A further common trait is the absence of indigenous Carnivores. A last remarkable example, this time of convergence, was noticed by Mourer-Chauviré *et al.* (1994). On the Hawaiian archipelago the genus *Grallistrix*, a small endemic owl of the Strigidae probably close to *Strix*, has undergone allopatric speciations (Olson & James, 1991). This genus is characterized by very lengthened hindlimbs and shortened wings. All of the four species are extinct. On the Mascarene Islands several allopatric speciations also occurred, in the extinct endemic genus *Mascarenotus*, probably close to *Otus* (Mourer-Chauviré *et al.*, 1994). *Mascarenotus* also shows very lengthened hindlimbs and shortened wings. The two archipelagoes had in common their remoteness and the absence of any non-flying mammal. These three examples show the importance – among others - of the characteristics of the mammal community in shaping the community of Strigiformes, and provide help to define the main island types biologically. The really oceanic islands are those devoid of non-flying mammals (including the Pleistocene Eivissa, Balearic archipelago, Alcover *et al.*, 1994). A further intermediate type should be defined: the islands lacking Carnivores (with the possible exception of some otters), but where some non-flying mammals (e.g. Rodents) are present. This is the case of some Caribbean Islands, including those where live *Gymnoglaux lawrencii* and *Otus nudipes*, both having lengthened hindlimbs, but not as much as *Grallistrix* and *Mascarenotus*.

Incidentally, it is remarkable that in Corsica are concentrated two rare types of evolution of size in owls: the only known extinct dwarf owl *Bubo insularis*, and the extinct giant *Athene angelis* diverging from a small owl. In addition, *B. insularis* shows the greatest known decrease in size from such a large mainland ancestor as a European *B. bubo* of today, and *A. angelis* shows one of the greatest increases from such a small owl as *A. noctua*. Many Carnivores lived on this island in the Middle Pleistocene (Pereira, 2001) and this unusual circumstance could have been influential in several ways. But insularity in other ways was marked enough to make these two evolutionary trajectories possible, in a still unclear manner (Louchart, 2001, 2002).

The selective extinctions and extirpations

The fossil record reveals the artifactual nature of the range of insular trends visible on the extant taxa alone. The selective nature of the extinctions in the Strigiformes can be summarized as follows (Figs. 2-4, 5): selective impacts have eradicated the largest species faster and more easily. Similarly the taxa resluting from extreme evolutionary pathways went extinct first. Larger species have lower population densities than the smaller ones (Peters, 1983). Therefore, insular populations of larger species, limited in surface area, are less numerous than are those of smaller species, which makes them more vulnerable to extinction risks (Soulé, 1987). The taxa with longer hindlimbs and/or shorter wings also experienced relatively more extinctions. A major reason lies in their vulnerability to predation, being more terrestrial. Even the perception of the relation between size and size evolution is affected when extinct taxa are not considered (Figs. 7-8).

Both extinctions and extirpations occurred among island birds due to anthropogenic impacts (e.g. Steadman, 1995). For owls, extinctions seem by far the most frequent, from the fossil record available. These extinctions may have a priori two origins: natural (changes in sea level, climate; volcanic eruptions, cyclonic events, land bridge due to a tectonic or eustatic event and allowing non-indigenous animals to colonize…), or anthropogenic. The latter were by far the most common on islands, mainly in the Holocene. For the Strigiformes, even if the exact causes are often very difficult to establish, it was demonstrated in almost all the individual cases that they were anthropogenic.

CONCLUSION

There is no general trend in the insular evolution of body size for owls. Neither is there an 'island rule' for this group. This also seems to be the case for birds as a whole, but a comprehensive study including the recent fossil record remains to be done. As summarized by Case (1978), an rule is more powerful if it explains the numerous exceptions to the general trends. But such a model tends to comprise many « amendments » to the « law ». Even in mammals, the 'island rule' would better be called just an island trend. For every size, only a majority of taxa follow the rule, but still all the other ones show either no change or change in the opposite way (e.g. Lomolino, 1985, Meiri *et al.*, 2004). Then, a simple rule may hide many converging or diverging factors, acting differently on the different taxa, size categories, etc. Such a rule is likely to be an emerging property of a very complex system (sensu Gell Mann, 1994). Finally, many islands display marked idiosyncrasies (e.g. Quammen, 1996; Grant, 1998; Laman, 2000), which perturb the recognition of general trends. But the idiosyncrasy of many islands must be emphasized, because it is a third reason to preserve island biotas, along with their role as museums – for palaeoendemics, and laboratories – for [partly] neoendemics (Cronk, 1997, in Sadler, 1999).

Body size may not be the powerful estimator of many ecological traits, as it has been thought. It is likely to be influenced by too many factors, sometimes in opposition, related to climate, competition, predation, among others (e.g. Peters, 1983; Meiri *et al.*, 2004), and such intricate relationships make both the recognition and explanation of a clear pattern very difficult. Some allometries seem to be more informative than body size considering owls. A trend for pedal digits and claws to get stronger in island owls is reported, and seems related to unusually large prey.

Trends for longer hindlimbs and shorter wings are observed, and are the same as those known in island birds in general. The most general explanations lie in terrestriality, special diets, and sedentarity. These characteristics are in turn linked with isolation and particular indigenous faunas, including prey and predators, the latter factor being partly a consequence of the previous.

The special case of Corsica is emphasized, as an original, alternative Middle Pleistocene insular context with several Carnivores, which among others revealed the extinct giant *A. angelis*, and the extinct dwarf *B. insularis*.

The probably most important intrinsic characteristics which need to be better investigated for some island owls are: their diet; other traits of their ecology like their degree of terrestriality; their territoriality (the original one of their mainland ancestor). The most important extrinsic, insular characteristics, which also need more precise quantifications, include the type and size of preys available; more generally the kinds of mammals present on the island (in part linked to, but as influential *per se* as the distance from the mainland). Here again, the palaeontological input is necessary, to reveal the original indigenous faunas, mammalian as well as reptilian for example. An intermediate type of biological islands should be defined: the islands lacking Carnivores (with the possible exception of some otters, depending on their diet), but where some non-flying mammals (e.g. Rodents) are present; as opposed to other continental islands where Carnivores are (or were recently) present.

The fossil record is indispensable to understand the insular evolutionary phenomena in owls. It is even possible to integrate quantitatively the extant and extinct records, which provides a closer approximation of the natural trends.

It is probable that the results of the bivariate analyses, carried out with extant taxa alone, are distorted too, due to the problem of selective extinctions. It is not possible to integrate the fossil data in these analyses yet. More indirectly, problems arise also from the fact that the ecology (diet for example) of living species is affected today by recent anthropogenic impacts to their habitats, available prey etc.

The fossil record is indispensable in two main ways:

- It reveals unique evolutionary pathways, the results of which are more likely to be extinct when they are extreme, for example in terms of giantism or strong allometries. The original protective nature of islands, especially in terms of release of predation, allowed the survival of such endemics. But the same islands became a trap when man appeared. The extreme adaptations to insular contexts became a handicap. The remaining extant range of evolutionary potentials of islands is very distorted and incomplete. Incidentally, the fossil record is also necessary for purposes of insular biogeography, because in this domain it becomes evident that in situ evolutions have to be taken in account (e.g. Lomolino, 2000; Lomolino & Weiser, 2001).

  N.B.: Taking in account the forms recently extinct from other causes than anthropogenic ones (rare cases, but existing), is important for taxon-scale studies of evolutionary possibilities.
- It is the only way to approximate the natural communities, contemporaneous with these evolutionary events, and which disappeared or changed drastically. The present insular communities are known to be highly residual and artificial since the human impacts, which have already been shown to make the fossils necessary in insular biogeography (e.g. Steadman, 1995). In terms of insular evolution, the best possible knowledge of the past, natural communities, is necessary because these determine the special interactions partly responsible for many changes. Alongside the owls themselves, the whole community of birds, mammals and other groups need the same palaeontological approach.

Such an integrated approach is still unusual, and surely it will require some time before biologists and palaeontologists really share the same interests. Well beyond the domain of owls, the same issue applies to birds in general, mammals, reptiles, and many other living organisms on islands, because few have escaped the anthropogenic waves of extinctions. A striking example is that of the Mascarene Islands where, unlike on the Hawaiian Islands for example, all the extinctions are due to the European colonizers since the XVIIth Century (Blanchard, 2000).

Perspectives for the study of insular owls

The data in the extant and extinct records need to be regularly updated, because new owls are discovered quite often on islands, living as well as fossil. More precise data are needed on allometries – including toes and claws - and size for many taxa, living and fossil. The phylogenetic relationships must be ascertained between many island and mainland taxa. More ecological data are also needed. The whole record of strictly continental taxa will be integrated for the Strigidae. It will be also necessary to make analyses segregating the small and large islands (as suggested for biogeography by Lomolino & Weiser, 2001), as well as the oceanic, intermediate, and continental ones, biologically speaking.

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16

THE INTERPRETATION OF CARIBBEAN PALEOGEOGRAPHY: REPLY TO HEDGES

Ross D. E. MacPhee & Manuel A. Iturralde-Vinent

MacPhee, R.D.E. & Iturralde-Vinent, M. 2005. The Interpretation of Caribbean Paleogeography: Reply to Hedges. *In* Alcover, J.A. & Bover, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: ***-***.

Resum

La hipòtesi de GAARlàndia (Iturralde-Vinent & MacPhee, 1999) especifica que una llengua de terra, capaç d'actuar com a via de dispersió per a organismes terrestres, va connectar les futures Antilles Majors amb la vorera del nord-oest de Sud Amèrica durant un període curt cap a la transició Eocè/Oligocè. Hedges (2001) ha criticat aquesta hipòtesi sota diferents prismes, i a aquest treball tractam de replicar algunes de les seves objeccions, tenint en compte l'evidència més recent que tenim sobre les següents tres qüestions: (1) Quant ha durat la presència dels ambients terrestres actuals de la conca del Carib? (2) Quines han estat les dates d'emergència més probables per a les illes que tenen aquests ambients? (3) Quin efecte tenen les corrents de superfície marines sobre la distribució dels objectes que suren a l'àrea del Carib? Primer, en contra del que diu Hedges, encara no hi ha evidència geològica per a donar suport a una continuïtat als ambients terrestres del Carib abans de fa 37 Ma. A llavors, la pretensió d'Hedges que com a mínim algunes entitats biòtiques haurien persistit *in situ* per períodes de més de 37 Ma (la data més primerenca suportada per tal evidència), com a mínim a algunes de les illes actuals, encara no es pot mantenir sobre bases geològiques. Segon, l'esdeveniment d'importància decisiva en l'emergència de GAARlàndia no fou la baixada del nivell eustàtic de la mar, sinó l'aixecament d'un arc insular tot seguint el final de la seva fase magmàtica. A llavors, notar, com Hedges fa, que l'emergència de GAARlàndia no va estar correlacionada amb una baixada identificable principal –encara que fos correcte- no és pertinent al problema plantejat. Ni ho són les incerteses de les datacions, tant de les baixades com de l'esdeveniment d'aixecament. Finalment, encara que el moviment de les corrents de superfície marines està afectat per la força de Coriolis, el vent és molt més important per al moviment dels objectes sobre la superfície. Experiments reals revelen que aquests moviments són significativament caòtics, cosa que condueix a que el transport passiu virtualment mai esdevindrà en línia recta. Com a resultat, encara que els objectes transportats pels rius de Sud Amèrica eventualment poden embarrancar a les costes del Carib, els temps de trànsit són probablement llargs. Aquest fet, tal volta més que qualsevol altre, condueix a que les llargues estades a la mar siguin un mètode improbable de dispersió exitosa per a moltes castes d'organismes. Òbviament, les investigacions geològiques i paleontològiques no poden falsar escenaris històrics, però poden subministrar *termini ad quem* per precisament el tipus d'esdeveniments en que els biogeògrafs insulars haurien d'estar interessats, tals com quan apareixen per primera vegada a una àrea ambients desitjables per organismes terrestres, i quins organismes (representats per les seves restes) eren els primers en disposar de l'avantatge d'aquestes noves terres.

Paraules clau: Carib, biogeografia, paleogeografia, tectònica, vertebrats.

Abstract

The GAARlandia hypothesis (Iturralde-Vinent & MacPhee, 1999) specifies that a landspan, capable of acting as a dispersal conduit for terrestrial organisms, connected the future Greater Antilles with the margin of northwestern South America for a short period around the time of the Eocene/Oligocene transition. Hedges (2001) has criticized this hypothesis on various grounds, and in this paper we seek to reply to several of his objections by considering the most recent evidence bearing on these three questions: (1) How long have the present land environments of the Caribbean basin been in existence? (2) What are the likeliest emergence dates for the islands supporting those environments? (3) What effect do sea-surface currents have on the distribution of flotsam in the Caribbean area? First, *contra* Hedges, there is still no geological evidence for *continuity* in Caribbean land environments earlier than 37 Ma. Therefore, Hedges' claim that biotic entities on at least some of the present islands have persisted *in situ* for periods longer than 37 Ma (the earliest date supported by such evidence) still cannot be sustained on geological grounds. Secondly, the event of overriding importance in the emergence of GAARlandia was not drawdown in eustatic sea level, but uplift in the island arc following the termination of its magmatic phase. Therefore, noticing as Hedges does that the emergence of GAARlandia was not correlated with an identifiable major drawdown—even if correct—has no pertinence to the issue at hand. Neither do uncertainties in the dating of either drawdowns or the uplift event. Finally, although the movement of sea-surface currents is affected by the Coriolis force, wind is much more important for the motion of objects on the surface (flotsam). Actual experiments reveal that such motions are significantly chaotic, which means that passive transport will virtually never occur in a straight line. As a result, although objects carried by South American rivers may eventually wash up on Caribbean shores, transit times are likely to be long. This fact, perhaps more than any other, makes long seas journeys an improbable method of *successful* dispersal for many kinds of organisms. Among such organisms we count most land mammals, for a host of autecological and physiological reasons. For other kinds of organisms, including herps, different considerations may apply. Obviously, paleontological and geological investigations cannot falsify historical scenarios, but they can provide *termini ad quem* for precisely the kinds of events that island biogeographers should be interested in, such as when environments suitable for land organisms first appeared in an area, and what organisms (as represented by their remains) were the first to take advantage of these new lands.

Key words: Caribbean, biogeography, paleogeography, tectonics, vertebrates.

INTRODUCTION

The GAARlandia hypothesis (Iturralde-Vinent & MacPhee, 1999) specifies that, close to the Oligocene/Eocene transition, a landspan (i.e., a land "bridge" connecting a mainland to a suite of islands) formed by the spine of the emergent Aves Ridge briefly (~1 Ma? [million years]) joined northwestern South America to at least three of the present Greater Antilles (Fig. 1; the involvement of tectonic blocks that now comprise the eastern part of Jamaica is possible but unconfirmed). The GAARlandia landspan episode ended with the onset of subsidence along the Aves Ridge and, conterminously, with the subdivision of the Greater Antillean Ridge into tectonic blocks and terranes and therewith the creation of the islands in approximately their current form (Iturralde-Vinent & MacPhee, 1999; MacPhee *et al.*, 2003). The degree to which GAARlandia (Greater Antillean + Aves Ridges) constituted a continuous subaerial feature at any given instant cannot yet be reconstructed empirically with available data. However, as discussed in the papers cited, the available evidence strongly indicates that much of it could have been exposed as dry land during its short existence during the Eocene/Oligocene transition. Refinements to the model continue to be made (e.g., MacPhee *et al.*, 2003), although truly decisive data will probably have to await a program of deep-sea drilling along the Aves Rise.

The GAARlandia hypothesis has generated a certain amount of controversy (cf. Graham, 2003a). Although opinion does not really divide along disciplinary lines, at present the idea seems to enjoy greater favor among paleontologists (e.g., Sánchez-Villagra *et al.*, 2000; Polcyn *et al.*, 2002) than among neontologists (e.g., Hedges, 2001; Dávalos, 2004). Hedges (2001) in particular has criticized several elements of the GAARlandia hypothesis. Our purpose here is to briefly reply to the points he raises that seem to us to be the most germane to Caribbean historical biogeography. These are:

- Permanency of land environments in the Caribbean basin
- Emergence dates for GAARlandia
- Generation of sea-surface currents and their effect on flotsam.

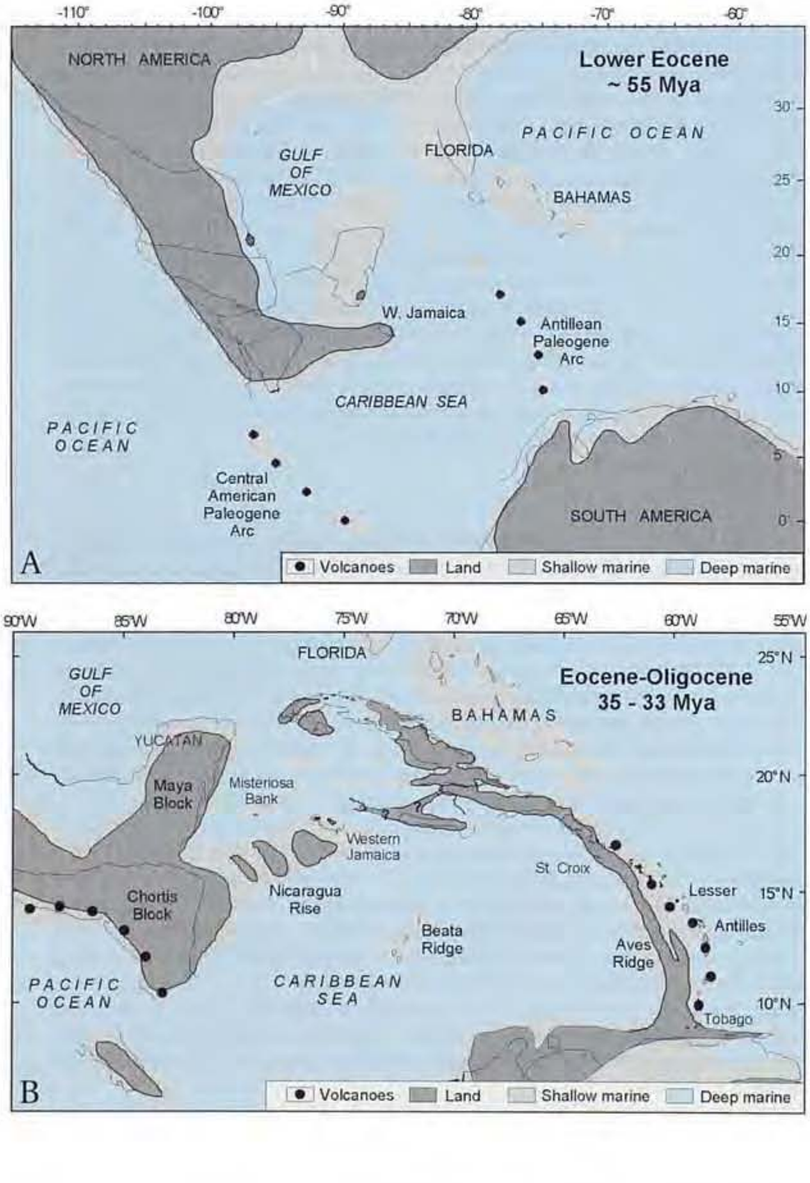

Fig. 1. Caribbean region in earlier (**A**) and later (**B**) Paleogene. In **A**, the small islands indicated along the spine of the Paleogene island-arc are indicated for purposes of illustration only. Although such islands doubtless existed, their disposition is not known. As part of the leading edge of the Caribbean plate, the basement of these islands would have been strongly deformed as they were incorporated into the Antillean foldbelt—the core of later GAARlandia. Note the existence of the broad Panamanian Seaway, which would have greatly influenced oceanic circulation and therewith the climate and sea-surface current patterns in the Caribbean region. In **B**, the GAARlandia landspan is depicted as it might have existed at its maximum extent for a short period around the time of the Eocene-Oligocene transition. For additional discussion see Iturralde-Vinent & MacPhee (1999).

*Fig. 1. La regió caribenya al Paleògen primerenc (**A**) i tardà (**B**). A la figura **A**, les illes petites indicades al llarg de l'espina de l'arc insular del Paleògen només estan indicades amb finalitat il·lustrativa. Encara que indubtablement aquestes illes varen existir, la seva situació no és coneguda. Com part de la vorera capdavantera de la placa caribenya, el basament d'aquestes illes hauria estat fortament deformat a mesura que s'incorporessin al cinturó del plegament antilleà – el cor de la posterior GAARlàndia. Noteu l'existència de l'ampli canal panameny, que hauria influït en gran mesura la circulació oceànica, juntament amb els patrons de corrents superficials marines i el clima a la regió caribenya. A la figura **B**, la llengua de terra de GAARlàndia es representa com podria haver existit en la seva extensió màxima durant un curt període de temps de la transició Eocè-Oligocè. Per a una discussió addicional, veure Iturralde-Vinent & MacPhee (1999).*

PERMANENCY OF LAND ENVIRONMENTS IN THE CARIBBEAN BASIN

First, Hedges (2001) takes issue with our claim that existing land environments within the Caribbean Sea are of relatively recent origin (i.e., Late Eocene and later). In his view, at least some Antillean land environments have been in continuous existence for a much longer period, perhaps since the late Mesozoic. We agree that there were land environments in the Caribbean prior to the end of the Paleogene, but our view of their origin and paleogeographical history is rather different from that espoused by Hedges. In our 1999 paper we provided empirical evidence for several such environments, and in more theoretical terms we included pre-Late Eocene terrestrial facies in our general model of the paleogeographical evolution of the Caribbean and circumjacent mainlands (e.g., Iturralde-Vinent & MacPhee, 1999, fig. 12, p. 53). However, our objective was to review the available evidence for judging the *permanency*, not the mere prior existence, of such land environments. The critical point here is that there is ample stratigraphic evidence throughout the Caribbean region for repeated marine transgressions that would have swamped any islands existing during the late Mesozoic and early Paleogene. Thus these earlier land environments—whatever their nature—cannot be regarded as being connected by an unbroken succession of subaerial conditions that persisted to the present. In post-Paleogene times, by contrast, the geological record supports the view that Neogene transgressions have been less complete (except in the case of western Jamaica; cf. Iturralde-Vinent & MacPhee, 1999). Thus at least on larger islands, terrestrial deposition, soil formation, and other indications of persistent subaerial conditions can be continuously traced from approximately 37 Ma at the earliest to the present—that is, from the time during the Late Eocene when the cores of the Greater Antilles were first uplifted following the termination of active volcanism, but before they coalesced into a unitary structure (GAARlandia) over which conditions were broadly subaerial to nearly subaerial. Although our model is more elaborate than others that have been proposed for Antillean Cenozoic paleogeography (e.g., Rosen, 1975, 1985), our basic framework builds on work by others interested in making regional biological history and earth history congruent (e.g., MacFadden, 1980; Perfit & Williams, 1989).

Nevertheless, Hedges (2001) argues that in the case of Hispaniola and Puerto Rico there is evidence that permanent land environments have existed much longer than we allow. In support of his position he cites two papers, one by Larue (1994) and the other by Donnelly (1992). As Larue's paper does not contradict any aspect of the GAARlandia model, including the time of uplift of Puerto Rico, we cannot explain why Hedges (2001) cited it. Indeed, Larue summarizes the late Paleogene history of Puerto Rico in terms that are entirely consistent with ours: "Cessation of volcanism, uplift of several kilometers, deformation and rotation of the arc massif in the late Eocene to middle Oligocene in Puerto Rico..." (Larue, 1994: 161; see also Larue & Ryan, 1998).

Donnelly (1992), by contrast, argued that parts of the Greater Antilles Arc (specifically Hispaniola and Puerto Rico) have been subaerial since the Albian (ca. 100-110 Ma), "and in these places emergence persisted to the present." Hedges (2001) fails to note, however, that Donnelly's argument for continuous emergence is not based on stratigraphic evidence per se, but on considerations of isostasy (as laid out by Donnelly [1990]). The scale of this approach, however, is far too gross to be useful in the present context. Relative buoyancy of crustal material is determined by mass relationships within the lithosphere, and has nothing to do with ambient sea level. If it did, then light, positive continental areas would not be subject to marine transgression. (The repeated appearance of epicontinental seas in North and South America during the Phanerozoic [cf. Hallam, 1989] is sufficient evidence to the contrary.)

True, crust becomes thicker and lighter—and, in consequence, more buoyant—during island-arc evolution. Indeed, this is why any island arc will experience general uplift immediately subsequent to the termination of volcanism, as one consequence of the exhaustion of magmatic chambers and the crystallization of large plutons beneath it (Iturralde-Vinent & MacPhee, 1999). In the case of the Cretaceous and Paleogene Caribbean arcs, on stratigraphic grounds we were able to document general uplift for short periods during latest Campanian-Maastrichtian and Middle-Late Eocene. Each phase of arc uplift was followed by later subsidence and major transgressions, also determined by stratigraphic evidence. In the case of the Cretaceous arc, no terrane has yet been identified by our methods that remained above sea level up to the present. In the case of the Paleogene arc, there is abundant evidence of continuous emergence only after magmatic extinction in the Middle Eocene. Thereafter, extinct arc segments were generally exposed from the late Eocene onwards, even during times of significant marine invasion of lowland areas.

During the last decade, one of us (MIV) has visited all the localities referred to by Donnelly (1992) as well as others of a similar nature in Cuba to obtain relevant samples for the purpose of verifying age and paleoenvironmental contexts. Results are collated, with the recent observations of many other workers, in table 1 of our paper (Iturralde-Vinent & MacPhee, 1999). In sum, this evidence shows that marine rocks of virtually every stage from Early Cretaceous through Late Eocene are well developed in the volcanic arc portions of present-day Puerto Rico, Hispaniola, Cuba and Jamaica. Terrestrial conditions certainly existed from time to time, but in our investigations older land indicators were everywhere succeeded by younger marine beds, indicating that any islands which existed were transitory.

Some heights-of-land may have avoided inundation during the pre-Late Eocene transgressions just mentioned, surviving as small islands until a later period. This is suggested by the occurrence in stratigraphic records of coarse-grained terrestrial conglomerates and montane plant fossils, both suggestive of elevated topography (Iturralde-Vinent & MacPhee, 1999, appendix 1; Graham, 2003b). However, the handful of late Paleogene island environments that have been investigated suffered later inundation and are therefore not examples of continuous survival (e.g., Cretaceous island masses exposed near Canal Paso Bonito a Cruces in Cuba; Iturralde-Vinent & MacPhee, 1999, p. 24; Eocene Guy Hill Fm terrestrial sandstone in Jamaica, op. cit., p. 39; and section diagrams in op. cit., appendix 1). In the few places where it has been possible to build up a good regional paleogeographic record, as in the case of the Havana area and the Sierra Maestra (Bresznyanzki & Iturralde-Vinent, 1978, 1985), land and marine indicators establish that there were many instances of emergence/submergence/reemergence of land during the later Mesozoic and early Paleogene. Such events had to have had a substantial effect on any terrestrial biota that managed to reach whatever islands there were prior to the Late Eocene (e.g., Donnelly, 1990, p. 607). In our view that effect would have been extinction.

Hedges (2001) does not discuss the fact that Donnelly (e.g., 1988: 26ff) also presented arguments to the effect that, during some part of the Paleogene, the northern Greater Antilles may have formed a continuous landmass; that island-island vicariance, affecting animals and plants resident thereon, might have occurred along this axis (Donnelly, 1990: 606); and that, most tellingly in view of the present discussion, a topographic high "either on the site of the present Aves Ridge, or along the present Lesser Antilles" formed a barrier to deep-water circulation between the Pacific and the Atlantic beginning "about 45 million years ago and was essentially complete at about 35 million years." (Donnelly, 1990: 601-602).

It should not be concluded from preceding paragraphs that Donnelly either presaged or would now accept the idea of GAARlandia as we present it. Indeed, Donnelly (e.g., 1989) even doubts the existence of a Caribbean "plate" as a rigid, coherent body, and situates the Greater and Lesser Antilles more or less where they are now for all of the Cenozoic. He is also everywhere careful to say that there is no persuasive evidence for a continuous landbridge/landspan on the spine of the Aves Ridge or that the ridge was ever connected to South America. On the other hand, a fair reading of the geological evidence does not lead him to reject all such possibilities out of hand, which is the point we wish to make here.

With regard to Hedges' molecular evidence for very long existence (since ?late Mesozoic) of a small number of herp lineages in the Caribbean basin, we (Iturralde-Vinent & MacPhee, 1999) note in our figure 9 and accompanying text that there is too much inherent uncertainty in his supporting arguments to accept that a molecular clock used to date phylogenetic divergences can be directly used to date colonization events (for exhaustive review of the methodological issues involved, see Crother & Guyer, 1996). It is well appreciated in the literature that there are a host of issues in linking divergence estimates, with their typically large CIs (95% credibility intervals), with specific events in earth history (for a pertinent West Indian example, see Roca et al. [2004]). By making various assumptions about tectonic scenarios and rates of molecular evolution, Crother & Guyer (1996) show that as little as 30% and as much as 90% of the available ID (immunological distance) data on herp lineages can be made to conform with one or another Antillean vicariance model. (These authors, who concluded that continent-island vicariance probably played a substantial role in determining Antillean vertebrate distributions, did not consider the GAARlandia hypothesis as an alternative explanation for concordant dispersal.) If, for example, the interpretation of the ID data for the endemic Cuban xantusiid *Cricosaura typica* by Hedges *et al.* (1992) is to be accepted at face value, it would be necessary to conclude that the lineage represented by this terminal taxon has been permanently resident in the same "place" since the Santonian (~87-83 Ma). This seems unlikely in view of the fact that "Cuba" did not exist as such at that time. Since Santonian time the components of the present Cuban foldbelt have been tectonically transported, stacked, and also transgressed at least once during each of the Campanian, Maastrichtian, Paleocene, and Eocene Stages/Epochs, all of which would have had dramatic effects on their topography.

Hedges *et al.* (1992) refer to one other mega-event, the giant tsunamis that would have been produced by the impact that struck Chicxulub in Yucatan at the K/T boundary, but they claim survival should still have been possible for some species (e.g., those distributed in montane areas). At least in the case of the Caribbean region, the most recent work (Bralower *et al.*, 1998; Tada *et al.*, 2000; Kiyokawa *et al.*, 2003; Tada *et al.*, 2004) on the magnitude of the impactor's effects seem to us to militate against survival of any terrestrial taxa (but see Crother & Guyer, 1996). In any case, impactor scenarios, no matter how violent, only address the matter of proximate cause. For the biota the knock-on consequences of the impactor event, in terms of catastrophic climatic and environmental change, were just as important (if not more so) than the event itself.

The case for Mesozoic origin of some lineages living in the Greater Antilles has recently been augmented by the work of Roca *et al.* (2004). Using molecular evidence, these authors showed that the divergence of *Solenodon* from other placentals is consistent with a calibrated origination date for the former of 76 Ma (95% CI, 72-81 Ma). Since solenodons occur nowhere else than the Greater Antilles, and since the sister-group of Solenodontidae remains persistently uncertain (Asher *et al.*, 2002), it is tempting to conclude that these insectivores have essentially always been where they are now. This temptation is redoubled if the xantusiid datum noted above is viewed as a sort of independent corroboration of very early land-vertebrate colonization of landmasses in the Caribbean Sea. However, divergence dates and colonization dates are two quite different things, and in the absence of relevant fossil evidence (for either group, in this case), there is no warrant for conflating the two. The lemurs of Madagascar are equally unique biogeographically, but to our knowledge no one has suggested that this clade originated vicariantly in the mid-Jurassic, when Madgascar and eastern Africa parted company (cf. Yoder *et al.*, 1996).

Clearly, this aspect of the debate will have no resolution without some new data, and the nature of the data needed are obvious. If there was a pre-Cenozoic Antillean fauna, then surely it consisted of more than a few herp taxa. If so, where was it and where are the fossils to document it?

EMERGENCE DATES FOR GAARLANDIA

A second group of Hedges' (2001) criticisms concerns our methodology for revising the emergence time of GAARlandia. Hedges makes two observations: (1) Originally, MacPhee & Iturralde (1994) defined the emergence date of GAARlandia as falling within the range 30-27 Ma, but later on they (Iturralde-Vinent & MacPhee, 1999) used another, older interval of 35-33 Ma for the same emergence event. (2) The reason for the change was that a sloth fossil from Puerto Rico, dated to the Early Oligocene on the basis of invertebrate faunas in associated beds (MacPhee & Iturralde-Vinent, 1995), was too "early" for the first emergence interval. Accordingly, the interval was altered to make sure that the emergence of GAARlandia preceded the deposition of the fossil. Hedges (2001) concluded that Iturralde-Vinent & MacPhee therefore biased their interpretations to make their geological sequences conform to their fossil discoveries.

Hedges (2001) is correct in noting the change, but incorrect in his characterization of the rationale for it. In the early 1990s, when we first considered the possibility of a dryland route to the large islands, the uplift event that is the fundamental basis for the GAARlandia hypothesis was very poorly constrained. Recognizing this, we originally said (MacPhee & Iturralde-Vinent, 1994, p. 10) that "a possible optimum for colonization [of the Greater Antilles] occurred between the end of the Middle Eocene and the beginning of the Late Oligocene" in concert with the Pyrenean orogenic event. We went on to hazard the possibility that the point of greatest landspan emergence might turn out to be centered on the Early/Late Oligocene boundary, since a major sea level drop, dated to 29 Ma by Haq *et al.* (1987), occurred at about that time. With further work over the next few years we were able to verify that the uplift event was actually centered several million years earlier than this, around the time of the Eocene/Oligocene transition. This was the consideration that put the 29 Ma drawdown out of contention.

It is also relevant to note that the estimated chronometric position of the Eocene/Oligocene boundary was also in a state of flux through the early 1990s, with estimates ranging from nearly 38 Ma to about 32 Ma (Prothero & Swisher, 1992). Clearly, it would have been an excess of refinement to settle on a particular chronometric estimate until a consensus on the boundary emerged. The estimate that we use presently for the Eocene/ Oligocene boundary is 33.9 Ma, which is the geomagnetic polarity time scale value published by the Geologic Time Scale 2004 project (Gradstein *et al.*, 2004). The Yauco sloth, which has not been dated chronometrically, is and will remain Early Oligocene age on the basis of biostratigraphic associations. Its relative age, accordingly, will always be younger than the Eocene/Oligocene boundary, whatever its estimated absolute date may be now or in the future.

In further criticism of our 1999 paper Hedges (2001, p. 28) goes on to say that "However, the sea level drop shown by Miller *et al.* (1996) at 35 mya was not a redating of the major Oligocene drop (Haq *et al.*, 1987) used by MacPhee & Iturralde (1994), now considered to be 32.2 mya (Miller *et al.*, 1996), but rather another sea level drop altogether. This inconsistent use of evidence shows that their paleogeographical model was influenced by their biogeographical model (i.e., the need to have the land bridge in place before the sloth fossil date)."

This passage displays confusion on several levels, not least over the interpretation of sea level position (several major fluctuations occurred during the later Eocene and Early Oligocene). What we (Iturralde-Vinent & MacPhee, 1999, p. 27) actually said was that "general tectonic uplift coincided with a major eustatic sea level drop at ca. 35 Ma (Miller *et al.*, 1996). As a result, subaerial exposure within the Caribbean basin was probably more extensive than at any other time in the Cenozoic, including the late Quaternary." This passage has nothing to do with the mid-Oligocene drawdown, which we had already discarded as too late. Instead, we were making the point that, because of the scale of uplift, the correlated drawdown at ca. 35 Ma would have led to a relatively greater amount of subaerial exposure in the Caribbean basin than at any other time. This is not implausible. Perhaps it needs to be re-emphasized for non-geologists that, because the Caribbean basin is and always has been an active tectonic region, earth movements may outstrip the rate of eustatic sea level change. Thus it is rather dangerous to rely too heavily on the latter for reliable paleogeographic information. Instead, we consistently based our reconstructions on stratigraphic considerations, using well-defined and well-understood land and marine indicators documented for specific time intervals in multiple rock sections (Iturralde-Vinent & MacPhee, 1999, appendix 1). We only noted correspondences with the eustatic sea-level curve when the correlation seemed especially interesting.

As we repeatedly emphasize in our paper (Iturralde-Vinent & MacPhee, 1999; see also Iturralde-Vinent, 2003), the most significant land indicators for the inferred exposure of GAARlandia around the time of the Eocene/ Oligocene boundary is the widespread occurrence of depositional hiatuses and the so-called "conglomerate event" that we see registered in sections throughout the Caribbean basin and its North and South American margins. *Uplift, on a geographically massive scale, is the only conceivable interpretation of this evidence.* The eustatic sea-level curve is not in conflict with this interpretation, because by definition it excludes relative changes in sea level due to local coastline subsidence or elevation.

In summary, with continuing refinements due to discoveries and reanalysis in many different areas, we expect to be able to shed additional light on the timing and consequences of the GAARlandia hypothesis. Far from being "inconsistent" with the evidence, we find ourselves fully in accord with the scientific method that treats relevant new facts and interpretations as useful occasions to test old ideas, including our own.

SEA-SURFACE CURRENTS AND THEIR EFFECT ON FLOTSAM

Finally, Hedges (2001) criticizes our modeling of sea-surface currents during the mid- and late Cenozoic. As in previous papers (e.g., Hedges, 1996a, b), Hedges (2001) continues to emphasize the overarching importance of the Coriolis force for imposing direction on the drift of flotsam, and repeats his earlier statement that "because the Caribbean always has been north of the equator during geological history, the Coriolis Force would have produced the same clockwise current flow in the past, even while a water connection to the Pacific was in existence" (Hedges, 1996b, p. 118). Because of this, he argues, the movement of flotsam will always be from the southeast toward the northwest in the Caribbean and adjacent tropical Atlantic, and this phenomenon (alone or in combination with powerful storms) can completely explain the origin of the Antillean fauna by overwater transport. This viewpoint was recently repeated without comment or modification by Hower & Hedges (2003): "If this clade [*Ameiva*] were an ancient product of proto-Antillean vicariance, the divergence time estimate between it and mainland species should be greater (e.g., 70-80 Mya) than we observe (25-30 Mya). Therefore, the West Indian Clade [of *Ameiva*] most likely arose by a single fortuitous dispersal event over water on floating debris (flotsam)." It is not made clear, or even addressed, why overwater dispersal is "most likely" when the landspan phase of GAARlandia existed at much the same time and could have provided a dryland route. Indeed, given inherent errors in both geological and molecular methods of estimating elapsed time—Hedges' earlier immunological distance estimate for the appearance of the *Ameiva* clade in the West Indies was ~36 Mya (Hedges *et al.*, 1992)—this near-approximation by investigators using quite different techniques must be regarded as little short of astounding.

Hedges gives no more than passing attention to several critical factors that might have appreciably influenced sea-surface currents in the Caribbean region during the Cenozoic, such as alterations in sea-bottom topography, presence or absence of submarine or subaerial topographic barriers, interoceanic connections, and climate change. Several of these issues were discussed by us previously (Iturralde-Vinent & MacPhee, 1999) and we continue to believe that they are important. Further, we continue to regard explanations that simply assume overwater transport under all conditions to be overstated as to the significance of the Coriolis force on "current flow" and simplistic as to the implied constancy of direction of motion of flotsam. We will close this paper with some additional observations on these two matters, which to us appear to go to the core of the "high" likelihood of overwater transport in the Caribbean region:

1. **Generation of sea-surface currents**. In discussing "current flow" in the Caribbean Sea and adjacent Atlantic, Hedges pays virtually no attention to the role of variables such as wind force and direction in the generation of surface currents. Wind and water currents that are attributable to the Coriolis force (plus the horizontal pressure gradient) are generally denoted as "geostrophic," in contrast to "surface" winds and currents whose direction and patterns are influenced by temperature gradients, the earth's surface relief, atmospheric pressure differentials, local climate, and other factors that induce or modify frictional forces (Levitus, 1982; Pickard & Emery, 1990; Berggren & Hollister, 1974). In the case of atmospheric motion, it is crucial to note that geostrophic winds are generally found at altitudes above 1000 m, and because of this are little influenced by the earth's surface except in montane areas. By contrast, surface winds are significantly influenced by ground- and sea-surface conditions, and these will in turn affect prevailing wind direction at such surfaces.

We cannot provide here the relevant data on wind mapping and wind power density estimates for surface winds in the Caribbean, but we can refer the reader to useful on-line wind energy resource atlases for the Dominican Republic and Puerto Rico (Elliott *et al.*, 2002; also follow links at http://rredc.nrel.gov/). Information for Cuba is contained in the *Atlas Nacional de Cuba* (1970). Windrose directional information indicates that, at the level of the sea surface, winds may come in from virtually any direction during the course of the year on these islands. However, by far the commonest direction recorded at coastal and near-coastal recording stations is either ENE or due E. This is tangent to the inertial effect provided by the Coriolis force rather than parallel to it, and prevailing sea-surface wind direction is unlikely to have been different in the Caribbean region in the past (except to the degree to which local relief will considerably affect winds in the immediate vicinity of islands as they blow onto, or off of, emergent land).

These observations do not necessarily diminish the strength of Hedges' argument regarding the pre-eminence of overwater transport, as long as it is reasonable to believe that animal-bearing flotsam could travel toward the Antilles from positions that lie to the E or ENE of these islands. To evaluate this, we must now consider the flotsam contribution of large South American rivers.

2. **Flotsam formation and travel times**. In our paper we showed that the largest Cenozoic river systems in northern South America were never particularly well situated for sending propagules into the Caribbean, before or after the closing of the Panamanian isthmus. Hedges (2001, p. 26) criticized us for concentrating on "the rivers of northwestern (rather than northeastern) South America...because, even today, they are less likely to be major contributors of flotsam to the Greater Antilles." The major rivers in question—Demarara, Berbice, Courantyne, Oyapock, and several others—are all quite short, with lengthy flood plains, and small annual discharges in comparison to that of the Amazon or Orinoco. These rivers are well south of the usual tracks followed by hurricanes at the present day. Thus any variation in discharge rate is likely to be essentially seasonal, with large storms having only occasional effects. Nevertheless, according to Hedges (2001, p. 26), the important point is that flotsam coming out of these rivers would always have been pushed relatively northwestward due to the Coriolis force, and therefore "at least some flotsam from northeastern South America would have been deposited on the Aves land bridge (i.e., part of the Antilles) and directly on the Greater Antilles."

We agree. Generalizing from the drift bottle experiments we cite in our paper (Iturralde-Vinent & MacPhee, 1999), the evidence is clear that flotsam in this region will go practically everywhere—eventually. Time, however, is the central problem. Whatever capacities herp species may have for surviving long-distance overwater transport, mammals such as insectivores and primates (let alone rodents and sloths) are unlikely to match them, especially when travel requires long periods in the open sea. Indeed, a primary reason for our suspecting that there must be a mechanism other than overwater transport to account for most Antillean land mammal distributions is the nature of the physiological constraints operating on small mammals. As Lindstedt (1980, p. 163) noted, "...the smallest animals are first to experience the effects of perturbations in their microclimate as their body temperatures are more directly affected by the physical environment (wind, radiation, temperature, etc.) than are those of larger animals." For a *Nesophontes*-sized animal, it is hard to cotemplate a microclimatic perturbation more severe than spending a long time on a small natural raft (for interesting speculations regarding the ability of monkeys to survive long sea journeys, see Houle, 1999).

It is reasonable to infer from the information presented on prevailing surface winds that flotsam originating from rivers draining the Guiana Highlands must first travel northward before there is much chance of it being sent into the Caribbean. The named current that is the likeliest transporter of flotsam northward along the Atlantic coast of northeastern South America is the North Brazil (or Guiana) Current, although Hedges (2001) does not name it as such. One of the distinctive features of the North Brazil Current is that it produces very large (~400 km) anticyclonic eddies or "rings" that continually spin off from the main trunk of the current in the region of 6-8°N, i.e., along the coasts of the Guianas (Fratantoni, 2001). These rings, whose origin is not well understood, remain intact for long periods, passing roughly northwestward where they eventually decay. Because of their potential importance for transporting upper-ocean water across the equatorial-tropical gyre boundary into the Atlantic, ring formation and translation is being intensively studied by physical oceanographers using drifters and satellite imagery (Fratantoni, 2001; Fratantoni & Glickson, 2002). Drifters are submersible buoys that travel at operator-determined depths and relay various kinds of data (position, current speed, temperature, pH, etc.) on a specific schedule to monitoring satellites. Although there are no data on the effect of rings on the movement of the kind of flotsam of interest here, the fact that phytoplankton distribution is affected by these massive eddies suggests that other kinds of surface objects will be as well (Muller-Karger & Aparicio Castro, 1994). In one series of experiments monitored in 1998-2000 (Fratantoni, 2001; Fig. 2), drifters released at positions between approximately 9ºN and 7ºN (approximately the latitude of the mouths of the Orinoco and of Georgetown, Guyana), well away from the continental shelf. The most frequent drift pattern seen was lengthy entrapment in an eddy, with eventual release northwards (see fig. 2 and movie clip at http://science.whoi.edu/users/dfratantoni/NBC%20Rings/drifter_car.mov). Some drifters were caught in Atlantic surface currents that took them away from land, to eddy in positions east of Bahamas for the period of the experiment (fig. 2A, C). Others (not shown) actually went east, evidently caught by the Atlantic Equatorial Countercurrent which extends several degrees north of the equator because of the northern offset of the warmest tropical water. Still others—those of greatest interest—passed into the Caribbean Sea through inter-island channels (i.e., between individual islands in the Lesser Antilles, or between the northern Greater Antilles and Bahamas/Turks and Caicos Islands). Transit times varied greatly (fig 2B, D), but the majority of drifters that entered Caribbean waters took *weeks to months* to cover the distance between their release point and the inter-island channel providing egress

As noted, for very small mammals with high metabolic rates living in the tropics, it is the capacity to withstand high temperatures that often determines survival (Vogel, 1980; Churchfield, 1990). Although metabolic rates are relatively lower in tropical as compared to temperate shrews (Vogel, 1980), we judge that a *Nesophontes*-sized insectivore would stand no chance of surviving a sea journey of more than a few hours in the Caribbean, because heat stress, exposure, and lack of food would surely kill it. Although it is a popular view that rodents are constitutionally more likely to survive a rafting event than are most other small mammals, this is unsupported assumption. Spennemann (1997), minutely reviewing the distribution of *Rattus rattus* and *R. norvegicus* in the Marshall Islands, concludes that these species have only invaded successfully when individuals managed to disembark along ropes and planks from moored vessels. Spennemann (1997) was unable to find any evidence of successful colonization from shipwrecks, as rats do not swim well enough to negotiate the surf. Like any anecdote-based argument, this conclusion can be challenged. However, it is surely germane to consider how difficult even short trips must necessarily be for most small mammals.

The fact that oryzomyin sigmodontines outside of the West Indies were also able to attain the Galápagos (Steadman, 1986) and Fernando da Noronha (Carleton and Olson, 1999) without any evident assistance from tectonics is a relevant counterclaim to our position, but such cases should not be overemphasized. In our view, physiological limits on propagules, whether actual or estimated, provide the only avenue for constraining the automatic appeal to rafting as nearly the sole (Hedges' "> 99%") mechanism of vertebrate faunal formation in the Antilles. If some kinds of reptiles can survive for long periods on rafts, as may be possible (e.g., Guadaloupean green iguanas rafting for ~ 1 month before reaching Anguilla; Censky *et al.*, 1998), then perhaps no constraint is feasible for this group. For mammals, we suspect that journeys of this length are normally out of the question. Finding a way of empirically verifying such a view, without appeal to mere anecdote, is the next challenge of Caribbean vertebrate biogeography.

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This is Contribution 10 to the series "Origin of the Antillean Land Mammal Fauna". Figure 1 was composed by MIV and fig. 2 by Patricia Wynne. We thank Clare Flemming for a critical reading of the manuscript version of this paper.

Fig. 2. Tracks of five drifters based on data originally compiled for Fratantoni's (2001) investigation of massive eddies in the North Brazil Current. The ones selected (out of several dozen released) for representation here were chosen to show diversity in the nature and direction of passive drift and in travel times between start/finish. Actual motion of drifters is considerably more complex than shown in the artist's renditions. "Origin area" refers to general area in which drifters were released from shipboard, at varying distances from NE coast of Brazil (for specific locations see movie clip noted in text). Colors indicate speed of drifters along different sections of their route (see scale). Four positions (in year/month/day format) are detailed for each drifter, to provide a sense of elapsed time en route. Original data grouped in ~10 day parcels, which is therefore the limit of precision. In all cases, "1" is point at which clock started for depicted drifter (and is never the same as actual release date, which is earlier by days or even weeks); "4" is point at which clock stopped (because drifter stopped transmitting, or because data collecting for this project ended in May 2000). Points "2" and "3" were chosen arbitrarily to give some idea of position vs. elapsed time along intermediate parts of each drifter's route. Examples chosen are average with respect to direction of drifter movement and speed. Although the general sense of movement is toward the NW, over short distances each drifter's track appears to be chaotic (unpredictable), involving frequent changes in direction and lengthy periods of slow or even retrograde motion.

Panel A, illustrating drifter bypassing Lesser Antilles and continuing into central Atlantic NE of Bahamas. 1, 1999/03/28—1999/04/08; 2, 1999/08/03—1999/08/13; 3, 2000/03/24—2000/04/03; 4, 2000/05/08—2000/05/18. Total elapsed time: beginning of April 1999 to mid-May 2000 (~13 months). Drifter passed close to northern Lesser Antilles, but left the region by August 1999 without coming close to any of them.

Panel B, illustrating two rather different drifter tracks involving central Caribbean Sea. The first drifter passed around the Lesser Antilles to enter the Caribbean Sea through the Mona Passage, eventually passing into the Gulf of Mexico and thence along the E side of Florida before leaving the monitoring area. 1, 1999/03/23—1999/04/01; 2, 1999/09/07—1999/09/17; 3a, 1999/08/01—1999/08/10; 3b, 1999/11/03—1999/11/13; 4, 2000/04/01—2000/04/11 (drifter continued N off map). Passage from origin along the Lesser Antilles chain and thence to Mona Passage took ~5 months. Thereafter drifter passed into a complicated series of eddies in the central Caribbean for two months, then traveled relatively quickly through the western Caribbean and along Yucatan coast. Changed direction to E to pass through Strait of Florida.

The second drifter passed almost directly westwards through the Lesser Antilles, across the Caribbean and thence into the Gulf of Mexico, terminating near the Mississippi delta. 1, 1999/03/23—1999/04/01; 2, 1999/12/15—1999/12/25; 3a,1999/10/07—1999/10/16; 3b, 1999/12/21—1999/12/31; 4a, 2000/02/08—2000/02/18; 4b, 2000/05/08—2000/05/18. Total elapsed time: beginning of April 1999 to mid-May 2000 (~13 months). Like the first drifter, the second drifter was caught in eddies (not shown) in the central Caribbean for a considerable period (October-December 1999) before being passed through the western Caribbean to the Yucatan Channel. From there it moved rapidly N (instead of E), crossing the Gulf of Mexico in ~2 weeks to eddy at its end point.

Panel C, illustrating route of drifter caught for ~3 months in a series of large rings propagating off NW coast of South America and continuing along E side of Lesser Antilles. 1, 1999/02/08—1999/02/18; 2, 1999/03/19—1999/03/28; 3, 1999/05/03—1999/05/12; 4, 1999/06/21—1999/07/01 (hereafter drifter followed path similar to one depicted in panel A, and remained in central Atlantic until end of experiment). Although drifter speed was comparatively high within rings, actual distance traveled along a straight line was much less.

Panel D, illustrating drifter passing into the Caribbean Sea and terminating off NW coast of Puerto Rico. 1, 1999/02/07—1999/02/17; 2, 1999/03/09—1999/03/19; 3, 1999/04/08—1999/04/17; 4, 1999/06/10—1999/06/20 (ceased transmitting). Total elapsed time: mid-February to mid-June 1999. From origin to passage through the Lesser Antilles took approximately one month. However, travel to point of termination off Puerto Rico took an additional 3 months because of eddying in central Caribbean. Thus despite this route's apparent "directness", the trip took 4 months—a long time for a terrestrial mammal, at least, to be at sea.

Fig. 2. *Rastres de cinc boies basats en dades originalment agrupades per la recerca de Fratantoni (2001) sobre remolins massius a la Corrent Nord Brasilera. Les que s'han seleccionat (d'algunes dotzenes llençades), per a la seva representació aquí, varen ser triades per mostrar la diversitat en la natura i direcció de la deriva passiva i en la durada del viatge entre el començament i el final. El moviment real de les boies és considerablement més complex que el que es mostra a les recreacions artístiques. L'"àrea d'origen" es refereix a l'àrea general en la qual les boies varen ser llençades des d'un vaixell, a distàncies variables de la costa NE de Brasil (per a veure les localitzacions exactes, moure el tros de pel·lícula indicat al text). Els colors indiquen la velocitat de les boies al llarg de diferents seccions de les seves rutes (veure escala). Es detallen quatre posicions (en format any/mes/dia) per a cada boia, per subministrar una idea del temps transcorregut en ruta. Les dades originals estaven agrupades en parcel·les de devers 10 dies, el qual és, a llavors, el límit de precisió. En tots els casos "1" és el punt en que el rellotge va començar a funcionar per a la boia representada (i mai és el mateix que la data real de llençament, la qual és uns dies o àdhuc unes setmanes anterior); "4" és el punt en que el rellotge es va aturar (degut a que la boia va deixar de transmetre o degut a que l'obtenció de dades per aquest Projecte va acabar el Maig del 2000). Els punts "2" i "3" varen ser triats arbitràriament per tenir alguna idea de la posició vs. el temps transcorregut al llarg d'indrets intermedis de la ruta de cada boia. Els exemples triats són el promig respecte la direcció del moviment i la velocitat de les boies. Encara que el sentit general del moviment és NW, sobre distàncies curtes el rastre de cada boia sembla ser caòtic (impredictible), amb canvis freqüents en direcció i llargs períodes de moviment lent, o fins i tot retrògrad.*

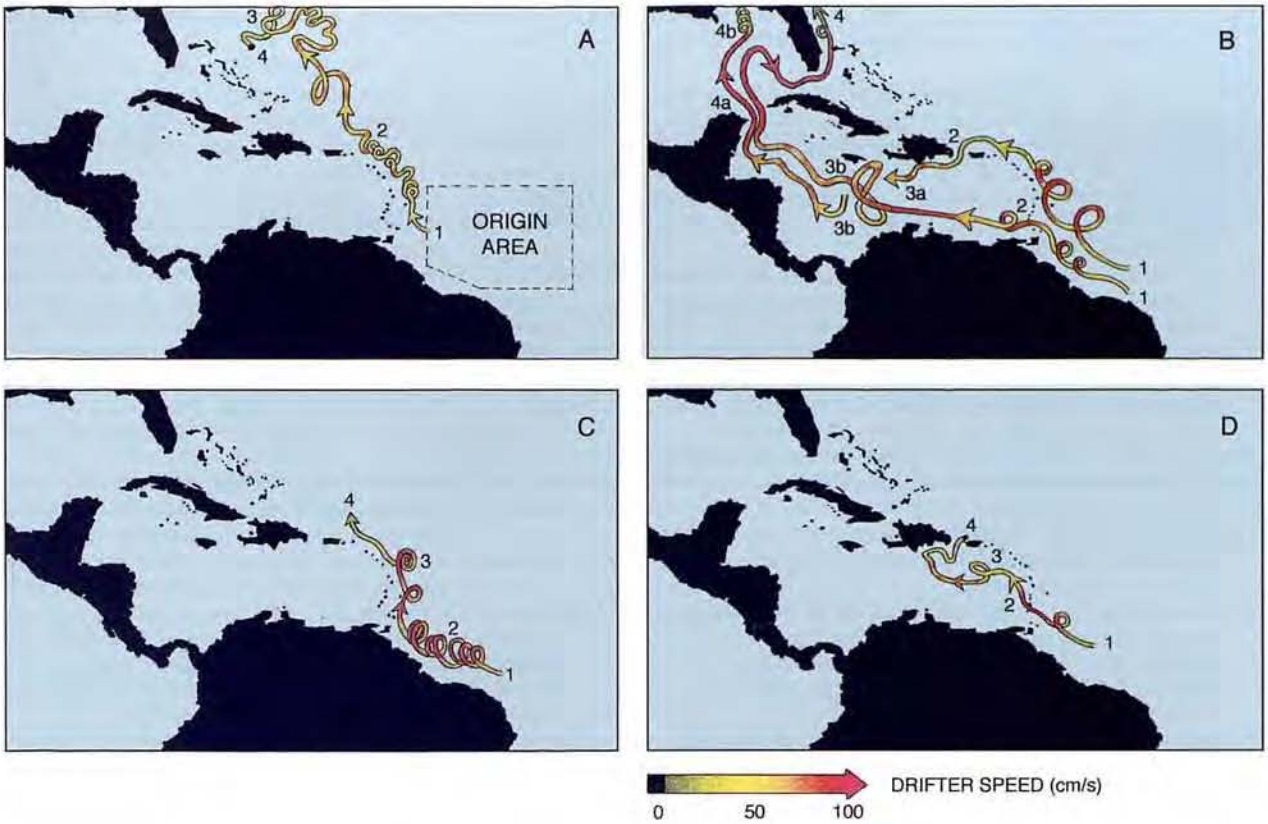
El **Panell A** *il·lustra el pas de la boia per les Antilles Menors i la seva continuació cap a l'Atlàntic central, NE de Bahames. 1, 1999/03/28—1999/04/08; 2, 1999/08/03—1999/08/13; 3, 2000/03/24—2000/04/03; 4, 2000/05/08—2000/05/18. Temps total emprat: començaments d'abril de 1999 fins a mitjans maig 2000 (devers 13 mesos). La boia va passar prop de les Antilles Menors septentrionals, però va deixar la regió l'agost de 1999, sense tornar-s'hi apropar.*

El **Panell B** *il·lustra dos rastres de boia més aviat diferents, afectant la Mar del Carib central. La primera boia va passar al voltant de les Antilles Menors per entrar a la Mar del Carib a través del Pas de Mona, passant al Golf de Mèxic i d'aquí al llarg de la costa E de Florida abans de deixar l'àrea de control. 1, 1999/03/23—1999/04/01; 2, 1999/09/07—1999/09/17; 3a, 1999/08/01—1999/08/10; 3b, 1999/11/03—1999/11/13; 4, 2000/04/01—2000/04/11 (la boia continuà cap al N del mapa). El pas des de l'origen al llarg de la cadena de les Antilles Menors i d'aquí al Pas de Mona va durar devers 5 mesos. A llavors la boia va passar per una sèrie de remolins complicats al Carib central durant dos mesos, a llavors va viatjar relativament aviat a través del Carib occidental i la costa del Yucatán. Va canviar de direcció cap a l'Est per passar a traves de l'estret de Florida.*

La segona boia va passar quasi directament cap a l'oest a traves de les Antilles Menors, creuant el Carib i d'aquí cap al Golf de Mèxic, acabant prop del delta del Mississipí. 1, 1999/03/23—1999/04/01; 2, 1999/12/15—1999/12/25; 3a,1999/10/07—1999/10/16; 3b, 1999/12/21—1999/12/31; 4a, 2000/02/08—2000/02/18; 4b, 2000/05/08—2000/05/18. Temps total transcorregut: des de començaments d'abril de 1999 fins a mitjans maig del 2000 (devers 13 mesos). Igual que la primera boia, la segona boia va ser capturada per remolins (no mostrat) a l'àrea central del Carib durant un període de temps considerable (d'octubre de 1999 a desembre de 1999) abans de passar a traves del Carib occidental al Canal de Yucatán. Des d'aquí es va moure ràpidament cap al N (en lloc de cap a l'Est), creuant el Golf de Mèxic en devers dues setmanes, fins arremolinar-se en el seu punt final.

El **Panell C** *il·lustra la ruta d'una boia capturada durant devers tres mesos a una sèrie d'anells que es propagaven lluny de la costa NW de Sud-Amèrica i continuaven al llarg del costat E de les Antilles Menors. 1, 1999/02/08—1999/02/18; 2, 1999/03/19—1999/03/28; 3, 1999/05/03—1999/05/12; 4, 1999/06/21—1999/07/01 (a partir d'aquí la boia va seguir un camí similar a un representat al Panell A, i va restar a l'Atlàntic central fins el final de l'experiment). Tot i que la velocitat de la boia va ser relativament alta dintre dels anells, la distància real recorreguda en línia recta va ser molt més petita.*

El **Panell D** *il·lustra el pas d'una boia al Carib central i acabant lluny de la costa NW de Puerto Rico. 1, 1999/02/07—1999/02/17; 2, 1999/03/09—1999/03/19; 3, 1999/04/08—1999/04/17; 4, 1999/06/10—1999/06/20 (va deixar de transmetre). Temps total transcorregut: des de mitjans de febrer fins mitjans juny de 1999. Des de l'origen fins el seu pas a traves de les Antilles Menors va transcórrer aproximadament un mes. No obstant això, viatjar fins al punt final lluny de Puerto Rico va implicar una duració addicional de tres mesos, degut als remolins del Carib central. Per això, tot i la semblança d'una ruta directa, el viatge va durar 4 mesos -un temps com a mínim massa llarg com per a que un mamífer terrestre estigui a la mar.*



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17

THE ENDEMIC VOLE *MICROTUS* (*TYRRHENICOLA*) (ARVICOLIDAE, RODENTIA) FROM MONTE TUTTAVISTA (SARDINIA, ITALY): NEW PERSPECTIVES FOR PHYLOGENY AND BIOCHRONOLOGY

Federica MARCOLINI, Marisa ARCA, Tassos KOTSAKIS & Caterinella TUVERI

MARCOLINI F., ARCA M., KOTSAKIS T. & TUVERI C. 2005. The endemic vole *Microtus* (*Tyrrhenicola*) (Arvicolidae, Rodentia) from Monte Tuttavista (Sardinia, Italy): new perspectives for phylogeny and biochronology. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 185-192.

Resum

Microtus (*Tyrrhenicola*) *henseli* és un talpó fòssil endèmic que va viure a Còrsega i Sardenya des del Pleistocè Mitjà a l'Holocè. S'han reconegut diferents poblacions de *Tyrrhenicola* a través de diferents graus evolutius que presenten una posició sistemàtica encara controvertida. S'han duit a terme algunes anàlisis de diverses poblacions de *Tyrrhenicola* provinents de les fissures recentment estudiades de Monte Tuttavista. Les poblacions estudiades mostren diferents distribucions de morfotipus que permeten reconèixer diferències als graus evolutius que faciliten la ubicació de les diferents poblacions a la seqüència fossilífera.

Paraules clau: Sardenya, Pleistocè, micromamífers, *Tyrrhenicola*, morfometria

Abstract

Microtus (*Tyrrhenicola*) *henseli* is an endemic fossil vole widespread in Sardinia and Corsica during Middle Pleistocene and Holocene. Though different evolutionary degrees have been recognised between different populations of *Tyrrhenicola* its systematic position is still controversial. Some analyses on several populations of *Tyrrhenicola* from the recently studied fissure fillings of Monte Tuttavista have been carried out, the studied populations show different morphotype distributions that allowed recognising differences in evolutionary degrees helping the sequencing of the different populations.

Keywords: Sardinia, Pleistocene, small mammals, *Tyrrhenicola*, morphometry.

INTRODUCTION

The genus *Tyrrhenicola* has been instituted by Forsyth Major in 1905 to describe the insular fossil vole remains coming from Corsica and Sardinia discovered by Cuvier in 1823 and is now considered a subgenus of *Microtus*. Though considering it at a subgeneric level, for a purpose of simplicity from now on it will be called just *Tyrrhenicola*. *Tyrrhenicola* (Arvicolidae, Rodentia, Mammalia) is an endemic fossil vole widespread in Sardinia and Corsica during Middle Pleistocene and Holocene, including a single described species *Tyrrhenicola henseli*. Though different evolutionary degrees have been recognised between different populations of *T. henseli* (Mezzabotta *et al.*, 1995), the systematic position and the phylogenetic relationships of *Tyrrhenicola* are still controversial.

After the institution of the new genus *Tyrrhenicola* by Forsyth Major, Chaline (1972), following the considerations of Hinton (1926), not only suggested that it represented an insular differentiation of *Terricola*, because of its skull features and the presence of a pitymyan rhombus in the first lower molars, but also that they belong to the same subgenus *Microtus* (*Terricola*) and proposes an evolution from some *Allophaiomys* forms like the other *Terricola*.

On the contrary, van der Meulen (1973) believes the similarities with *Terricola* to be only a parallelism and propose an evolution from *Allophaiomys pliocaenicus*, suggesting immigration to Sardinia during Early Pleistocene.

Later on, Brunet-Lecomte & Chaline (1990) further suggest that *Tyrrhenicola henseli* may represent an archaic branch of the Mediterranean group of *Terricola* they suppose to be derived from an evolved form of *Allophaiomys*, *A. chalinei*, which might have reached Sardinia and Corsica during the early Middle Pleistocene.

Mezzabotta *et al.* (1995), on the basis of some morphometric analyses, propose an evolution from the *Allophaiomys ruffoi-burgondiae* group and an immigration event dated late Early or early Middle Pleistocene throughout the Tuscan archipelago.

With the exception of the paper of Brandy (1978), all the *Tyrrhenicola* populations recovered until a few years ago in Sardinia or Corsica seem to be already evolved, none of them presenting archaic features that could help us in correlating with continental species. Indeed Brandy

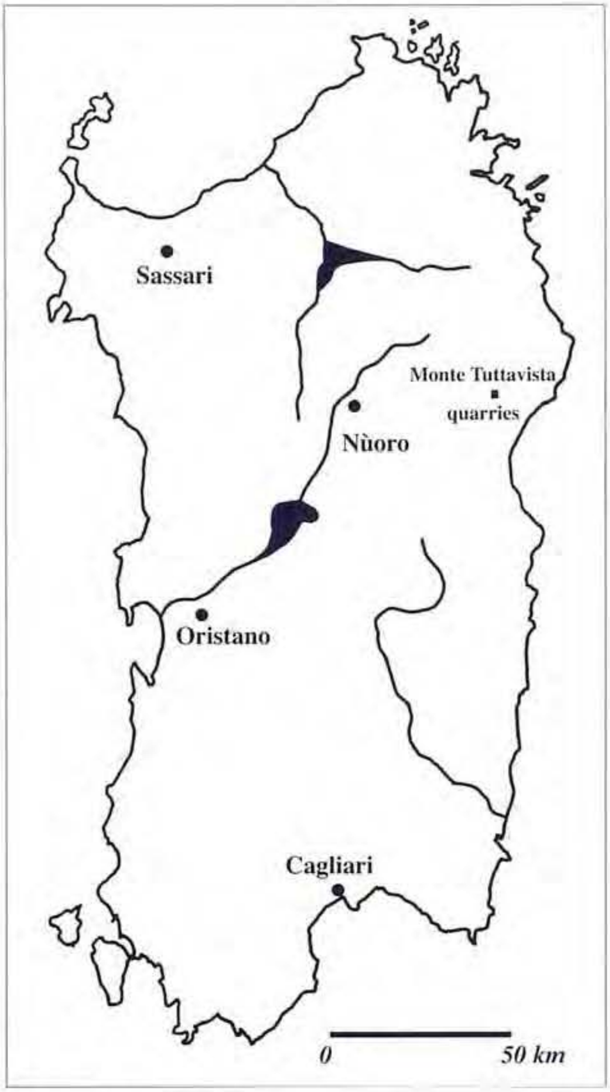

Fig. 1. Localization of Monte Tuttavista quarries.

Fig. 1. Localització de les pedreres de Monte Tuttavista.

(1978), studying the remains from Capo Figari (Sardinia), recognised the presence of a *Tyrrhenicola* more archaic than those recovered before. Later on Cordy (1997) and Sondaar (2000) quote a small sized species from quarry Xg3 of Monte Tuttavista (Sardinia). All these authors suggest it to be a different species from *Tyrrhenicola henseli* and emphasize its smaller size. Indeed size increase in insular small mammal faunas is a well known evolutionary pattern, that affects different families of small mammals in different islands. The Pleistocene Sicilian giant dormouse *Leithia melitensis* (Adams, 1863) and the Late Miocene (and Early Pliocene?) murids of the genus *Microtia* and cricetids of the genus *Hattomys* in the palaeoisland(s) of Gargano (Southern Italy) are perfect examples (Freudenthal, 1976, 1985; Abbazzi *et al.*, 1993; Petruso, 2002). The Cretan Pleistocene murids of the endemic genus *Kritimys*, with the temporal succession of three species, *Kritimys* aff. *K. kiridus* – *Kritimys kiridus* (Bate, 1942) – *Kritimys catreus* (Bate, 1912), are another good example of an evolutionary lineage whose members increase in size (Mayhew, 1977). Still in Sardinia the evolution from the small sized form *Rhagapodemus azzarolii* Angelone & Kotsakis, 2001 (Mandriola, early Middle Pliocene) through *Rhagapodemus minor* (Brandy, 1978) (found also in Capo Figari and quarry Xg3) to the bigger *Rhagamys orthodon* (Hensel, 1856) (widespread in Sardinia during late Middle Pleistocene and Late Pleistocene) is very representative (Angelone & Kotsakis, 2001).

New analyses on several populations of *Tyrrhenicola* from the recently studied fissure fillings of Monte Tuttavista (Abbazzi *et al.*, 2004; Rook *et al.*, 2004) have been carried out. The studied populations show different morphotype distributions that allowed to recognise differences in evolutionary degrees, helping the sequencing of the different populations and showing a general trend towards an increase in the complexity of the anteroconid, with a progressive development of T7 and sometimes the presence of incipient T6 and T9.

MATERIALS AND METHODS

Monte Tuttavista (Orosei, Nuoro) is located in the north-eastern side of Sardinia (Fig. 1) and on its flanks numerous limestone quarries are active. Thanks to the collaboration between the Soprintendenza per i Beni Archeologici delle Province di Sassari e Nuoro and the quarries owners, it has been possible to recover the bony breccias filling of these calcareous fissures (Cordy, 1997). Both large and small mammals, as well as amphibians, reptiles and birds have been recovered and more than 80.000 specimens have been collected. After a preliminary analysis, about 70 taxa have been identified. They can be ascribed to four different faunal complexes, ranging in time from the Late Pliocene to the Late Pleistocene (Palombo *et al.*, 2003; Abbazzi *et al.*, 2004). In the present paper results will be presented about the *Tyrrhenicola* remains coming from 5 of these fissure fillings that take their names from the quarries where they have been recovered: quarry VI banco6, quarry X g3, quarry XI g3, quarry XI "canide" and quarry XI "dic. 2001".

Hundreds of *Tyrrhenicola* specimens were present in each quarry, but a sample of about 30 to 40 first lower molars *per* quarry have been chosen. They have been described and attributed to the main morphotypes recognized by Mezzabotta *et al.* (1995) and frequency percentages have been calculated for each quarry. Moreover twenty-three different measurements on the occlusal surface of M_1s have been taken following Brunet-Lecomte (1990) method (Fig.2), as well as 7 indices:

$\mathrm{AL} = (\mathrm{V6}-\mathrm{V3})/\mathrm{V6} * 100$
$\mathrm{LW} = \mathrm{V6}/\mathrm{V21}$
$\mathrm{LW2} = \mathrm{V6}/\mathrm{V27}$
$\mathrm{LW3} = \mathrm{V6}/\mathrm{V2}$
$\mathrm{RP} = (\mathrm{V4}-\mathrm{V3})/\mathrm{V6} * 100$
$\mathrm{IAT2T3} = \mathrm{V26}/\mathrm{V27} * 100$
$\mathrm{IAT4T5} = \mathrm{V24}/\mathrm{V21} * 100$

Principal Component Analyses and ANOVAs have been performed. Analyses have been carried out using SPSS 11.0 for Windows installed on a PC of the University of Roma Tre.

RESULTS

After a description and a qualitative analysis, several differences showed up between the different populations from Monte Tuttavista quarries (Fig. 3). As to quarry VI banco6 the majority of the specimens showed a narrow neck between LRA4 and BRA3, a T7 well developed and T6 almost always present even if with different developmental stages.T4 and T5 opposite and confluent and always verging towards the posterior part of the tooth. On the contrary, specimens from quarry X g3 had a very slightly developed anteroconid. T6and T7 only outlined, while T9 was always lacking. The neck between LRA4 and BRA3 was always large and T4T5 not confluent.

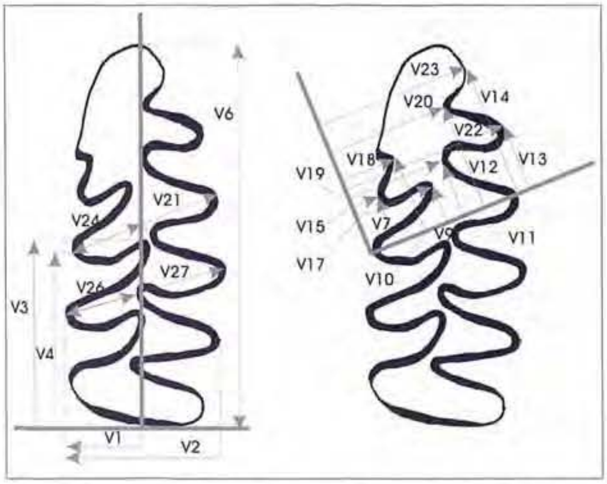

Fig. 2. Main measurements taken on the occlusal surface of *Microtus (Tyrrhenicola)* M_1, modified from Brunet-Lecomte (1990): V1: width of the lingual part of the tooth; V2: total width across the axis; V3: length along the axis of the posterior part on BRA2; V4 length along the axis of the posterior part on BSA2; V6: total length along the axis; V7: length of BSA3 across the T4T5 axis; V9: length of BRA3 across the T4T5 axis; V10: length of BSA4 across the T4T5 axis;V11: length of LRA4 across the T4T5 axis;V12: length of LRA5 across the T4T5 axis; V13: length of LSA4 across the T4T5 axis; V14: length of LSA5 across the T4T5 axis;V15: distance of BSA3 from T4 along T4T5 axis; V17: distance of BRA3 from T4 along T4T5 axis; V18: distance of BRA4 from T4 along T4T5 axis; V19: distance of LRA4 from T4 along T4T5 axis; V20: distance of LRA5 from T4 along T4T5 axis; V21: width along T4T5; V22: distance of LSA4 from T4 along T4T5 axis; V23: distance of LSA5 from T4 along T4T5 axis; V24: width of the buccal part of T4T5; V26: width of the buccal part of T2T3; V27: width along T2T3. Terminology follows van der Meulen (1973).

Fig. 2. Mesures principals preses a la superfície oclusiva de l'M_1 de Microtus (Tyrrhenicola), *segons Brunet-Lecomte (1990), modificat. V1: amplària de la part lingual de la dent; V2: amplària total a través de l'eix; V3: llargària al llarg de l'eix de la part posterior de BRA2; V4 llargària al llarg de l'eix de la part posterior de BSA2; V6: llargària total al llarg de l'eix; V7: llargària de BSA3 a través de l'eix T4T5; V9: llargària de BRA3 a través de l'eix T4T5; V10: llargària de BSA4 a través de l'eix T4T5;V11: llargària de LRA4 a través de l'eix T4T5;V12: llargària de LRA5 a través de l'eix T4T5; V13: llargària de LSA4 a través de l'eix T4T5; V14: llargària de LSA5 a través de l'eix T4T5;V15: distància de BSA3 des de T4 al llarg de l'eix T4T5; V17: distància de BRA3 des de T4 al llarg de T4T5; V18: distància de BRA4 des de T4 al llarg de l'eix T4T5; V19: distància de LRA4 des de T4 al llarg de l'eix T4T5; V20: distància de LRA5 des de T4 al llarg de l'eix T4T5 axis; V21: amplària al llarg de T4T5; V22: distància de LSA4 des de T4 al llarg de T4T5; V23: distància de LSA5 des de T4 al llarg de l'eix T4T5; V24: amplària de la part bucal de T4T5; V26: amplària de la part bucal de T2T3; V27: amplària al llarg de T2T3. La terminologia segueix van der Meulen (1973).*

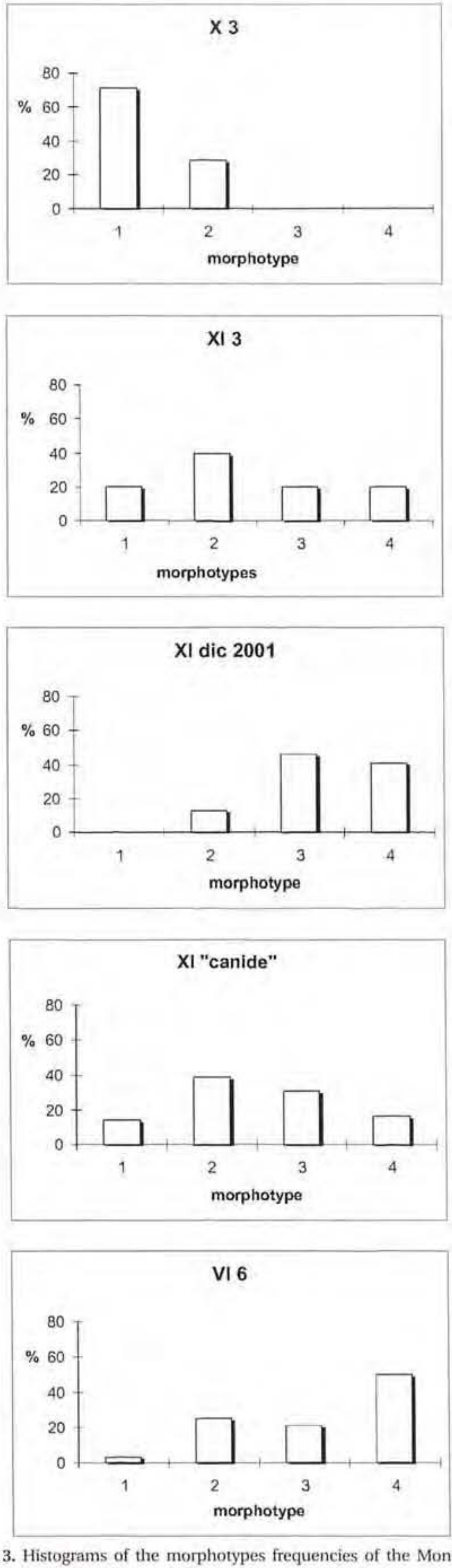

Fig. 3. Histograms of the morphotypes frequencies of the Monte Tuttavista populations (expressed as a percentage).

Fig. 3. Histogrames de les freqüències de morfotipus de les poblacions de Monte Tuttavista (expressats com a percentatges).

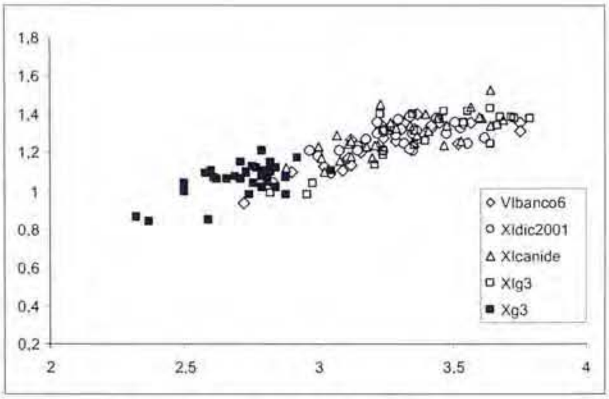

Fig. 4. Length against width plot for all the populations.

Fig. 4. *Relació entre la llargària I l'amplària per a totes les poblacions.*

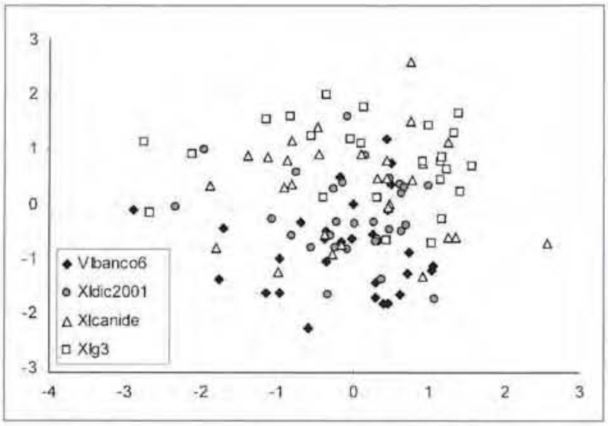

Fig. 5. Principal Component Analysis on V1, V2, V3, V4, V6, V21, V24, and V27 for quarry XI g3, XI "canide", XI "dic.2001" and VI banco6.

Fig. 5. *Anàlisi de Components Principals de V1, V2, V3, V4, V6, V21, V24, i V27 per a les pedreres XI g3, XI "canide", XI "dic.2001" i VI banco6.*

The other quarries populations showed intermediate features such as a short and rounded anteroconid in quarry XI g3 specimens, or T6 and T7 retrovergent but with a narrow neck in quarry XI "dic. 2001", or with a very variable neck – from very narrow to very wide – in quarry XI "canide" specimens.

Once described, the teeth have been attributed to the four main morphotypes of Mezzabotta *et al.* (1995), and percentage frequencies have been calculated. The calculation of frequencies showed interesting patterns (Table 1): quarry X g3 specimens belong only to morphotypes 1 and 2, with a clear prevalence of number 1 (71.4%). First lower molars of XI g3 have been attributed to all the four morphotypes, with a prevalence for number 2 (40%). Quarry XI "canide" has an almost equal percentage of morphotypes 2 and 3 (38,8% and 30,6% respectively), while the populations from VI banco6 and XI "dic. 2001" seem to be the more evolved, with a prevalence of morphotypes 3 and 4. It has been therefore possible to establish a sort of relative sequence between Monte Tuttavista fissures (Fig. 4) on the basis of the prevalent morphotype within the populations, where quarry X g3 is the more archaic and VI banco6 and XI "dic. 2001" the more evolved.

Quarries	Morphotype frequencies (%)			
	1	2	3	4
X g3	71.4	28.6		
XI g3	20	40	20	20
XI "canide"	14.3	38.8	30.6	16.3
XI "dic. 2001"		12.8	46.2	41.0
VI banco6	3.6	25.0	21.4	50.0

Table 1. Morphotype frequency percentages of the five quarries.

Taula 1. *Percentatges de freqüència dels morfotipus a les cinc pedreres.*

Component	Total	% of Variance	Cumulative %
1	6.086	76.072	76.072
2	0.934	11.672	87.745
3	0.266	3.319	91.063
4	0.230	2.876	93.940
5	0.202	2.520	96.459
6	0.148	1.853	98.312
7	0.088	1.104	99.416
8	0.047	0.584	100

Table 2. Eigenvalues of Principal Component Analysis on V1, V2, V3, V4, V6, V21, V24, V26 and V27 for quarry XI g3, XI "canide", XI "dic.2001" and VI banco6.

Taula 2. *Eigenvalues de l'Anàlisi de Components Principals sobre V1, V2, V3, V4, V6, V21, V24, V26 i V27 per a la pedrera XI g3, XI "canide", XI "dic.2001" i VI banco6.*

Variables	Component	
	1	2
V1	0.905	-0.052
V2	0.961	0.023
V3	0.745	0.584
V4	0.530	0.821
V6	0.801	0.283
V21	0.964	-0.026
V24	0.914	-0.115
V27	0.929	0.112

Table 3. Factor Loadings of Principal Component Analysis on V1, V2, V3, V4, V6, V21, V24, V26 and V27 for quarry XI g3, XI "canide", XI "dic.2001" and VI banco6.

Taula 3. *Factor Loadings de l'Anàlisi de Components Principals sobre V1, V2, V3, V4, V6, V21, V24, V26 i V27 per a la pedrera XI g3, XI "canide", XI "dic.2001" i VI banco6.*

Another simple analysis, such as the relationship between width and length of the M_1, has been performed (Fig. 5), showing a high correlation coefficient (R^2 = 0,746) and a differentiation in two main groups: one composed mainly by quarry Xg3 specimens and the other by the other populations.

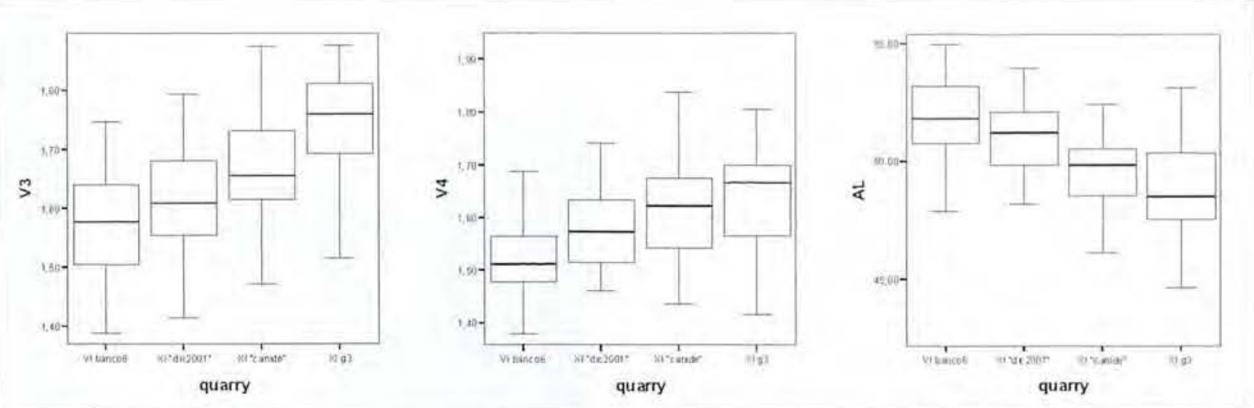

Fig. 6. Boxplots of a: V3; b: V4; c: AL.

Fig. 6. Boxplots de a: V3; b: V4; c: AL.

Quarry	N	V3		V4		V6		AL	
		Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.	Mean	Std. Dev.
VI banco6	30	1.58	0.09	1.52	0.08	3.28	0.23	51.90	1.75
XI "canide"	30	1.67	0.11	1.61	0.09	3.31	0.23	49.56	1.37
XI "dic2001"	30	1.62	0.08	1.58	0.09	3.29	0.19	50.79	1.94
XI g3	25	1.74	0.11	1.64	0.09	3.39	0.26	48.73	2.44
ANOVA		p<0.0001		p<0.0001		N.S.		p<0.0001	

Table 4. ANOVAs results for V3, V4, V6 and AL.

Taula 4. Resultats de l'ANOVA per V3, V4, V6 i AL.

It is therefore simple to identify quarry Xg3, though none of the above mentioned analyses has been able to discriminate between the other four quarries populations. That is why we decided to apply a simple morphometric method such as that of Brunet-Lecomte (1990) measurements, with the aim to determine if a difference between the populations exists and, in that case, which are the variables responsible for such a differentiation.

Several Principal Component Analyses have been performed. A first one with all the variables together, then using only the measurements of the anteroconid complex, or using both the variables of the main body of the tooth and the horizontal measurements of the anteroconid, or the contrary: the variables of the main body of the tooth and the vertical measurements of the anteroconid. The best resolution we obtained was using only the main variables of the tooth excluding those describing the anteroconid (Table 2). In this case, a good differentiation is visible on a bivariate plot along Axis 2, where two main groups are visible (Fig. 6): one composed by quarry VI banco6 and quarry XI "dic.2001" and the other formed by XI g3 and XI "canide". As results from Table 3 the second principal component weight is given mainly by V3 and V4, representing the length of BSA2 and BRA2, respectively, along the tooth axis.

ANOVAs and post-hoc tests have been therefore performed on these two variables to determine their significance in the differentiation of the populations and on V6, the total length, to have a final clue whether the size shows a significant variation or not.

Both V3 and V4 show a significant ANOVA (p<0.0001 in both cases; table 4) while the analysis on V6 is not significant, meaning size in itself does not vary significantly within the studied populations.

(I) Quarry	(J) Quarry	Mean Difference (I-J)	Std. Error	Sig.
VI banco6	XI "dic2001"	-0.042	0.026	0.437
	XI "canide"	-0.090*	0.026	0.008
	XIg3	-0.159*	0.027	0.000
XI "dic2001"	VI banco6	0.042	0.026	0.437
	XI "canide"	-0.048	0.026	0.325
	XIg3	-0.117*	0.027	0.001
XI "canide"	VI banco6	0.090*	0.026	0.008
	XI "dic2001"	0.048	0.026	0.325
	XIg3	-0.069	0.027	0.090
XIg3	VI banco6	0.159*	0.027	0.000
	XI "dic2001"	0.117*	0.027	0.001
	XI "canide"	0.069	0.027	0.090
* The mean difference is significant at the .05 level.				

Table 5. Scheffè test results for V3.

Taula 5. Resultats del test d'Scheffè per a V3.

Scheffé test has been performed (Table 5) showing for V3 a significant difference between means of quarry VI banco6 and XI g3 / XI "canide", as well as a difference between quarry XI "dic.2001" and XI g3. The analysis of the homogeneity of subsets of the means (Table 6) shows

Quarry	N	Subset 1	2	3
VI banco6	30	1.576		
XI "dic2001"	30	1.618	1.618	
XI "canide"	30		1.666	1.666
XI g3	25			1.735
Sig.		0.458	0.346	0.078

Table 6. Univariate Homogeneous Subsets for V3.

***Taula 6.** Subconjunts homogenis univariats per a V3.*

(I) Quarry	(J) Quarry	Mean Difference (I-J)	Std. Error	Sig.
VI banco6	XI "dic2001"	-0.066*	0.023	0.048
	XI "canide"	-0.094*	0.023	0.001
	XIg3	-0.125*	0.024	0.000
XI "dic2001"	VI banco6	0.066*	0.023	0.048
	XI "canide"	-0.028	0.023	0.678
	XIg3	-0.060	0.024	0.113
XI "canide"	VI banco6	0.094*	0.023	0.001
	XI "dic2001"	0.028	0.023	0.678
	XIg3	-0.031	0.024	0.643
XIg3	VI banco6	0.125*	0.024	0.000
	XI "dic2001"	0.060	0.024	0.113
	XI "canide"	0.031	0.024	0.643

* The mean difference is significant at the .05 level.

Table 7. Scheffè test results for V4.

***Taula 7.** Resultats del test d'Scheffè per a V4.*

Quarry	N	Subset 1	2
VI banco6	30	1.519	
XI "dic2001"	30	1.584	1.584
XI "canide"	30		1.613
XI g3	25		1.644
Sig.		0.057	0.100

Table 8. Univariate Homogeneous Subsets for V4.

***Taula 8.** Subconjunts homogenis univariats per a V4.*

three subsets, meaning that the means of VI banco 6 and XI "dic.2001" do not differ significantly, that the means of XI "dic.2001" and XI "canide" do not differ significantly and that the means of XI "canide" and XI g3 do not differ significantly. The same analysis (tables 7 and 8) performed on V4 shows two subsets, one composed by VI banco6 and XI "dic.2001", and the other by XI "canide" and XI g3 with XI "dic.2001" that stays in both subsets.

ANOVAs and post-hocs have been performed also on the indices. None of them result in a significant difference between the populations except for AL, the relative elongation of the anterior part of the tooth, (Table 4 and 9) and RP, but with a lower significance level. AL means of quarry VI banco6 and XI g3 / XI "canide" are significantly different, as well as between quarry XI "dic.2001" and XI g3. This leads to a subset pattern similar to that of V3 (table 10).

Discussion and Conclusions

The considerable amount of material recovered from the Monte Tuttavista quarries is leading to an extensive study not only of the *Tyrrhenicola* specimens, but also of the whole fauna of large and small mammals, allowing comparisons to be made either by an evolutionary and a biochronological point of view. At the beginning of our studies we possessed very few clues about the age of the fissures nor there was a biochronological framework of Sardinian mammal faunas, helping in the stratigraphic constraining of the faunas. Many of the recovered large mammal taxa were new species or even new genera, and the possibility to have even a relative sequence of the quarries was, at the beginning, unlikely.

Unfortunately the morphological qualitative analysis of the populations, even in presence of a high number of specimens, has not proven to be decisive, due to the highly variable characters of the anteroconid complex. The apparent predominance of some features is, in fact, not confirmed by a quantitative statistic analysis of the measurements of the anteroconid complex. As already stated by Mezzabotta *et al.* (1995) we are in presence of a clear mosaic evolutionary pattern, visible even in a very restricted area such as that of the Monte Tuttavista. This is not completely exact for quarry X g3 population that shows indeed a smaller size and a much simpler anteroconid than the other quarries populations. Such features have been already noticed by Cordy (1997) and Sondaar (2000) which suggested the possibilities of a new species of *Tyrrhenicola*, possibly related to those archaic remains of Capo Figari quoted by Brandy (1978). Such a possibility is indeed confirmed by the present study, where all the signs indicate a marked difference between quarry Xg3 and all the other *Tyrrhenicola* up to day recovered, both qualitatively and quantitatively. The anteroconid is less developed and complicated, leading to a definitely smaller size, the total absence of morphotypes number 3 or 4, and the predominance of number 1; they all strongly suggest for the *Tyrrhenicola* of quarry X g3 to be the ancestor species of *T. henseli*. Further morphometric studies and comparisons of this archaic form with other continental taxa will likely help the identification of the ancestor of *Tyrrhenicola* (Marcolini *et al.*, in press).

Still uncertainties remained as to the possibility to identify different evolutionary degrees between the other four populations, supposing that they exist.

Morphotypes frequencies are giving the first clue for a possible sequence to be constructed (Fig. 4). Quarry XI g3 and XI "canide" have almost the same percentage of morphotype 2, but while the latter has also a high percentage of number 3, the first has almost equal weights on the other three. Same stands for quarry VI banco6 and

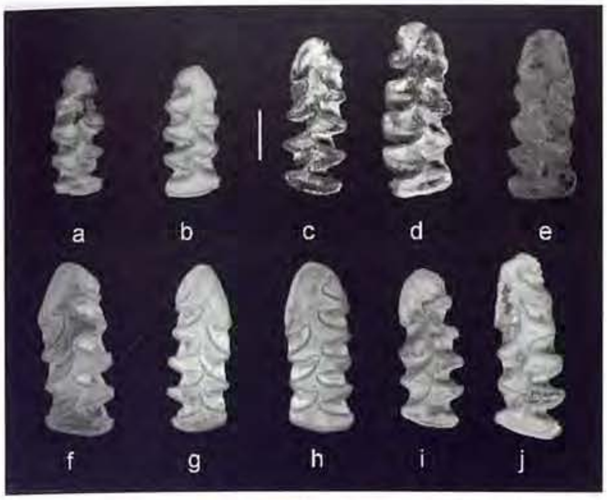

Plate 1. *Microtus (Tyrrhenicola)* first lower molars from Monte Tuttavista: **a, b:** quarry X g3, specimens ORX3ty5 and ORX3ty9; **c, d:** quarry XI g3, specimens ORXI3ty39 and ORXI3ty 45; **e, f:** quarry XI "canide", specimens ORXIcty82 and ORXIcty 87; **g, h:** quarry XI "dic.2001", specimens ORXI2001ty123 and ORXI2001ty129; **i, j:** quarry VI banco6, specimens ORVI6ty162 and ORVI6ty168. Scale bar represents 1 mm.

Làmina 1. Primers molars inferiors de Microtus (Tyrrhenicola) *de Monte Tuttavista.* ***a, b:*** *pedrera X g3, espècimens ORX3ty5 i ORX3ty9;* ***c, d:*** *pedrera XI g3, espècimens ORXI3ty39 i ORXI3ty 45;* ***e, f:*** *pedrera XI "canide", espècimens ORXIcty82 i ORXIcty 87;* ***g, h:*** *pedrera XI "dic.2001", espècimens ORXI2001ty123 i ORXI2001ty129;* ***i, j:*** *pedrera VI banco6, espècimens ORVI6ty162 i ORVI6ty168. L'escala representa 1 mm.*

XI "dic. 2001", where number 4 and 3 are the more represented respectively, while the other frequencies are more variable.

On this basis a possible sequence of the quarries, from the oldest to the youngest, can be XI g3, XI "canide", XI "dic. 2001" and VI banco6. Such an interpretation is in good agreement with the pieces of information coming from the other small mammals and from large mammals (Abbazzi *et al.*, 2004). In order to ameliorate the global knowledge on the stratigraphy of all the quarries, we compared the morphotype percentage frequencies with those of other Sardinian and Corsican sites we were able to find in literature. Unfortunately no radiometric dates exist for any of the Sardinian faunas, while a few are available for Corsica. Published data on *Tyrrhenicola* for Capo Figari, Dragonara, Siniscola, Monte San Giovanni, Bonaria (Mezzabotta *et al.*, 1995), Punta di Calcina and Castiglione 3CG (Pereira *et al.*, 2001) have been compared with the percentages we calculated for Monte Tuttavista quarries (Table 11). We were thus able to obtain a relative sequencing of the Sardo-Corsican faunas where *Tyrrhenicola* is present and abundant, awaiting for the possibility to obtain radiometric dates of some of the Sardinian sites.

Still the problem risks to remain unsolved for all those sites where only a few first lower molars of *Tyrrhenicola* are present. Moreover when we deal with single specimens or a very reduced population, where reliable frequency percentages cannot be computed, to determine with good certainty which is the evolutionary stage of the species – and therefore of the containing

(I) Quarry	(J) Quarry	Mean Difference (I-J)	Std. Error	Sig.
VI banco6	XI "dic2001"	1.111	0.487	0.163
	XI "canide"	2.337*	0.487	0.000
	XIg3	3.165*	0.510	0.000
XI "dic2001"	VI banco6	-1.111	0.487	0.163
	XI "canide"	1.226	0.487	0.102
	XIg3	2.053*	0.510	0.002
XI "canide"	VI banco6	-2.337	0.487	0.000
	XI "dic2001"	-1.226	0.487	0.102
	XIg3	0.828	0.510	0.456
XIg3	VI banco6	-3.165*	0.510	0.000
	XI "dic2001"	-2.053*	0.510	0.002
	XI "canide"	-0.828	0.510	0.456
* The mean difference is significant at the 0.05 level.				

Table 9. Scheffè test results for AL.

Taula 9. Resultats del test d'Scheffè per a AL.

Quarry	N	Subset	
		1	2
XI g3	25	-2.635	
VI banco6	30	-1.716	-1.716
XI "canide"	30	-1.571	-1.571
XI "dic2001"	30		-1.004
Sig.		0.234	0.587

Table 10. Univariate Homogeneous Subsets for AL.

Taula 10. Subconjunts homogenis univariats per a AL.

	morphotype frequencies (%)			
	1	2	3	4
X g3	71.4	28.6		
Capo Figari*	11.1	33.3	44.4	11.1
Dragonara*	21.1	42.1	26.3	10.5
XI g3	20	40	20	20
Punta di Calcina°	18.8	46.9	28.2	6.3
XI "canide"	14.3	38.8	30.6	16.3
Siniscola C*	11.1	44.4	22.2	22.1
Monte San Giovanni*	6.9	24.1	58.6	10.3
Siniscola E*		16.7	66.7	16.7
Bonaria*		47.4	39.5	13.1
XI "dic. 2001"		12.8	46.2	41.0
VI banco6	3.6	25.0	21.4	50.0
Castiglione 3CG°		2.7	56.2	41.1

Table 11. Tentative relative sequence of Corsican and Sardinian *Microtus (Tyrrhenicola)* faunas; * data from: Mezzabotta *et al* (1995); ° data from: Pereira *et al.* (2001).

Taula 11. Seqüència relativa tentativa de les faunes de Microtus (Tyrrhenicola) *corses i sardes; * dades de: Mezzabotta* et al *(1995); ° dades de: Pereira* et al. *(2001).*

fauna – is quite impossible, which is the reason why PCAs have been performed. When we determined all the measurements, especially those taken on the anteroconid, and we performed the PCAs we were hoping to obtain a good resolution in the differentiation of the morphological fields of the species *T. henseli*. What happened instead is that we were able to glimpse a small differentiation only excluding the measurements of the anteroconid features and used only the main tooth variables. This is certainly due to the mosaic evolutionary pattern of which *Tyrrhenicola* is a perfect example. Such a small differentiation, given mainly by V3 and V4, perfectly fits the pattern obtained with the morphotype analysis, with the two main groups composed by quarries VI banco6/XI "dic. 2001" and quarries XI "canide"/XI g3. It is also in good agreement with the patterns summarized by Mezzabotta *et al.* (1995) of an increase in the complexity of the AC and an elongation of the ACC even if we were not able to distinguish a consequent statistically significant increase in the size of the tooth.

Following the Scheffè's test results and its proposed subsets it is possible to hypothesize a more detailed evolutionary sequence of the populations. It starts with quarry XI g3 followed by XI "canide" and XI "dic. 2001" and ending with VI banco6. Within this sequence, size in itself does not vary significantly, as suggested by the PCA and confirmed by the ANOVA, still the complexity and the size of the anteroconid – even if following a mosaic pattern – increase, determining a significant variation in the AL index and a reduction of V3 (Fig. 7). The reduction of V4 attests to the trend toward a backward vergence of triangles T4 and T5 as exemplified in morphotype 4 of Mezzabotta *et al.* (1995, fig. 8).

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18

PLEISTOCENE HIPPOPOTAMUSES OF MEDITERRANEAN ISLANDS: LOOKING FOR ANCESTORS

Antonella Cinzia MARRA

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Resum

Al registre fossilífer del Pleistocè de les illes mediterrànies es coneixen hipopòtams que presenten adaptacions als ambients insulars: *Hippopotamus pentlandi* a Sicília i Malta, *Hippopotamus melitensis* a Malta, *Hippopotamus creutzburgi* a Creta, *Phanourios minutus* a Xipre. Hi ha incerteses en la recerca dels ancestres dels hipopòtams insulars, les quals es deuen al desenvolupament de caràcters endèmics i a la confusió existent a la sistemàtica de les espècies continentals europees. A aquest treball es compara la morfologia craniana i la biometria dels hipopòtams insulars del Pleistocè amb la de les espècies continentals, i s'introdueix una discussió sobre la seva sistemàtica. *Hippopotamus amphibius* podria ser l'ancestre d'*Hippopotamus pentlandi*, el qual a la seva volta podria ser l'ancestre d'*Hippopotamus melitensis*. *Hippopotamus antiquus* sembla ser l'ancestre d'*Hippopotamus creutzburgi*. Les característiques de *Phanourios minutus* similars a *amphibius* podrien estar relacionades amb una relació filogenètica amb aquesta espècie.
Keywords: Hippopòtams, Pleistocè, illes mediterrànies.

Summary

Hippopotamuses, having endemic adaptations related to insular environment, are known in the Pleistocene fossil record of Mediterranean islands: *Hippopotamus pentlandi* in Sicily and Malta, *Hippopotamus melitensis* in Malta, *Hippopotamus creutzburgi* in Crete, *Phanourios minutus* in Cyprus. The uncertainties in searching for ancestors of the insular hippopotamuses are caused by the development of endemic characters and by the confusion in the systematics of European mainland species. In this paper, skull morphology and biometry of Pleistocene insular hippopotamuses are compared with those of mainland species, introducing a discussion on their systematic. *Hippopotamus amphibius* could be the ancestor of *Hippopotamus pentlandi*, which in its turn could be the ancestor of *Hippopotamus melitensis*. *Hippopotamus antiquus* seems to be the ancestor of *Hippopotamus creutzburgi*. The *amphibius*-like characters of *Phanourios minutus* could be related to a relationship with this species.
Keywords: Hippopotamuses, Pleistocene, Mediterranean islands.

INTRODUCTION

The Pleistocene record of Mediterranean Islands often released hippopotamus remains: *Hippopotamus pentlandi* in Sicily and Malta, *Hippopotamus melitensis* in Malta, *Hippopotamus creutzburgi* in Crete, *Phanourios minutus* in Cyprus (Fig. 1). The real problem in studying hippopotamuses of the islands is in distinguishing the endemic features from the phylogenetic ones. Furthermore, uncertainty in systematics of the mainland species causes confusion in naming possible ancestors.

In this paper, morphology and biometry of the insular species skull are compared with those of the mainland species. Considerations on the possible ancestors are done. The possible ancestors spread in Europe during Pleistocene are: *Hippopotamus antiquus* (= *H. major*, Faure, 1983), *Hippopotamus amphibius* (*H. incognitus*, Faure 1983, 1984; Guérin, 1996) and *Hippopotamus tiberinus* (Mazza, 1991, 1995).

ANCESTORS

The search for ancestors of Pleistocene hippopotamuses starts from mainland forms. Two species of hippopotamus are commonly thought to be present in the Pleistocene of Europe: *Hippopotamus antiquus* and *Hippopotamus amphibius*.

Hippopotamus antiquus was present in Europe from the beginning of the Lower Pleistocene to the early Middle Pleistocene (Mazza, 1991, 1995; Guérin, 1996; Gliozzi *et al.*, 1997). Certain authors consider it as a subspecies of *H. amphibius*: *Hippopotamus amphibius antiquus* (e.g., Kahlke, 1987). It was a large-sized hippopotamus. Its cranium has an elongated face and elevated orbits. The neurocranium is short if compared to the face; the sagittal crest is steep. A rather developed diastema is present between P^2 and P^3. The mandible typically has an elongated and low horizontal branch.

Fig. 1. Mediterranean Islands mentioned in the text.

Fig. 1. *Illes mediterrànies esmentades al text.*

Hippopotamus amphibius, still living in Africa, is recorded in Europe from the Middle Pleistocene to the Late Pleistocene (Mazza, 1995; Guérin, 1996). Its cranium is shorter than that of *Hippopotamus antiquus*, it has a longer cranium and less elevated orbits. It has a long face, with a marked constriction of the muzzle at first molar-fourth premolar level. The mandible has a short and high horizontal branch.

Mazza (1991, 1995) recognized a new species of hippopotamus in Europe, *Hippopotamus tiberinus*, showing differences from the skulls of both *H. antiquus* and *H. amphibius*: more protruding occipital condyles, very short postorbital region and sagittal crest, and very elevated and forward directed orbits. *H. tiberinus* could be derived from the European *H. antiquus* stock (Mazza, 1991, 1995). Mazza (1991, 1995) observed that the morphology of *Hippopotamus antiquus* is similar to the most primitive representatives of the *Hippopotamus gorgops* lineage of East Africa (Olduvai Bed I and II, Coryndon, 1970), while *H. tiberinus* shows similarities to the most derived forms. According to Coryndon (1970, 1977a and b) and Mazza (1991), *H. gorgops* has a clear trend from the specimens found in Bed I, which show primitive *amphibius*-like characters (short and depressed skull, fairly long postorbital region, rather low orbits, very reduced P^2-P^3 diastema), to the specimens from more recent levels, which show an increasing specialization (elongation of the face, shortening of the postorbital region, uplifting of the nuchal crest, steepening of the parietal profile, elevation of the orbits, elongation of the diastema between second and third premolar). Although showing affinities with *H. gorgops* from Bed IV, *H. tiberinus* seems an autochthonous offspring from the European *H. antiquus*, on the basis of morphological characters. The two species could have formed a line somewhat parallel to that of *H. gorgops* in Africa (Mazza, 1991).

H. antiquus, present in Europe before the beginning of Elsterian, seems to evolve to *H. tiberinus*, that appears in the Villafranchian-Galerian transition. In the course of the Middle Pleistocene *H. tiberinus* dispersed in Central Europe, apparently disappearing at the beginning of the Saalian, withdrawing to more southern areas (e.g., Italy). In the transition to the Late Pleistocene, *H. tiberinus* returned to Central Europe, from which definitively disappeared before the fist glacial. *H. amphibius* spread in Europe from Africa in the course of Eemian and moved away during the first part of the first Pleniglacial.

Cranium	
LPN	prosthion - nuchal crest lenght
LPOc	prosthion – occipital condyle lenght
LCN	canine alveolus – nuchal crest length
LnnOr	nasal notch – orbital cavity lenght
LCOr	canine alveolus – orbital cavity lenght
HZOr	zygomatic arch – orbital height
HOpA	opisthion – akrocranion height
HBA	basion – akrocranion height
HFm	height of the foramen magnum
BFm	breadth of the foramen magnum
BN	breadth of the nuchal crest
Botot	otion – otion breadth
BOc	breadth across the occypital condyles
BTl	breadth between the temporal lines
Bee	euryon – euryon breadth
BF	frontal breadth
BZ	zygomatic breadth
BOrOr	breadth between the orbital cavities
BiOr	infraorbital breadth
BC	breadth across the canine alveoli
BCa	breadth between the canine alveoli
BI1a	breadth between the first incisor alveoli
BI2	breadth across the second incisor alveoli
BI2a	breadth between the second incisor alveoli
BP2	breadth between the second premolar alveoli
BM1	breadth between the first molar alveoli
BM3	breadth between the third molar alveoli
Mandible	
LGcC	gonion caudalis – canine alveolus length
LcC	mandibular condyle – canine alveolus length
LGcM3	gonion caudalis – posterior border of the M/3 alveolus length
LM3I	posterior border of the M/3 alveolus – incisor alveolus length
LS	length of the mandibular symphysys
BC	breadth of the two halves across the condyles
BCo	breadth of the two halves across the coronoid processes
Ban	breadth of the two halves across the angular processes
BFo	outer breadth of the rostral fan
BFi	inner breadth of the rostral fan
HGvc	gonion ventralis – condyle height
HGvs	gonion ventralis – sygmoid incisure heigth
HGvco	gonion ventralis – coronoid process heigth
H3M	heigth of the horizontal ramus at level of M/3
H4P	heigth of the horizontal ramus at level of P/4
H2P	heigth of the horizontal ramus at level of P/2
Teeth	
P/2	second upper premolar
P/3	third upper premolar
P/4	fourth upper premolar
M/1	first upper molar
M/2	second upper molar
M/3	third upper molar
P2/	second lower premolar
P3/	third lower premolar
P4/	fourth lower premolar
M1/	first lower molar
M2/	second lower molar
M3/	third lower molar
OL	outer length
IL	inner length
AB	anterior breadth
PB	posterior breadth
Lpt	lenght of the posterior tubercle (M3)

Table 1. List of measurements of tables 2-5 (after Mazza, 1995).

Taula 1. *Llista de les mesures de les taules 2-5 (a partir de Mazza, 1995).*

Faure (1984) thought that the Pleistocene *H. amphibius* had to be identified as *Hippopotamus incognitus*, whose holotype was the specimen D3980 from Barrington (UK), previously described by Reynolds (1922). Compared with the living *H. amphibius*, *H. incognitus* is larger in size, the cheek teeth are more bulky and the proportions of the limb bones are different (Faure, 1984). Faure (1984) attributed the three species to three distinct phylogenetic lineages originating from the same Pleistocene African stock.

Mazza (1995) considered the hippopotamus from Barrigton an ancient form of *H. amphibius*, characterized by rather large-sized individuals. According to Petronio (1995), *H. incognitus* and *H. tiberinus* are not valid species, being the first referred to *H. amphibius* and the second to *H. antiquus*. Coryndon (1970, 1977a and b) dubitatively related *H. antiquus* with *H. amphibius* and/or *H. gorgops* stocks. In this scenario, the search for ancestors appears problematic.

HIPPOPOTAMUS PENTLANDI OF SICILY AND MALTA

In Sicily, *Hippopotamus pentlandi* is associated with a Late Middle Pleistocene - Late Pleistocene fauna (*Elephas mnaidriensis* Faunal Complex) and disappears in the following Late Pleistocene fauna (Bonfiglio *et al.*, 2002). The fauna is impoverished but balanced if compared to the mainland one and represents an almost complete turnover with respect to the Early Middle Pleistocene Sicilian fauna, which was strongly oligotypical and endemic (Bonfiglio *et al.*, 2002; Marra, 2005). In Malta, assemblages related to *E. mnaidriensis* Faunal Complex are impoverished if compared to Sicilian ones.

Cranium (Tables 1, 2 & 4; Plate 1)

Dorsal view

The sagittal crest may be narrow and prominent or broad and flattened. Although variable, it is short, intermediate between *H. antiquus*, where it is shorter, and *H. amphibius*, where it is longer. The frontal bone is widely concave, less than *H. antiquus* and more than *H. amphibius*. The postorbital length is proportionally longer than *H. antiquus* and shorter than *H. amphibius*. The zygomatic arches are little prominent and meet the muzzle forming a wide curve, as in *H. amphibius*. In *H. antiquus*

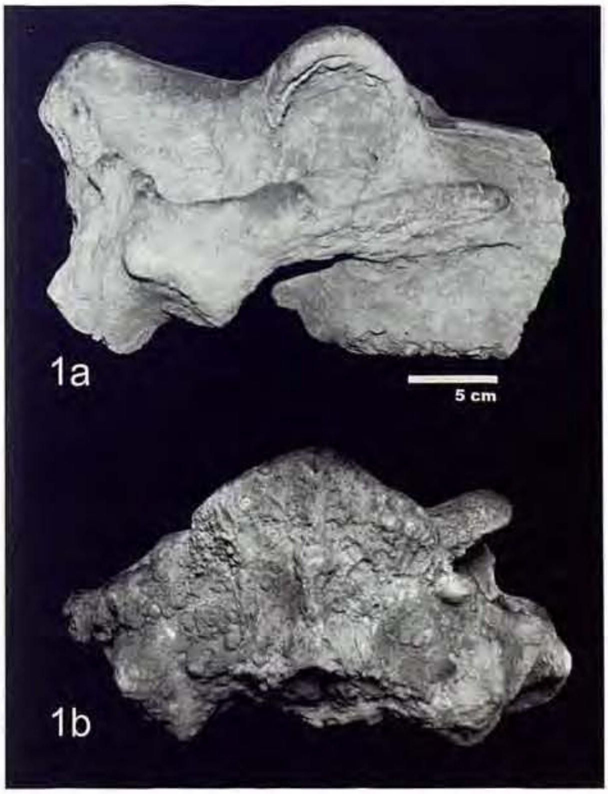


Plate 1. Cranium of *Hippopotamus pentlandi* from Sicily. **1a**: lateral view. **1b**: occipital view (specimen stored in the Museo di Paleontologia, University of Catania, Italy).

Làmina 1. *Crani d'*Hippopotamus pentlandi *de Sicília. **1a**: vista lateral. **1b**: vista occipital (espècimen conservat al Museu de Paleontologia, Universitat de Catània, Itàlia).*

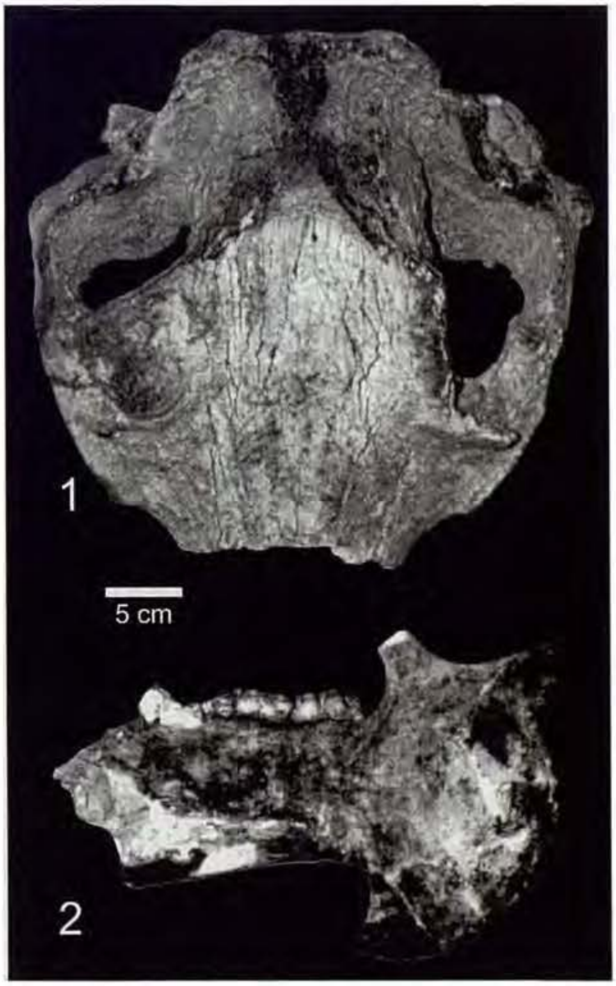


Plate 2. *Hippopotamus pentlandi* from Sicily. **1**: cranium in dorsal view (specimen stored in the Museo di Paleontologia, University of Catania, Italy). **2**: mandible in lateral view (specimen stored in the Museo Civico di Storia Naturale, Milan, Italy)

Làmina 2. Hippopotamus pentlandi *de Sicília. **1**: vista dorsal (espècimen conservat al Museu de Paleontologia, Universitat de Catània, Itàlia). **2**: mandíbula en vista lateral (espècimen conservat al Museo Civico di Storia Naturale, Milan, Itàlia).*

the zygomatic arch meets the muzzle with a prominent and accentuated angle. A little prominent crest is present on the side of the maxilla, anteriorly to the zygomatic process. This crest seems to divide the maxilla in a dorsal and an alveolar portion, as observed in *H. antiquus*. The facial part of the cranium is proportionally shorter than *H. antiquus* and more similar to *H. amphibius*. Anteriorly, the muzzle is narrow.

Lateral view

The sagittal crest is short and steep, proportionally less than *H. antiquus* and more than *H. amphibius*. Nasal bones have a peculiar curved profile: they describe a curve low in the posterior portion, high in the medial portion and again low anteriorly. This feature, observed in several specimens, is not attributable to plastic deformation and is similar to *H. antiquus*.

Occipital view

In subadult specimens, the occipital has a sub-triangular outline, similar to *H. antiquus*, while in the adult ones it is trapezoidal, as *H. amphibius*. The massive occipital condyles have a conic shape with the longer axis horizontally oriented, more than *H. antiquus* and considerably more than *H. amphibius*, where it is oblique. The foramen magnum has a quadrangular shape, as *H. antiquus*.

Ventral view

The basioccipital is sturdy. The nasal conchae open behind the third molar, as in *H. antiquus*. The glenoid fossae have a peculiar form, being wide in lateral and anteposterior directions. The palate is proportionally shorter than *H. antiquus* and comparable to *H. amphibius*. The tooth rows present a weak convergence at the first molar – fourth premolar. This convergence is marked in *H. amphibius* and almost absent in *H. antiquus*. The diastema between second and third molar, long in *H. antiquus* and short in *H. amphibius*, is absent in *H. pentlandi*. The molars (Plate 3, Figs. 1-3) are smaller than *H. antiquus* (about -20%) and *H. amphibius* (-10%), with some more differences in proportions. Upper molars are proportionally shorter on lateral side with respect to both mainland species. In the anterior side, they are narrower than *H.*

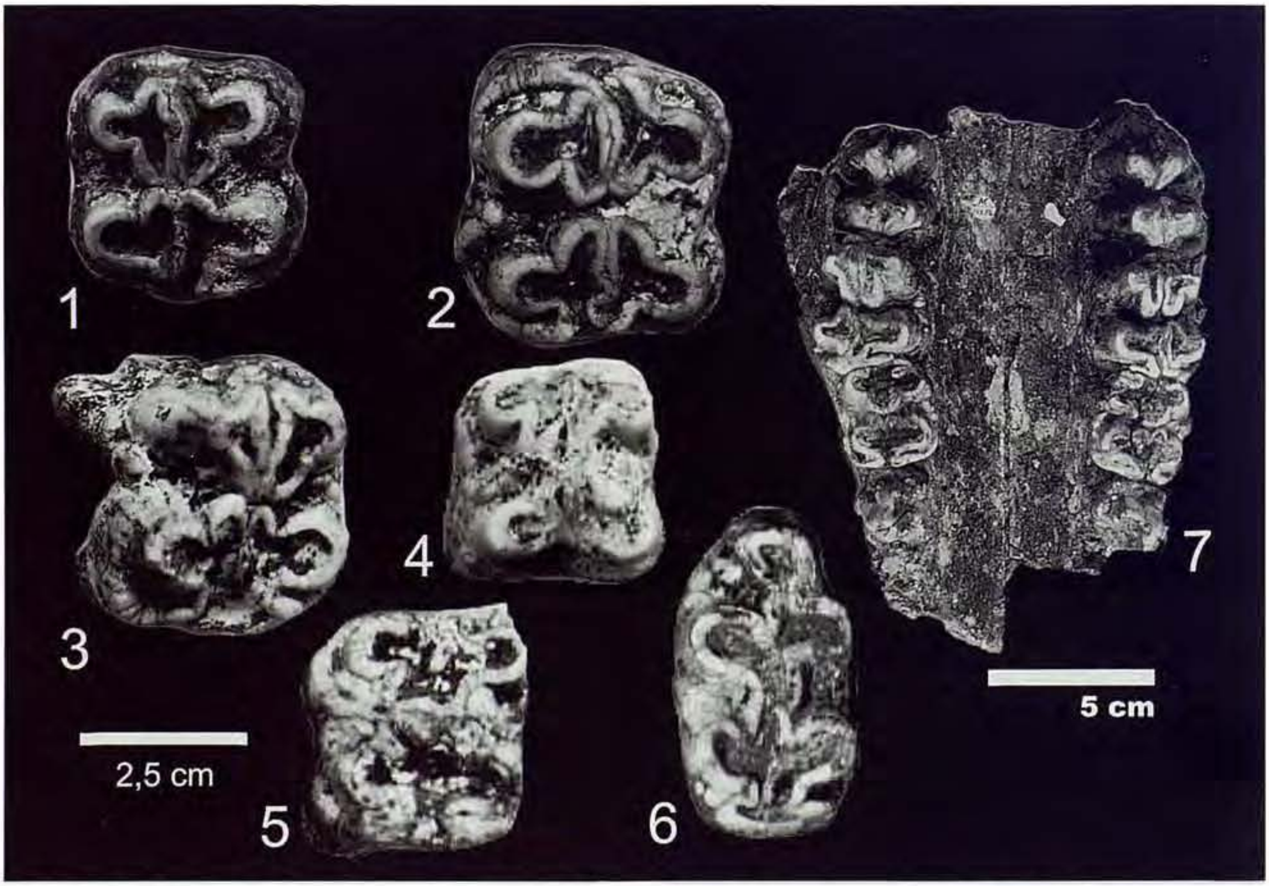


Plate 3. Teeth of *Hippopotamus pentlandi* from Malta. **1**, first upper molar. **2**, second upper molar. **3**, third upper molar (specimens stored in the Natural History Museum, London, UK; scale bar: 5 cm). Teeth of *Hippopotamus melitensis* from Malta: **4**, first upper molar. **5**, second upper molar. **6**, third lower molar (specimens are stored in the Natural History Museum, London, UK; scale bar: 5 cm). *Hippopotamus creutzburgi*: **7**, maxilla fragment (specimen stored in Natural History Museum, London, UK; scale bar: 2.5 cm).

Làmina 3. *Dents d'*Hippopotamus pentlandi *de Malta.* ***1****, primer molar superior.* ***2****, segon molar superior.* ***3****, tercer molar superior (espècimens conservats al Natural History Museum, London, UK; escala: 5 cm). Dents d'*Hippopotamus melitensis *de Malta.* ***4****, primer molar superior.* ***5****, segon molar superior.* ***6****, tercer molar superior (espècimens conservats al Natural History Museum, London, UK; escala: 5 cm).* Hippopotamus creutzburgi. ***7****, fragment de maxil·lar (espècimen conservat al Natural History Museum, London, UK; escala: 2,5 cm).*

antiquus. M^1 is wider and shorter than in *H. antiquus* and *H. amphibius*; M^2 is similar to *H. amphibius*, while it is internally shorter and posteriorly wider than *H. antiquus*; M^3 is internally shorter and anteriorly narrower than both *H. antiquus* and *H. amphibius*.

Mandible (Tables 1, 3 & 5; Plate 2)

Dorsal view

The mandibular branches diverge more than in *H. antiquus* and less than in *H. amphibius*. The tooth rows are almost straight, slightly convergent at the first molar – fourth premolar level. This convergence is marked in *H. antiquus* and almost absent in *H. amphibius*. The molars are smaller than *H. antiquus* (about -20%) and *H. amphibius* (about -10%) with some differences in proportions. M_2 is shorter than *H. amphibius* and is shorter and larger than *H. antiquus*. M_3 has similar proportions to *H. amphibius*, while is wider than *H. antiquus* and with a shorter posterior tubercle. M_2 and M_3 often present a "comma shaped" entoconide. The "comma shaped" wear pattern (*sensu* Mazza, 1995, 1999) derives from a reduced development or from a complete absence of the posterior style of the cusp. Columnar entoconides, without styles, are observed in M_3 of some individuals of *H. pentlandi*. The M_2 comma shaped entoconids are quite common in *H. antiquus* and rather frequent in fossil *H. amphibius*, while are occasional in living hippopotamuses (Mazza, 1991, 1995).

Lateral view

The mandible is slender, as in *H. antiquus*, but shorter. The lower outline of the horizontal branch is concave and the margin is sturdy. The height of the ascending branch is proportionally intermediate between *H. antiquus*, where is lower, and *H. amphibius*, where is higher. The coronoid process is thin, proportionally more than the mainland species. The sigmoid notch is wide rounded. The masseterine fossa is wide and deep as in *H. amphibius*. The posterior outline is straight, as in *H. antiquus*, not curved as in *H. amphibius*.

HIPPOPOTAMUS MELITENSIS OF MALTA

In Malta a hippopotamus smaller than *H. pentlandi*, *Hippopotamus melitensis*, was recorded, but its stratigraphical position and the possible associated fauna are unknown. The presence itself of *H. melitensis* in Malta was debated among authors, who alternatively doubted (Reese, 1975) or confirmed (Bate, 1923, 1925; Caloi & Palombo, 1983; Capasso Barbato & Petronio, 1983; Faure, 1983) the existence of a species smaller than *H. pentlandi*. The reason of these discordant opinions is the shortage of materials available for study.

The studied molars (tabs. 1, 4, 5; Plate 3, Figs. 4-6) have morphology similar to *H. pentlandi* and are consi-

CRANIUM													
H. pentlandi	LPN	LPOc	LCN	LnnOr	LCOr	HZOr	HOpA	HBA	HFm	BFm	BN	Botot	BOc
specimens	2	1	1	2	1	1	3	2	5	7	6	7	8
minimum	555	580	506	310	275	93	128	162	30	50	127	232	114
maximum	565	580	506	360	275	93	140	173	48	62	186	288,4	174
average	560	580	506	335	275	93	133	167,5	39,6	55,2	156	257,7	144,8
H. pentlandi	BTI	Bee	BZ	BorOr	BiOr	BC	BI2	BP2	BM1	BM3			
specimens	3	5	5	3	2	1	1	2	4	5			
minimum	5,1	113	312	232	90	303	182	67,7	58	60			
maximum	15	146	384	260	112	303	182	85	69	80			
average	10,7	129	350	244	101	303	182	76,35	64,3	71,6			
P. minutus	LCOr	HZOr	HOpA	HBA	HFm	BFm	BN	Botot	BOc	Bee	BZ	BorOr	BiOr
specimens	2	1	2	2	2	2	2	2	1	1	1	2	2
minimum	110	33	67	90	25,3	27,8	94	126	67	84	204	103	56
maximum	121	33	73	99	27,5	34,8	95	157	67	84	204	109	57
average	116	33	70	94,5	26,4	31,3	94	141,5	67	84	204	106	56,5
P. minutus	BC	BCa	BI1a	BI2	BI2a	BP2	BM1	BM3					
specimens	2	2	1	1	1	2	2	1					
minimum	104	73	29,1	73	47,7	43	27	37					
maximum	118	73	29,1	73	47,7	46	29	37					
average	111	73	29,1	73	47,7	44,5	28	37					

Table 2. Measurements of crania.

Taula 2. *Mesures dels cranis.*

derably smaller. They are proportionally shorter and larger than mainland species, while in the lingual side they are shorter than in *H. pentlandi*. The molars show a peculiar strong wear on the anterior and posterior talons. The hypocone of M^3 has a short posterior style, while the hypoconulid of M3 is clearly comma shaped.

HIPPOPOTAMUS CREUTZBURGI OF CRETE

Hippopotamus creutzburgi was recorded in Early Pleistocene – Middle Pleistocene assemblages (*Kritimys* biozone, in De Vos, 1996; Mayhew, 1996). The associated fauna (*Elephas creticus* and *Kritimys kiridus* in the Early Pleistocene; *Kritimys catreus* in the Early Middle Pleistocene) is endemic and strongly unbalanced, with an extremely low biodiversity (De Vos , 1996; Mayhew, 1996; Marra, 2005).

Cranium (Tables 1 &4; Plate 3)

The few cranial remains, mostly maxillae, are similar to *H. antiquus*: the palate is a little narrow, the tooth rows are quite straight and convergent at first molar – fourth premolar, the teeth are hypsodont. The premolars are peculiarly larger than molars and forward directed. The molars are considerably reduced in size with respect to *H. antiquus* (about -45%) and *H. amphibius* (about -35%) and their proportions are similar to *H. antiquus*. M^2 and M3 have comma shaped hypocone.

Mandible (Tables 1, 2 & 5; Plate 3)

The horizontal branches are straight, with sturdy inferior margin. The tooth rows are straight and close together. These features fit well with *H. antiquus*. In lateral view, the horizontal branch is lower than in *H. antiquus*. The anterior margin of the mandible apophysis is straight, backward directed. The premolars are larger than molars and forward directed. A diastema between P^2 and P^3 is present, as in *H. antiquus*. The teeth are hypsodont, like *H. antiquus*. The molars are reduced in size of about 45% with respect to *H. antiquus* and about 35% with respect to *H. amphibius*. M2 is wider than *H. antiquus* and M3 has a very short posterior tubercle. M^2 and M_3 have a comma shaped endoconid.

PHANOURIOS MINUTUS OF CYPRUS

During the Pleistocene only one faunal complex was present in Cyprus (Reese, 1995). The fauna was strongly endemic, impoverished, unbalanced and with an extremely low biodiversity.

Plate 4. Mandible of *Hippopotamus creutzburgi*. **1a,** dorsal view. **2a,** lateral view (specimen stored in the Museo di Paleontologia, University of Rome "La Sapienza").

*Làmina 4. Mandíbula d'*Hippopotamus creutzburgi. *1a, vista dorsal. 2a, vista lateral (espècimen conservat al Museu de Paleontologia, Universitat de Roma "La Sapienza").*

When found in datable terrace deposits, hippo and elephant remains from Cyprus have an age coeval or posterior to Middle Pleistocene, while the only available dating on collagen bone of *Phanourios* offered the result TX -5976B: 9420±550 BP (10700 – 7300 cal BC; Wigand & Simmons, 1999).

The supposed hippo hunting by humans (Simmons, 1988; Simmons & Reese, 1993) was discussed and rejected (Olsen, 2000). In absence of clear evidences for co-existence of man and the endemic fauna, it is reasonable to think that the fauna became extinct before the human arrival or rapidly after it (Vigne *et al.*, 2000; Davis, 2003).

Cranium (Tables 1, 2 & 4; Plate 5)

The cranium is strongly modified with respect to the mainland species.

Dorsal view

The cranium is much more slender than in *H. amphibius* and *H. antiquus.* The sagittal crest is present only in young specimens and is absent in adult ones. The cerebral part of the cranium is longer than in *H. amphibius.* The frontal bone is flat, as in *H. amphibius.* The morphology of zygomatic arch can be deduced by some fragments. It seems very little expanded.

Lateral view

The parietal bones are convex, more than in *H. amphibius.* The nasal bones have a convex outline, similar to *H. amphibius.* The orbits are lower than in *H. amphibius* and *H. antiquus.*

Occipital view

The occipital is very different with respect to mainland species. It is proportionally very narrow and high. The occipital condyles are developed in vertical sense, having a long oval and vertical surface.

Ventral view

The glenoid fossa of the temporal zygomatic process is longer than in mainland species. The fourth premolar lacks in this species. The molars have a peculiar wear pattern, which produces pointed cusps and transversal grooves between anterior and posterior cones. The molars are reduced in size if compared with *H. antiquus* (about -55%) and *H. amphibius* (- 45%). The proportions of the molars are similar to *H. amphibius,* which has shorter molars than *H. antiquus.* The third upper molar present a comma shaped hypocone.

Mandible (Tables 1, 3 & 5; Plate 6)

Dorsal view

The mandibular branch are posteriorly closer each other than *H. amphibius* and *H. antiquus.* The lower molars are proportionally wider than mainland species. M_3 presents a comma shaped hypoconide.

Lateral view

As in *H. amphibius,* the horizontal branch is high, the sygmoid notch is shallow, the coronoid process is high and the posterior margin is curved and prominent over the condyle. The mandible apophysis is backward directed, unlike *H. amphibius* and *H. antiquus.*

MANDIBLE													
H. pentlandi	LGcC	LcC	LGcM3	LM3I	LS	Bc	Bco	Ban	BFo	BFi	HGvc	HGvs	H3M
specimens	2	2	5	6	6	2	1	2	3	4	2	2	7
minimum	410	472	115	290	107	315	176,5	400	300	220	229	201	100
maximum	435	532	165	345	178	326	176,5	450	385	330	260	222	127
average	422,5	502	138,2	326,67	144	320,5	176,5	425	345	260,5	244,5	211,5	113,4
H. pentlandi	H4P	H2P	*H. creutzburgi*		LM3I	LS	BFo	BFi	H3M	H4P	H2P		
specimens	4	3	specimens		2	3	1	3	2	2	2		
minimum	99	86	minimum		237	79	166	124	65	62	64		
maximum	123	124	maximum		312,3	130	166	198	100	98	105		
average	111,25	99,667	average		274,65	110,33	166	160,67	82,5	80	84,5		
P. minutus	LGcM3	LS	BFo	BFi	HGvc	HGvs	HGvco	H3M	H2P				
specimens	1	2	1	1	1	1	1	2	1				
minimum	80	67	112	75	116	98	127	47,5	57				
maximum	80	72,6	112	75	116	98	127	58	57				
average	80	69,8	112	75	116	98	127	52,75	57				

Table 3. Measurements of mandibles.

Taula 3. Mesures de les mandíbules.

DISCUSSION AND CONCLUSION

The phylogeny of *Hippopotamus pentlandi* was discussed by several authors, with discordant opinions. Accordi (1955), who gave the most complete morphological study, thought the Sicilian-Maltese species derived from *H. amphibius*. According to Capasso Barbato & Petronio (1983) and Petronio (1995), the morphological differences between *H. pentlandi* and *H. amphibius* enable only a sub-specific separation of the insular form, named *H. amphibius pentlandi*. The same authors supposed the possibility of several migrations from mainland, which biased the dwarfing processes of the species. Caloi & Palombo (1983) considered *H. pentlandi* derived from *H. amphibius*, attributing the similarities with *H. antiquus* to the dwarfing processes. Faure & Guérin (1991), Faure (1983, 1984, 1985) and Guérin (1996) attributed the derivation of *H. pentlandi* from *H. antiquus*. The derivation from *H. antiquus* was supposed also by me in my PhD thesis (Marra, 1998) and in a paper in collaboration (Marra & Bonfiglio, 1998).

The most impressive feature in *H. pentlandi* morphology is to having a mix of character intermediate between *H. amphibius* and *H. antiquus*. The strong similarities between the Pleistocene and the living *H. amphibius* specimens seems to exclude the derivation of the European *H. amphibius* from *H. antiquus*. A new spread of African *H. amphibius* in the Middle Pleistocene is more realistic. However, *H. antiquus* could be related to a wide *H. amphibius* group, probably spread from an archaic *H. amphibius*, as *H. gorgops* of the Olduvai Bed I, East Africa (Coryndon, 1970; Mazza, 1991, 1995). In this case, the "mixed" characters may be related with the common lineage of both *H. antiquus* and *H. amphibius*. *H. pentlandi* could come from the Pleistocene *H. amphibius* and the *antiquus*-like characters could be reminiscent of a common derivation from an ancestral *H. amphibius* stock. *H. pentlandi* is reduced in size of about 10-15% with respect to *H. amphibius* and about 20-25% with respect to *H. antiquus*.

In Sicily, *H. pentlandi* is present in a faunal complex characterized by a low degree of endemism, a relatively high biodiversity and a good ecological balance. In these conditions, the hippopotamus underwent a slight reduction in size, accompanied by interesting morphological modifications. In Malta, the Middle Pleistocene fauna seems to be impoverished with respect to Sicily. In Malta,

UPPER TEETH													
H. pentlandi	P2/OL	P2/IL	P2/AB	P2/PB	P3/OL	P3/IL	P3/AB	P3/PB	P4/OL	P4/IL	P4/AB	P4/PB	M1/OL
specimens	5	5	8	7	7	7	8	9	25	26	28	29	18
minimum	28,2	9,9	7	19,5	26,4	24,4	10,7	19,3	11	16,3	11,7	16,3	30,7
maximum	36,5	33,8	19	23	35,2	35,5	20	26,1	32	32,4	28	31,4	40,2
average	32,2	27,3	15,7	21,3	31,4	30,8	16,9	23,1	25,5	25,5	18,9	21,4	34,9
H. pentlandi	M1/IL	M1/AB	M1/PB	M2/OL	M2/IL	M2/AB	M2/PB	M3/OL	M3/IL	M3/AB	M3/PB		
specimens	19	17	17	27	27	28	28	22	22	21	22		
minimum	30,3	27,6	29	36,1	35	21,4	23	39,6	37,8	22,5	21,1		
maximum	39,2	39,7	42,2	47	44,2	46,3	50	55	45,4	47	49		
average	33,9	33,5	35,6	41,4	39,2	40,1	40,4	44,8	41,2	40,7	38,8		
H. melitensis	M1/OL	M1/IL	M1/AB	M1/PB	M2/OL	M2/IL	M2/AB	M2/PB	M3/OL	M3/IL	M3/AB	M3/PB	
specimens	2	2	2	2	3	28	28	27	5	5	5	5	
minimum	27,4	29,5	29,2	29	32	22,5	21,4	23	36	38	35,8	31	
maximum	29,7	30,2	31,4	30,1	37,6	44,2	46,3	50	38,4	42,5	40,2	35,9	
average	28,5	29,8	30,3	29,5	34,5	35,8	36,4	36,6	37,3	39,7	37,3	33,4	
H. creutzburgi	M1/OL	M1/IL	M1/AB	M1/PB	M2/OL	M2/IL	M2/AB	M2/PB	M3/OL	M3/IL	M3/AB	M3/PB	
specimens	7	7	7	7	9	9	9	9	7	7	7	7	
minimum	27,8	26	26,1	26,8	31,8	30,5	33,2	32	33,2	31,6	29,3	28	
maximum	31,6	32	31,7	32,4	38	35,5	38,8	37,6	41,8	37,8	39,6	36,2	
average	29,5	28,5	27,8	28,4	34,1	32,9	35,7	34,4	36,5	34,3	34,3	31,7	
P. minutus	M1/OL	M1/IL	M1/AB	M1/PB	M2/OL	M2/IL	M2/AB	M2/PB	M3/OL	M3/IL	M3/AB	M3/PB	
specimens	5	5	5	5	11	11	11	9	10	11	10	10	
minimum	19	17,6	18,5	18,9	21,9	21,1	23	21,2	24,2	24	23,6	18,2	
maximum	22	22	20	20,2	25,6	24,4	25,3	25	35,2	32	32,6	29	
average	19,9	19,3	19,2	19,6	23,9	22,7	23,7	23,2	26,9	25,9	25,9	22,8	

Table 4. Measurements of upper teeth.

Taula 4. *Mesures de les dents superiors.*

H. pentlandi faced a new environment with smaller island area and lower biodiversity. The few studied remains indicate that it stayed unchanged for an unknown time span, then gave probably rise to *H. melitensis*.

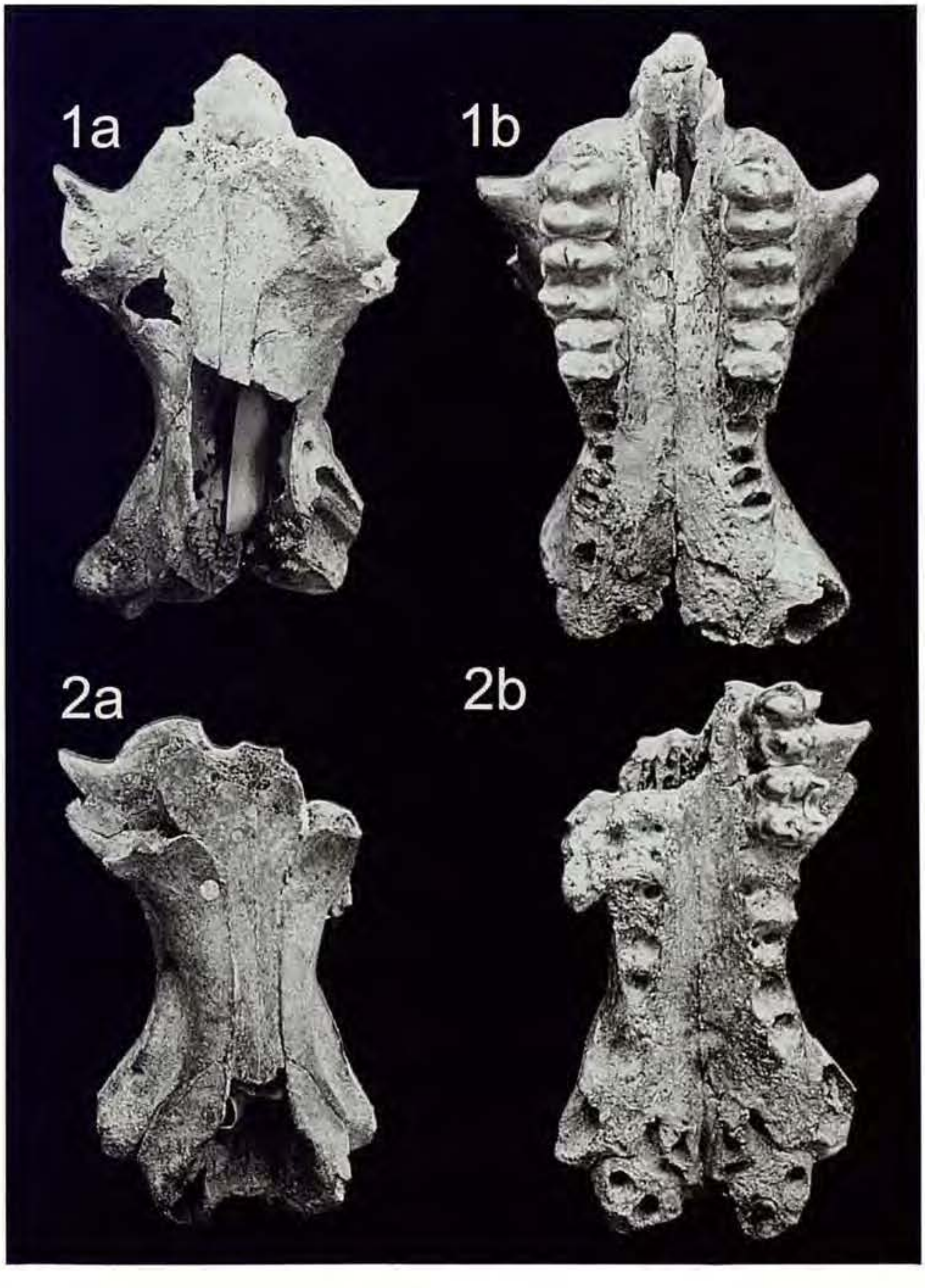
The derivation of *H. melitensis* from *H. pentlandi* was considered by Capasso Barbato & Petronio (1983) and Caloi & Palombo (1985). Data are too short to enable unquestionable phylogenetic considerations. The few molars studied in this paper shows a trend towards a reduction of the tooth row lenght. Derivation from *H. pentlandi* is probable, but a previous spread, although improbable, cannot be excluded.

The debate about the phylogeny of *H. creutzburgi* divided the authors, some of them being inclined to a derivation from *H. amphibius* (Boekschoten & Sondaar, 1966; Kuss, 1975), others being in favour of a relationship with *H. antiquus* (Sondaar, 1971; Coryndon, 1977; Dermitzakis & Sondaar, 1979; Capasso Barbato *et al.*, 1982; Caloi & Palombo, 1983; Faure, 1983). The presence of *H. creutzuburg parvus*, a smaller subspecies derived from *H. creuzburgi*, was proposed by Kuss (1975) on the basis of biometrical differences. Capasso Barbato *et al.* (1982) extended the number of specimens on new materials and rejected the hypothesis by Kuss (1975), considering the measurements within the normal variability of a species. Spaan (1996) and Caloi & Palombo (1996) discussed the current knowledge on *H. creutzburgi* and rejected the subspecies *parvus*.

The derivation of *H. creutzburgi* from *H. antiquus* seems supportable by morphological data. Moreover, the stratigraphical distribution of *H. creutzburgi* is consistent with the spread of *H. antiquus* on mainland (Lower Pleis-

Plate 5. Crania of *Phanourios minutus*: **1a**, **2a**, dorsal views. **1b**, **2b**, ventral views (specimens stored in the Natural History Museum, London, UK).

Làmina 5. *Cranis de* Phanourios minutus*: **1a**, **2a**, vistes dorsals. **1b**, **2b**, vistes ventrals (espècimens conservats al Natural History Museum, London, UK).*



tocene). The hippopotamus could have reached Crete following occasional ways thanks to its swimming capability. In conditions of strong isolation, small area of the island and low biodiversity, the hippopotamus underwent a considerable decrease in size (about -40% with respect to *H. antiquus*; about -30% with respect to *H. amphibius*), accompanied by a trend to slenderness. The persistence of the diastema between P^2 and P^3, characteristic of *H. antiquus*, is very interesting in presence of the general shortage of the tooth row, where the molars dcrease with respct to the premolars.

The phylogeny of *Phanourios minutus* of Cyprus was debated among authors. Coryndon (1977a) considered the species of Cyprus as *Hippopotamus minor*, derived from *Hippopotamus lemerlei* of Madagascar. Houtekamer & Sondaar (1979) attributed the small hippo to the genus *Phanourios* and the species *minor* in consideration of the strong modifications in size and morphology. The same authors considered *P. minutus* belonging to the "*H. amphibius* group", but derived from *H. antiquus*. Later, Sondaar (2000) used the more correct name *Phanourios minutus*.

The phylogeny of *Phanourios minutus* needs more investigations. At the state of the art, it presents a high endemism developed in strong insular conditions. The identification of morphological characters related to *H. amphibius* faces again the problem of relationships among the mainland hippopotamuses.

In conclusion, hippopotamuses from Mediterranean Islands show a common trend to slenderness and shortage of the face and of the tooth-row. In the molars, they preserve the comma shaped hypocone and hypoconulide, which are characteristic of the European Pleistocene hippopotamuses.

Hippopotamus antiquus may be considered the ancestor of *H. creutzburgi*, while *H. amphibius* may be the ancestor of *H. pentlandi*. The Sicilian-Maltese species could have inherited *antiquus*-like characters as a reminiscence of the derivation from an ancestral *H. amphibius* stock. In its turn, *H. pentlandi* may be the ancestor of *H. melitensis of Malta*. The ancestor of *Phanourios minutus* is still uncertain. Some *amphibius*-like characters could be inherited from the European *H. amphibius* as well as from the archaic *H. amphibius* stock, from which *H. antiquus* derived.

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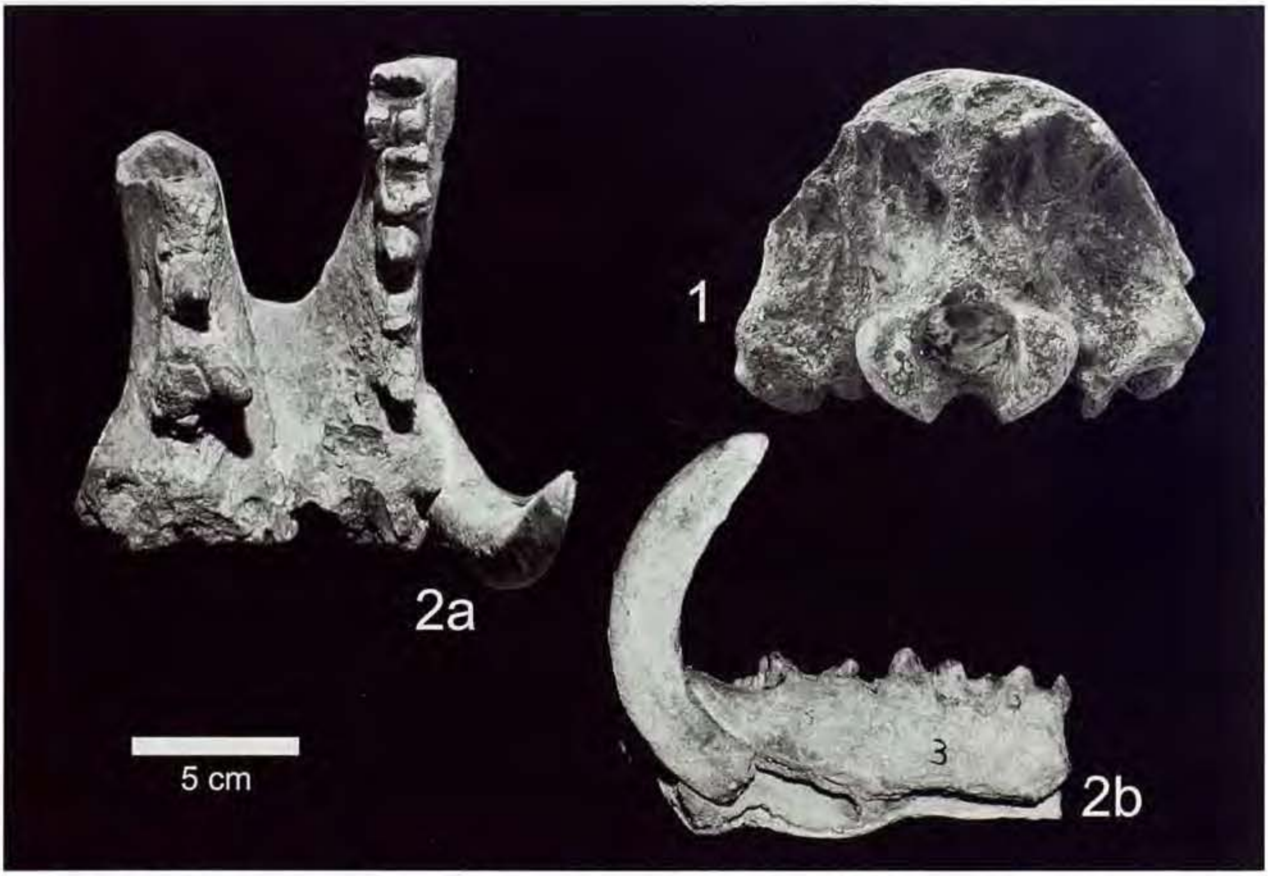

Plate 6. Cranium of *Phanourios minutus*: **1**, occipital view. Mandible of *Phanourios minutus* (specimen stored in the Natural History Museum, London, UK). Mandible of Phanourios minutus: **2a**, dorsal view. **2b**, lateral view (specimen stored in the Natural History Museum, London, UK).

Làmina 6. *Crani de* Phanourios minutus*: **1**, vista occipital. Mandíbula de* Phanourios minutus *(espècimen conservat al Natural History Museum, London, UK). Mandíbula de* Phanourios minutus*: **2a** vista dorsal. **2b**, vista lateral (espècimen conservat al Natural History Museum, London, UK).*

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LOWER TEETH													
H. pentlandi	P/2OL	P/2IL	P/2AB	P/2PB	P/3OL	P/3IL	P/3AB	P/3PB	P/4OL	P/4IL	P/4AB	P/4PB	M/1OL
specimens	11	11	13	13	11	14	12	15	15	17	16	18	11
minimum	25	26,9	12	15,6	28	24,8	13,2	18,6	16,5	17,6	14,2	20,2	32
maximum	33,3	32,4	17	19,4	34,5	32,3	23,6	323	35,8	34,4	23	29	43,5
average	29,6	29,6	14,6	17,9	31,1	30,5	16,8	42,3	27,8	28,3	18,4	23,8	36,5
H. pentlandi	M/1IL	M/1AB	M/1PB	M/2OL	M/2IL	M/2AB	M/2PB	M/3OL	M/3IL	M/3AB	M/3PB	M/3LPt	
specimens	10	10	12	16	15	15	16	23	23	24	25	23	
minimum	31,4	23,7	24,6	31,8	33,8	23	23,8	45	51,4	26,4	11,2	9,5	
maximum	42	32,6	38,6	45	46,5	35,3	38,3	69,5	70	40	43	27	
average	35,9	27,9	29,8	39,9	40,7	31,1	33,7	58,5	60,2	33,4	31,7	15,9	
H. melitensis	M/3OL	M/3IL	M/3AB	M/3PB	M/3LPt	*H. creutzburgi*		P/2OL	P/2IL	P/2AB	P/2PB	P/3OL	P/3IL
specimens	3	3	3	3	2	specimens		2	2	1	1	2	2
minimum	42,7	50,5	27,2	29,4	12	minimum		27	28	14,6	20,6	27	27,2
maximum	56,1	57	30,3	30,2	15,6	maximum		29,7	28,5	14,6	20,6	30,8	27,6
average	49,3	52,9	28,6	29,7	13,8	average		28,3	28,2	14,6	20,6	28,9	27,4
H. creutzburgi	P/3AB	P/3PB	P/4OL	P/4IL	P/4AB	P/4PB	M/2OL	M/2IL	M/2AB	M/2PB	M/3OL	M/3IL	M/3AB
specimens	2	2	2	2	2	2	4	4	4	4	9	9	8
minimum	15,3	21,6	22	26,2	21,8	23	19,4	22,4	17,2	17,3	44	45	25,4
maximum	20	22,4	25,7	30,3	22	27,8	40,7	42,4	29	30,7	64	63,5	31,8
average	17,65	22	23,85	28,25	21,9	25,4	31,575	32,95	24,4	25,2	48,5	49,5	27,3
H. creutzburgi	M/3PB	M/3LPt	*P. minutus*		M/2OL	M/2IL	M/2AB	M/2PB	M/3OL	M/3IL	M/3AB	M/3PB	M/3LPt
specimens	9	9	specimens		4	4	4	4	2	2	2	2	2
minimum	25,8	11	minimum		25	23,3	16,5	16,8	32,2	33	17,2	17,5	7,5
maximum	31,4	16,6	maximum		42,2	49	33,8	38	58	61,5	33,9	39,7	22,5
average	26,9	12,7	average		29,3	30,3	21,6	22,7	45,1	47,2	25,5	28,6	15

Table 5. Measurements of lower teeth.

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19

DESCRIPTION OF THE SKULL OF THE GENUS *SYLVIORNIS* POPLIN, 1980 (AVES, GALLIFORMES, SYLVIORNITHIDAE NEW FAMILY), A GIANT EXTINCT BIRD FROM THE HOLOCENE OF NEW CALEDONIA

Cécile MOURER-CHAUVIRÉ & Jean Christophe BALOUET

MOURER-CHAUVIRÉ, C. & BALOUET, J.C. 2005. Description of the skull of the genus *Sylviornis* Poplin, 1980 (Aves, Galliformes, Sylviornithidae new family), a giant extinct bird from the Holocene of New Caledonia. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears,* 12: 205-118.

Resum

El crani de *Sylviornis* mostra una articulació craniorostral completament mòbil, amb dos còndils articulars situats sobre el rostrum, el qual s'insereix al crani en dues superfícies articulars allargades. La presència de dos procesos rostropterigoideus sobre el basisfenoide del rostrum i la forma dels palatins permet confirmar que aquest gènere pertany als Galliformes, però les característiques altament derivades del crani justifiquen el seu emplaçament a una nova família, extingida, Sylviornithidae. El crani de *Sylviornis* està extremadament eixamplat i dorsoventralment aplanat, mentre que el rostrum és massís, lateralment comprimit, dorsoventralment aixecat i mostra unes cristae tomiales molt fondes. El rostrum exhibeix un ornament ossi gran. La mandíbula mostra una símfisi molt allargada, les branques laterals també presenten unes cristae tomiales fondes, i la part posterior de la mandíbula és molt gruixada. Es discuteix el possible origen i l'alimentació de *Sylviornis.*

Paraules clau: Aves, Galliformes, Extinció, Holocè, Nova Caledònia.

Abstract

The skull of *Sylviornis* shows a completely mobile craniorostral articulation, with two articular condyles situated on the rostrum, which insert into two elongated articular surfaces on the cranium. The presence of two rostropterygoid processes on the basisphenoid rostrum and the shape of the palatines make it possible to confirm that this genus belongs to the Galliformes, but the highly derived characteristics of the skull justify its placement in a new, extinct family Sylviornithidae. The cranium of *Sylviornis* is extremely widened and dorsoventrally flattened, while the rostrum is massive, laterally compressed, dorsoventrally raised and displays very sharp cristae tomiales. The rostrum bears a large bony ornament. The mandible shows a very elongated symphysis, the lateral branches also show sharp cristae tomiales, and the posterior part of the mandible is very thick. The possible diet of *Sylviornis* is discussed.

Key words: Aves, Galliformes, Extinction, Holocene, New Caledonia.

INTRODUCTION

The genus *Sylviornis* was described by F. Poplin (1980) from some very fragmentary postcranial remains, gathered by J. M. Dubois in a fossiliferous well situated at Ure, in the Kanumera bay, on Isle of Pines, to the south-east of the main island of New Caledonia. These remains were attributed to a ratite. More complete material was collected by F. Poplin and J. C. Balouet in 1980 and made it possible to show that this bird was in fact a galliform, which was attributed to the recent family Megapodiidae (Poplin *et al.*, 1983; Poplin & Mourer-Chauviré, 1985). Later, J. C. Balouet discovered several other fossiliferous localities on the main island and found very numerous remains of *Sylviornis* in one of the Pindai caves, in particular a cranium and a rostrum.

These elements of the skull of *Sylviornis* were described by Balouet in his doctoral dissertation, which has remained unpublished (Balouet, 1984), and were illustrated with a short description in two later papers (Balouet, 1986; 1991). We think that it is necessary to publish on this material in more details. Our paper will be limited to the description of the cranial material. The species *Sylviornis neocaledoniae* Poplin, 1980 was described from the material of Isle of Pines. The material from the main island differs from that of Isle of Pines by the absence of a pygostyle, whereas the pygostyle is present in the type-population. It is likely that the form from the main island represents a second species, but it will not be described here.

The Pindai caves are situated on the Nepoui peninsula, on the western coast of the main island. The *Sylviornis* remains described here come from the main Pindai cave, the description of which is given by Balouet and Olson (1989). Charcoal associated with *Sylviornis* or other extinct bird bones have given a radiocarbon age of 1750 ± 50 BP (Gif 6341). *Sylviornis* is the most abundant bird in this locality.

The 23 other bird species, studied by Balouet and Olson (1989) include 7 extinct species. The rest of the fauna includes very numerous Chiroptera (at least 4 species), a new family, genus and species of primitive crocodile, Mekosuchidae (Balouet & Buffetaut, 1987), the horned tortoise *Meiolania* (Gaffney *et al.*, 1984) and a monitor lizard, *Varanus* (Balouet, 1984; 1991).

SYSTEMATIC STUDY

Order Galliformes

Family **Sylviornithidae** nov. fam.

Type-genus: *Sylviornis* Poplin, 1980, the only included genus.

Remark: The genus *Sylviornis* was placed in the recent family Megapodiidae based mainly on characteristics of the postcranial skeleton. The study of the skull shows that this genus is highly derived. The characters that bring together *Sylviornis* and the Megapodiidae can be considered as plesiomorphic.

Family diagnosis: True mobile articulation between the cranium and the rostrum, with two articular condyles on the rostrum, formed by the anterior part of the embryonic nasal bones, which are inserted into two articular surfaces borne by the posterior parts of embryonic nasal bones, later fused to frontals. Lacrimals fused to frontals and forming a ventrally oriented lobe; this lobe bears a small articular surface which comes into contact with a tubercle situated on the rostrum. Cranium very flattened and widened posteriorly, with a very strong development of exoccipitals and squamosals. On the ventral surface, flexure of the posterior part of the cranium just posteriorly to the basipterygoid processes; the basitemporal plate makes an angle of ca. 135 ° relative to the plane of the basisphenoid rostrum. Occipital condyle situated almost in the center of the posterior surface of the cranium; its axis is parallel to the surface of the basisphenoid rostrum; occipital foramen situated just ventral to the dorsal surface. Rostrum very elevated and narrow and bearing a bony dorsal ornament; naris situated close to the posterior part in the adult; rostrum ending anteriorly in a pointed hook, with cutting tomial crests on the ventral surface. Quadratojugal with a sigmoid shape in the adult; its anterior part articulates with a surface situated at mid-length of the posterior border of the rostrum; posterior portion wide and paddle-shaped. Left and right palatines fused posteriorly in the adult. Vomer absent. Mandible with anterior part narrow and laterally compressed; mandibular symphysis very long and thick; posterior part very widened, with thick bone; long and thick retroarticular processes, not pointed posteriorly and dorsally but rather with a rounded profile. These characteristics are considered autapomorphic.

Distribution: Holocene of New Caledonia.

Genus *Sylviornis* Poplin, 1980

Sylviornis cf. *neocaledoniae* Poplin, 1980

Description of the cranial material from the main Pindai cave (the anatomical terminology generally follows Weber, 1996).

List of the material examined (this material is preserved in the collection of the Paris Muséum national d'Histoire naturelle):

Cranium, adult, NCP 241; Cranium, juv., NCP 260 + 262; Nasal, posterior part, juv., right, NCP 261; Frontals, juv., left, NCP 264-265; Squamosal, juv., left, NCP 262; Ethmoids, juv., NCP 316-319; Quadrates, left, NCP 41-45, 222-240; Quadrates, right, NCP 46-64, 244, 268-270; Quadrates, juv., NCP 272-276; Pterygoids, left, NCP 65-77, 245, 320-322, 325; Pterygoids, right, NCP 78-99; Pterygoids, juv., NCP 323-324; Palatines, right and left fused, NCP 121-136, 250, 277; Palatines, left, NCP 137-153; Palatines, right, NCP 154-168, 251, 278-279; Quadratojugals, left, complete, NCP 114-120; Quadratojugals, left, incomplete, NCP 169-177, 192-195, 281-283; Quadratojugals, right, complete, NCP 106-113, 246, 253-259; Quadratojugals, right, incomplete, NCP 178-191; Quadratojugals, left, juv., NCP 203-210, 284; Quadratojugals, right, juv., NCP 198-202, 247-249, 285-286; Jugals, juv., NCP 211, 287-289; Quadrate + pterygoid + quadratojugal, left, NCP 252, right, NCP 271; Rostrum, adult, NCP 242; Rostrum, juv., NCP 220, 263; Nasal, anterior part, juv., NCP 221, 290-293; Mandible, symphyses and fragments of symphyses, NCP 213, 215, 243, 294-295, 299, 310-312; Mandible, fragments of branches, NCP 216, 313;

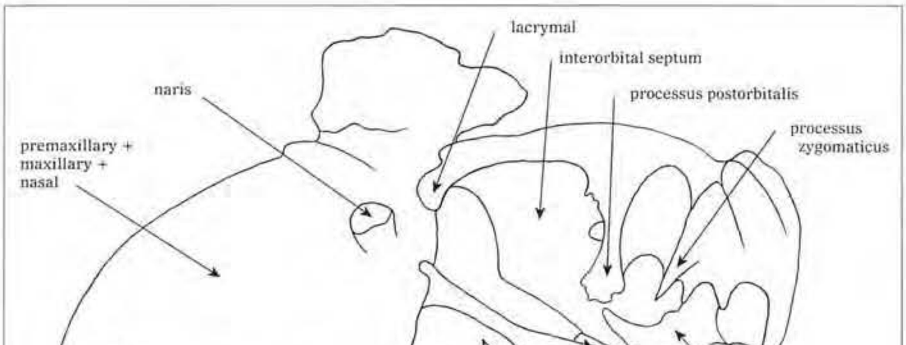

Fig. 1. *Sylviornis* cf. *neocaledoniae*. Reconstruction of the skull, showing the position of the different elements, left lateral view.

Fig. 1. Sylviornis *cf.* neocaledoniae. *Reconstrucció del crani, mostrant la posició dels diferents elements, norma lateral esquerra.*

Mandible, framents of articular parts, NCP 214, 217, 296-297; Articular, juv., NCP 219, 315; Angular, juv., NCP 212; Supraangular, juv., NCP 218, 314; Articular + supraangular + angular, right, juv., NCP 298.

In addition, several fragments of mandible collected in July 2003 by T. H. Worthy, A. Anderson, C. Sand, J. Jones, and F. Pechey in the same cave, have been examined on photographs. This material is at present deposited in the Museum of New Zealand Te Papa Tongarewa, Wellington, but has not been catalogued.

A restoration of the different cranial elements is given in figures 1 and 2.

Adult cranium (NCP 241, fig. 3)

The skull of *Sylviornis* is prokinetic and characterized by the presence of a true craniorostral hinge, with two parts completely separated. According to Bock (1964, p. 4): "the prokinetic skull is characterized by a hinge or region of bending at the junction of the nasal and frontal bones; hence the entire jaw moves as a unit". However Bock indicates that this articulation does not necessarily correspond to the suture between the embryonic nasal and frontal bones. The juvenile cranium (NCP 260 + 262) shows that the frontals are contiguous in the sagittal plane, but that their junction leaves a wide triangular space between them at their anterior end (fig. 4). This can also be seen on the juvenile cranium of other Galliformes, for example in the chicken (Jollie, 1957, fig. 2), or in a juvenile of the megapode *Alectura lathami* (Weber, 1996, fig. 3). The posterior part of the nasal (NCP 261) inserts in this triangular space. The juvenile material shows that the nasals consist of two different parts that articulated along a rectilinear hinge. The anterior part of the nasal is made up of two branches that later fuse with the premaxillary and the maxillary. The posterior part of the nasal later fuses with the frontal. In the juvenile the two parts of the nasal must have been held together by fibrous ligaments. From the juvenile elements it is possible to state that the hinge between the cranium and the rostrum was embryologically intranasal and not frontonasal. The features of the juvenile cranium also shows that a true craniorostral articulation was already present in the early stages of development of *Sylviornis*.

The adult cranium is extremely widened and flattened. This is largely due to the development of the exoccipitals in dorsal and lateral directions. The crista nuchalis transversa is rectilinear on the dorsal surface of the skull, then it continues laterally, forming two wide, projecting occipital crests at the level of the junction between the parietals and the squamosals with the supraoccipital and the exoccipitals, and then continues on ventrally along the paroccipital processes.

On the dorsal surface, the lacrimals are fused with the anterior part of the frontals. The fusion is still discernable by the presence of a large foramen on the left side. In some Galliformes, particularly in the Cracidae, the lacrimals are extended by a long process that penetrates inside the orbital cavity. In the Megapodiidae the lacrimals are very small, sometimes barely visible, and fused with the frontals and the nasals at the level of the craniofacial flexion zone. They do not have an orbital process. In *Sylviornis* the orbital process is also absent. The anterior part of the cranium, dorsal to the craniorostral hinge, is formed by the junction of the posterior part of the nasals with the ethmoid. This part shows, in the sagittal plane, a median tubercle flanked by two depressions, indicating the presence of a synovial joint. On the posterior part of the supraorbital ridge, there is a series of small foramina.

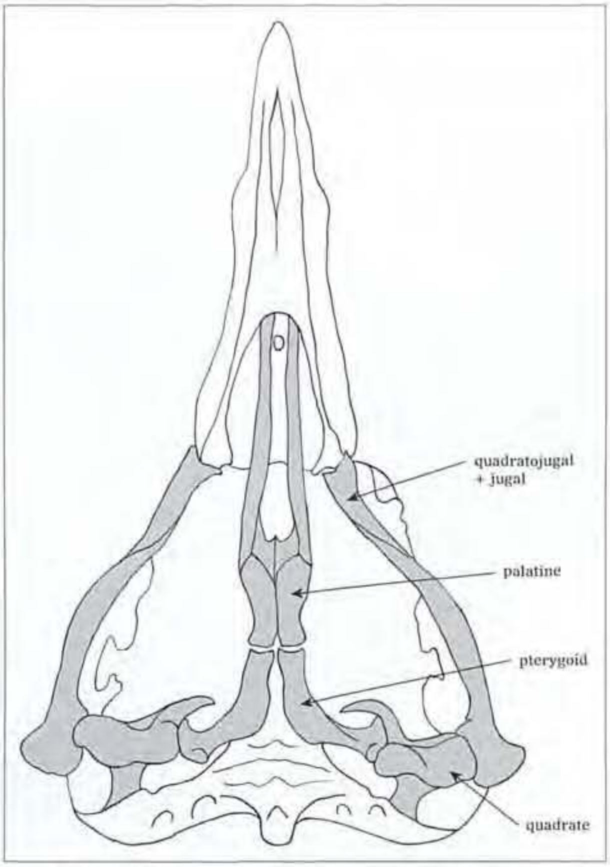

Fig. 2. *Sylviornis* cf. *neocaledoniae*. Reconstruction of the skull showing the position of the different elements, ventral view.

Fig. 2. Sylviornis *cf.* neocaledoniae. *Reconstrucció del crani, mostrant la posició dels diferents elements, norma ventral.*

The posterior surface is characterized by the very great enlargment of the exoccipitals, which is continued by the strongly ventrally projecting paroccipital processes. The supraoccipital bears a smooth median ridge. The occipital foramen is higher than wide and is situated just ventral to the dorsal surface. The occipital condyle is situated almost at the center of the posterior surface, its dorsal surface is slightly concave. On each side of the occipital condyle there are two well-marked depressions containing foramina for blood-vessels and nerves.

The ventral surface is characterized by the presence of two processus rostropterygoideus (Weber, 1996). They are oval in shape, slightly elevated relative to the surface of the basisphenoid rostrum, oriented in parallel in an anteroposterior direction, and separated by a wide space, ca. 140 % wider than the adjacent width of the rostropterygoid processes. These processes are situated at the base of the basisphenoid rostrum, which is triangular in shape, relatively short anteroposteriorly, and wide at its base. At the anterior end of the basisphenoid rostrum the interorbital septum widens and fuses with the ethmoid. Usually in birds the ventral part of the cranium is a relatively flat surface and the basitemporal plate (or basiparasphenoid plate in Ericson, 1996) is a horizontal plane in the prolongation of

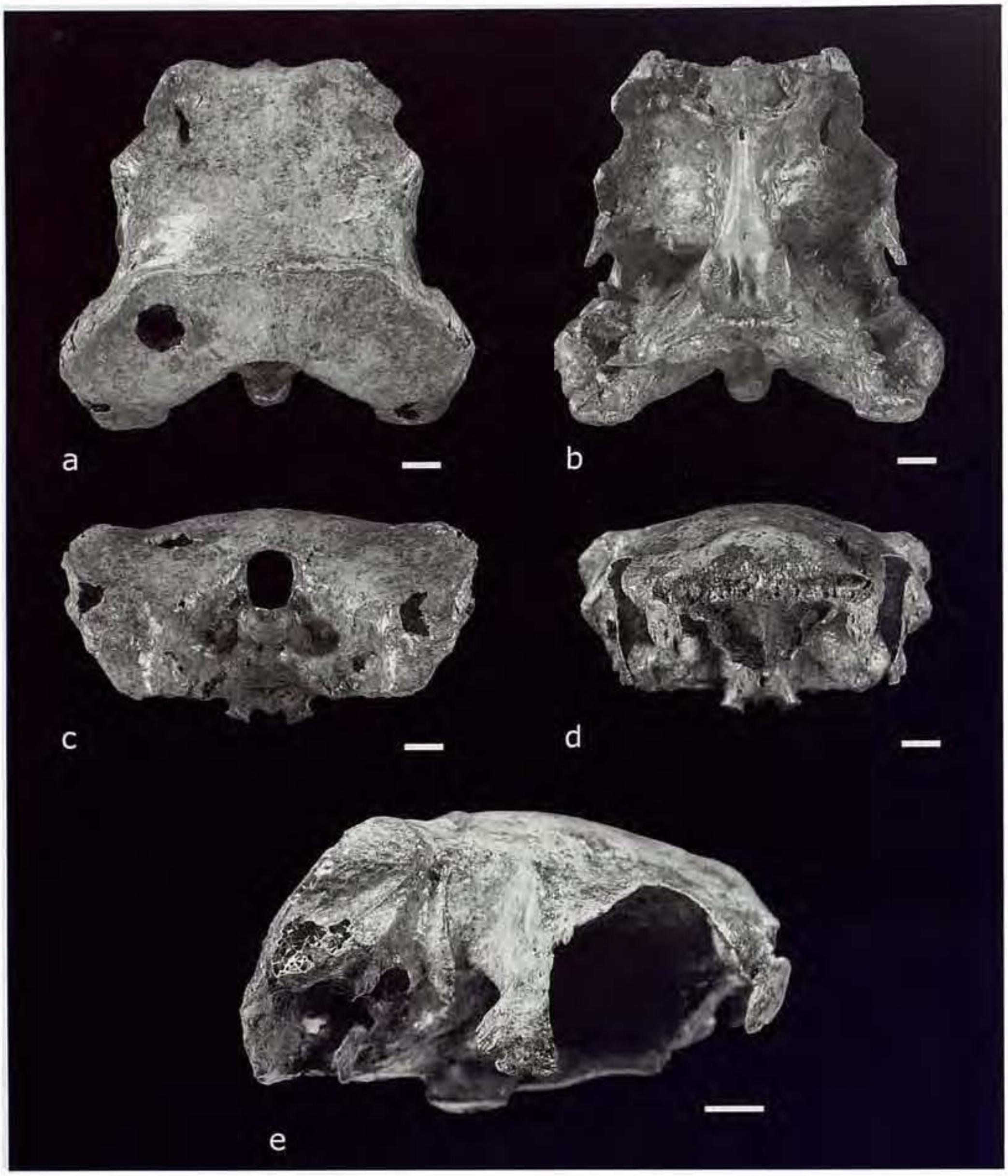

Fig. 3. *Sylviornis* cf. *neocaledoniae*. Adult cranium, NCP 241; a) dorsal view; b) ventral view; c) posterior view; d) anterior view; e) right lateral view. The scale bar represents 10 mm.

Fig. 3. Sylviornis *cf.* neocaledoniae. *Crani adult, NCP 241; a) norma dorsal; b) norma ventral; c) norma posterior; d) norma anterior; e) norma lateral dreta. L'escala representa 10 mm.*

the palate. In the posterior part of the cranium, there is a flexure between the ventral and the posterior surfaces, and this flexure is situated either at the level of the occipital condyle, or slightly ventrally relative to the condyle. In *Sylviornis* the flexure is situated between the basisphenoid rostrum and the basitemporal plate, just posterior to the basipterygoid processes. The basitemporal plate, rather than being near coplanar with the basisphenoid, makes an angle of ca. 135 ° with the ventral surface of the rostrum. In the recent megapodes, the flexure occurs at the posterior part of the basitemporal plate, which, unlike in *Sylviornis*, is slightly inflated.

On the lateral surface, the postorbital process is strongly developed and directed ventrally. It widens ventrally in the shape of a spatula, with an indented edge. This ventral part of the postorbital process probably corresponds to an aponeurosis ossificans (Zusi & Livezey, 2000). Posteriorly, there is a zygomatic process that is pointed, directed ventrally and slightly anteriorly, and is smaller than the postorbital process. This zygomatic process is very similar to that of some adult megapodes (genera *Alectura*, *Leipoa*, *Aepypodius*, *Macrocephalon*) but it is different in the genus *Megapodius*. Its ventral part is named by Zusi and Livezey (2000) aponeurosis zygomatica ossificans. Between the two processes is a temporal fossa corresponding to the insertion of M. adductor mandibulae externus (AME), pars coronoidea. This fossa is wide and deep, with a well-defined outline. Posterior to the zygomatic process is a second temporal fossa, or fossa temporalis secundaria (Weber 1996), for the insertion of M. add. mand. ext., pars articularis (Zusi & Livezey, 2000). This triangular-shaped fossa is delimited anteriorly by a ridge that is situated in the prolongation of the zygomatic process, and posteriorly by the thick and inflated crista nuchalis. Ventral to this fossa is the quadrate articulation, and posteriorly to the quadrate articulation is a very large tympanic cavity. Anterior to the postorbital process, the orbital fossa is closed medially by the interorbital septum, pierced on each side by a wide foramen opticum.

The anterior surface shows the craniorostral hinge with a median tubercle in the sagittal plane and, on each side, two medio-laterally oriented articular surfaces. On each side the lacrimals form anteriorly a lobe situated ventrally relative to the hinge and ventrally oriented. On the medial side of the lacrimals there is a small, rounded, articular facet, which comes into contact with a process of the rostrum, situated ventrally relative to the articular condyles of the hinge. Then, more ventrally, and medially situated there is the ethmoid, with a median ridge, and the two alae ethmoidales. On each side of the ethmoid there is a wide orbitonasal foramen, and ventral to the foramen a large articular surface, oval in shape and slightly concave. On a cast of the cranium it is possible to see that the right ala ethmoidale was extended in lateroventral direction by a thin, sharp process. This process was subsequently broken on the specimen NCP 241.

Juvenile cranium (NCP 260, 261, 262, fig. 4)

This juvenile cranium has been reconstructed from isolated unfused bones, based on matching sizes and shapes. As for the adult, its general shape is very wide and flat. The supraorbital region is much narrower than in the adult because the lacrimals are not yet fused with the frontals. The crista nuchalis transversa is much less developed and the cristae occipitales are less projecting in lateral and dorsal directions. The squamosal is anteroposteriorly elongated and does not show the enormous swelling of its posterior part that is seen in the adult.

Several juvenile ethmoids have been identified. They show a wide, flat part at their anterior side, and a ventral keel. On each side of the keel is the sulcus olfactorius. Dorsally the anterior part shows articular surfaces which in the adult are fused with the ventral surface of the nasals (fig. 5, g).

Rostrum (NCP 242, fig. 5, a-c))

The adult rostrum NCP 242 does not fit with the cranium NCP 241 and comes from a slightly larger individual. This rostrum is formed by the fusion of the anterior parts of the nasals, the premaxillaries, the maxillaries and the maxillo-palatines. It shows a true hinge, with two large articular condyles, which project ca. 1 cm from the lateral facies immediately in front of them and which insert into the articular surfaces of the posterior parts of the nasals. Its dorsal part bears in the adult a bony ornament, made of very thin cancellated bone, and is incompletely preserved. At the anterior part and at the base of this ornament, there is a groove and a flattened surface. Ventral to the articular condyle, there is a small process [3 mm by 3 mm] that articulates with the small articular surface situated on the ventral process of the lacrimal.

The beak is extremely high and narrow. Its surface has a shagreened aspect that indicates the presence, in adults, of a thick ramphotheca. On the juvenile specimens the surface of the beak is rather smooth. The nostril is rounded and situated almost at the posterior part of the rostrum. The anteriormost part of the beak is a narrow point, ventrally directed. The external tomial crest forms a dorsally oriented sinus, then a ventrally oriented lobe. In ventral view one can see two external tomial crests, two internal ones that continue onto the posteroventral angle of the beak, and one median crest. Anteriorly the adoral surface is formed by the ventral fusion of the premaxillaries. Posteriorly there is a secondary palate formed by the ventral fusion of the maxillaries.

In posterior view, ventral to the craniorostral hinge, there are the two processes that articulate with the lacrimal processes, then two large openings of the internal nares. On

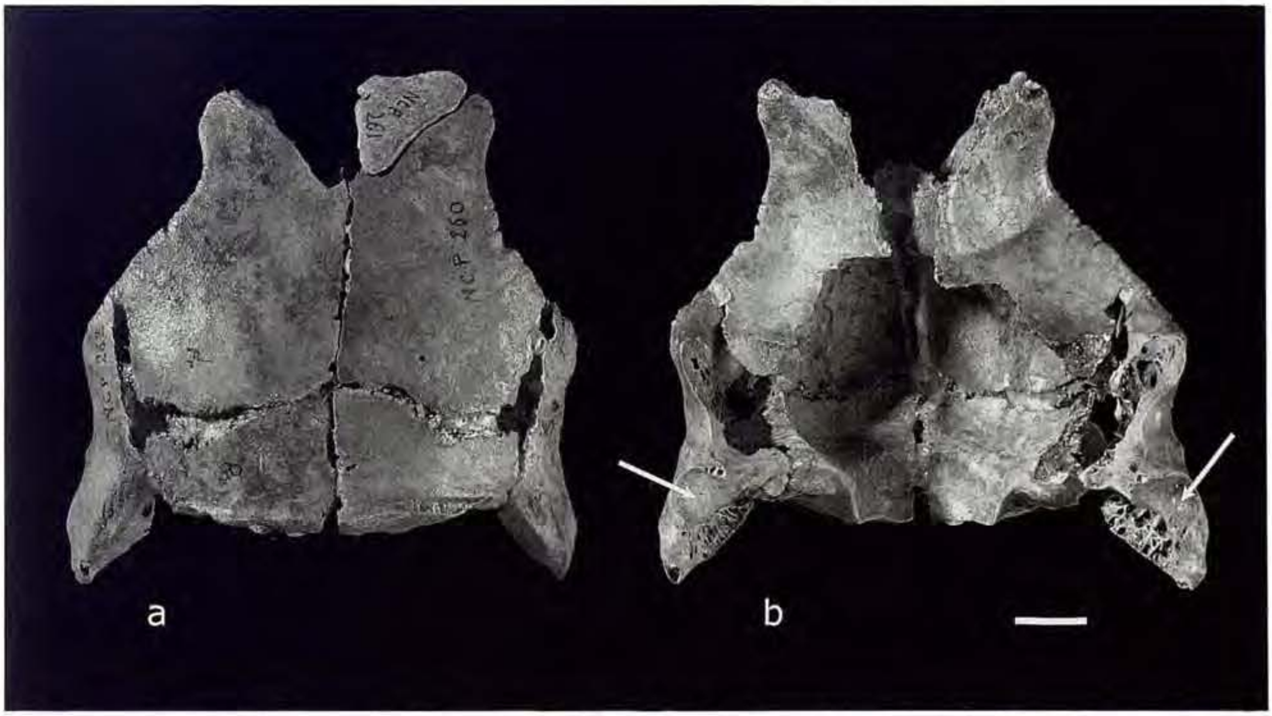

Fig. 4. *Sylviornis* cf. *neocaledoniae*. Reassembled juvenile cranium, NCP 260 + 262; a) dorsal view (the posterior part of the right nasal NCP 261 has been placed in the anterior opening of the frontals); b) ventral view without the nasal NCP 261. The arrows indicate the articular surfaces for the quadrates. The scale bar represents 10 mm.

Fig. 4. Sylviornis *cf.* neocaledoniae. *Crani juvenil remuntat, NCP 260 + 262; a) norma dorsal (la part posterior del nasal dret NCP 261 s'ha situat a l'obertura anterior dels frontals); b) norma ventral sense el nasal NCP 261. Les fletxes indiquen les superfícies articulars per als quadrats. L'escala representa 10 mm.*

Fig. 5. *Sylviornis* cf. *neocaledoniae.* Adult rostrum, NCP 242; a) right lateral view; b) posterior view (for a and b the thick arrow indicates the tubercle which corresponds to the articular surface found on the ventral process of the lacrimal, and the thin arrow indicates the indentation for the articulation with the anterior part of the quadratojugal); c) ventral view. Juvenile rostrum and left nasal, NCP 263, and right nasal, NCP 290; d) right lateral view (the thick arrow indicates the tubercle which later becomes the articular condyle of the adult and the thin arrow indicates the tubercle which corresponds to the articular surface found on the ventral process of the lacrimal); e) dorsal view. Right juvenile nasal, anteriorpart, NCP 221; f) medial view. Juvenile ethmoid, NCP 316; g) right lateral view (one can see the sulcus olfactorius). The scale bar represents 10 mm.

Fig. 5. Sylviornis *cf.* neocaledoniae. *Rostre adult, NCP 242; a) norma lateral dreta; b) norma posterior (per a a i b la fletxa gruixada indica el tubercle que correspon a la superfície articular que es troba sobre el procés ventral del lacrimal, i la fletxa prima indica la indentació per a l'articulació amb la part anterior del quadratojugal); c) norma ventral. Rostre juvenil i nasal esquerre, NCP 263, i nasal dret, NCP 290; d) norma lateral dreta (la fletxa gruixada indica el tubercle que posteriorment es transforma en el còndil articular de l'adult i la fletxa prima indica el tubercle que correspon a la superfície articular que es troba sobre el procés ventral del lacrimal); e) norma dorsal. Nasal juvenil dret, part anterior, NCP 221; f) norma medial. Etmoide juvenil, NCP 316; g) norma lateral dreta (es pot veure el sulcus olfactorius). L'escala representa 10 mm.*

each side there is a small indentation that corresponds to the articulation of the anterior part of the quadratojugal.

In the juvenile specimens, the anterior part of the nasal is not yet fused with the premaxillary (NCP 263 + 290, fig. 5, d-e). Anteriorly it shows two branches, a dorsal one, which inserts into a groove situated on the posterior part of the premaxillary (NCP 263), and a maxillary one, which probably rested against the maxillary (fig. 5, f). Posteriorly it presents, on each lateral side, a large tubercle that, in the adult, becomes the articular condyle, and ventrally a very small point that bears the articular surface for the lacrimal (fig. 5, d).

Quadrate (fig. 6, c-f)

The processus oticus ends dorsally in two articular condyles, the squamosal and the prootic ones, which are contiguous but distinct in the adults. The squamosal condyle is about twice as large as the prootic one. On the anterior surface of the processus oticus, the eminentia articularis is a poorly delimited tubercle, projecting dorsally. The processus orbitalis, triangular in shape, is very elongated, slightly incurved medially, and ends in a rounded lobe. The articular surface for the quadratojugal is a deep socket, surrounded by a thick rim. The mandibular articulation is made up of two obliquely elongated condyles,

Fig. 6. *Sylviornis* cf. *neocaledoniae.* Right and left fused palatines, NCP 250; a) dorsal view; b) ventral view. Right quadrate, NCP 244; c) medial view; d) lateral view; e) dorsal view; f) ventral view. Right quadratojugal, fused with the jugal, NCP 246; g) lateral view; h) dorsal view; i) medial view. Juvenile right palatine, unfused, NCP 251; j) ventral view. Adult left pterygoid, NCP 245; k) dorsal view; l) ventral view. Juvenile left pterygoid, NCP 323; m) ventral view. Three juvenile stages of right quadratojugals, still unfused with the jugals, medial views; n) NCP 247, juvenile; o) NCP 248, more juvenile; p) NCP 249, still more juvenile. The scale bar represents 10 mm.

Fig. 6. Sylviornis *cf.* neocaledoniae. *Palatins dret i esquerre fusionats, NCP 250; a) norma dorsal; b) norma ventral. Quadrat dret, NCP 244; c) norma medial; d) norma lateral; e) norma dorsal; f) norma ventral. Quadratojugal dret fusionat amb el jugal, NCP 246; g) norma lateral; h) norma dorsal; i) norma medial. Palatí dret juvenil, no fusionat, NCP 251; j) norma ventral. Pterigoide adult esquerre, NCP 245; k) norma dorsal; l) norma ventral. Pterigoide juvenil esquerre, NCP 323; m) norma ventral. Tres estadis juvenils de quadratojugals drets, encara no fusionats amb els jugals, normes medials; n) NCP 247, juvenil; o) NCP 248, més juvenil; p) NCP 249, encara més juvenil. L'escala representa 10 mm.*

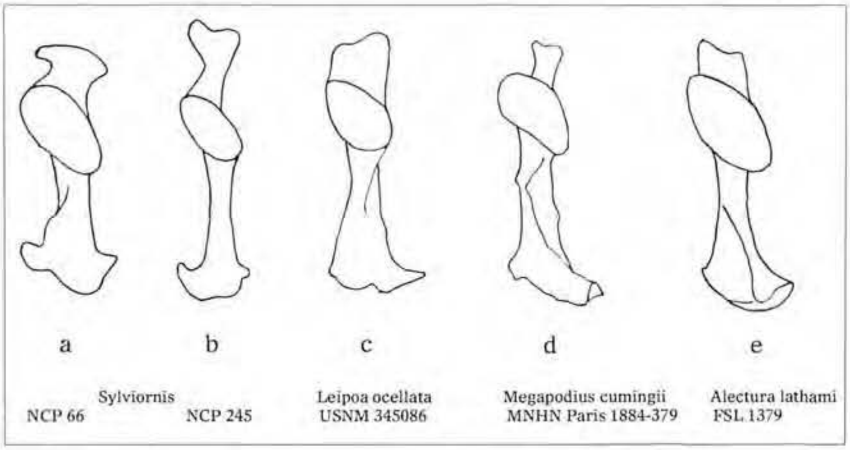

Fig. 7. Drawings of left pterygoids, dorsal view, in two different individuals of *Sylviornis* cf. *neocaledoniae* (a, b) and in three recent genera of megapodes (c, d, e). Not to scale.

Fig. 7. Dibuixos de pterigoides esquerres, norma dorsal, a dos diferents individus de Sylviornis *cf.* neocaledoniae *(a, b) i a tres gèneres recents de megàpodes (c, d, e). No a escala.*

medialis and lateralis, separated by a shallow groove. The lateral condyle is much larger than the medial one. At the anterior part of the medial condyle there is an almost hemispheric, convex, articular surface for the pterygoid (in recent megapodes this surface is more dorsally situated and clearly separated from the medial condyle). The articular surface for the pterygoid continues dorsally along the ventral border of the orbital process, on its medial side. On the medial surface, at the posterior end, dorsally relative to the condylus lateralis, there is a flattened surface for the retroarticular process of the mandible. A pneumatic foramen is present, in the middle of the medial surface of the bone, at the base of the otic process.

Pterygoid (fig. 6, k-m)

This bone shows a large, oval, articular surface for the processus rostropterygoideus, a surface that is oriented at about 45 ° in relation to the long axis of the bone. The ratio between the length of the articular surface and the length of the bone is highly variable. Some pterygoids are long with a small articular surface (NCP 245), others are short with a large articular surface (NCP 66; see fig. 7). At the anterior end of the pterygoid is the articular surface for the palatine, which is made up of an elongated surface on the ventral side, and a point on the dorsal side. The posterior end, widened and crescent-shaped, bears a rounded articular surface for the quadrate on the medial side, and a hook-shaped extension on the lateral side.

The articulation with the processus rostropterygoideus is not situated at the anterior end of the bone, but rather at its anterior third and this characteristic is also found in the recent megapodes that we have been able to study (see fig. 7), whereas in the Cracidae and Phasianidae, as well as the Anatidae, the articulation is situated at the anterior end. This characteristic cannot be considered as a synapomorphy of *Sylviornis* and the megapodes, however, because it is also present in the primitive Anseriformes Anhimidae and Anseranatidae (Dzerzhinsky, 1995), as well as in the Eocene Anseranatidae *Anatalavis* (Olson, 1999). This characteristic is therefore considered as plesiomorphic.

Palatine (fig. 6, a-b, j)

The palatine shows the charateristic shape of the Galliformes, with a narrow posterior part and a very elongated anterior branch. It is different form the anseriformes palatine, which has a wide, wing-like posterior part and a short anterior branch. On some specimens the right and left palatines are fused posteriorly, but this fusion probably occurred relatively late in development because in the available material, the number of individuals with fused vs. unfused palatines is about equal. Most unfused palatines come from small, juvenile, individuals, but there are also large-sized, unfused palatines. When the palatines are unfused, the medial surface is rough, indicating the presence of a fibrous joint.

The fused palatines show two branches that end cranially by a flattened paddle, with a rough and fibrous surface. These branches probably fit into the cavity between the primary and secondary palates, and were probably attached in this cavity by ligaments. The symphyseal part of the palatines shows, on its dorsal side, a point oriented dorsally and a median ridge. At its posterior part there are the two, clearly separated, rounded articular surfaces for the pterygoids. On its ventral side there are two elongate, slightly concave, muscle impressions. There is no contact for a possible vomer and no piece that could be interpreted as a vomer has ever been found.

Quadratojugal (fig. 6, g-i, n-p)

It is formed by the fusion of the quadratojugal sensu stricto with the jugal. Here also the fusion occurs late, as in some adult-sized individuals the jugal is still unfused. The adult quadratojugal has a very sinuous shape. It is dorsoventrally flattened on its anterior part, then latero-medially flattened on its posterior part, and it ends posteriorly in an oval paddle, with a strong dorsal tubercle on its medial side for the quadrate articulation. This shape changes according to age. Young individuals do not have a posterior paddle but only a tubercle for the quadrate (NCP 249, fig. 6, p), after which the paddle develops progressively (NCP 248, 247, fig. 6, o-n). Likewise young individuals have a much more rectilinear quadratojugal, and it becomes more sinuous as it grows. The anterior part of the quadratojugal is made up of a rough articular surface on the medial side, and a point on the lateral side. This articular surface and point rest against an indentation on the posterior side of the rostrum, where they must have been tied by ligaments, in such a way that the rostrum could move around the craniorostral hinge.

Mandible (fig. 8)

No complete mandible is known. The fragments indicate that the mandibular symphysis was very long (NCP

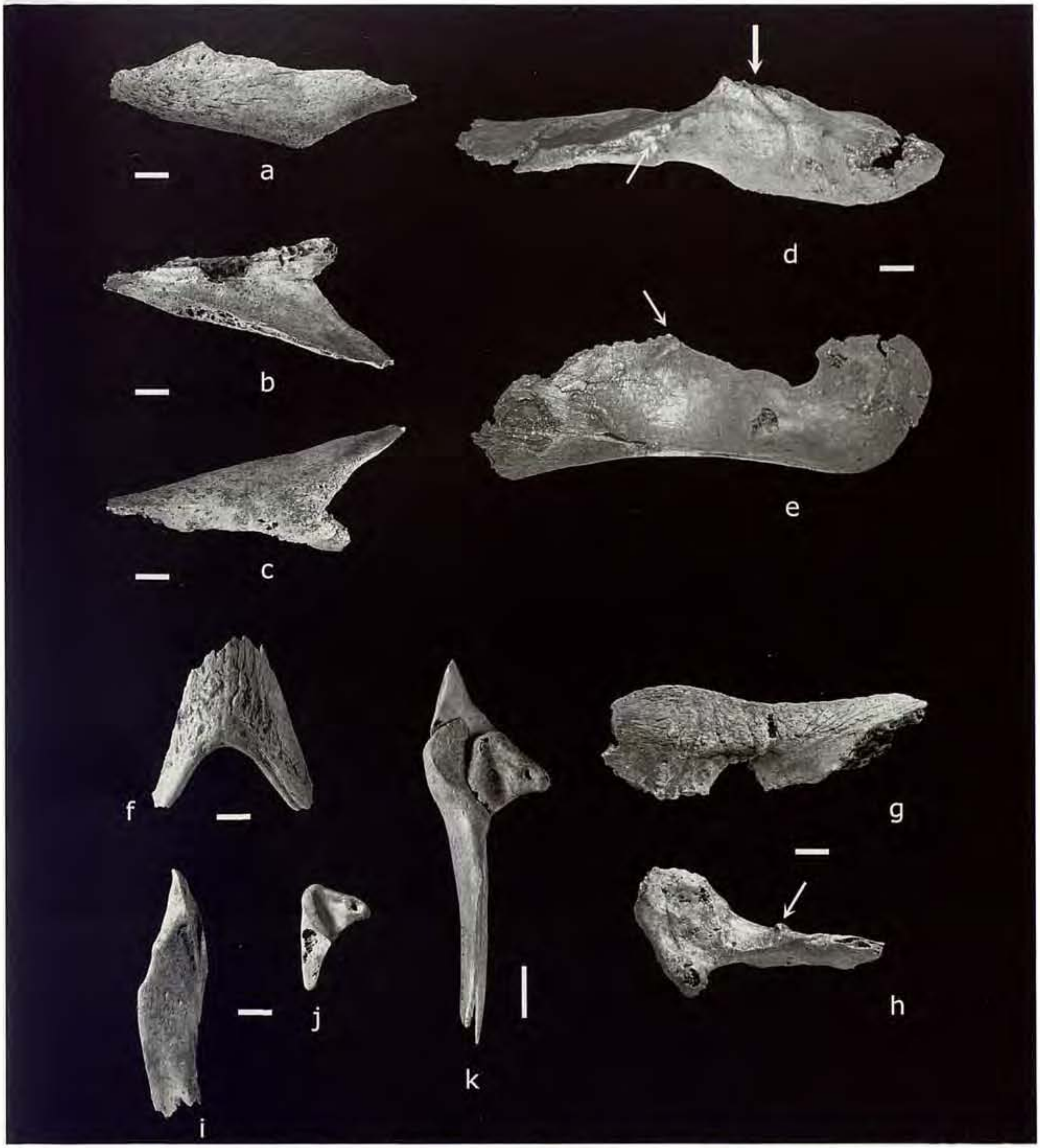

Fig. 8. *Sylviornis* cf. *neocaledoniae*. Symphysial part of juvenile mandible, NCP 243; a) left lateral view; b) dorsal view; c) ventral view. Part of a mandible, left ramus collected by T. H. Worthy *et al.*; d) dorsal view; e) lateral view (in d the thick arrow indicates the position of the processus mandibularis medialis which is broken on this specimen; in d and e the thin arrow indicates the processus coronoideus; the crista paracoronoidea caudalis is not visible on this mandible). Symphysial part of adult mandible, NCP 215, with a corrugated surface; f) ventral view. Intermediate part of left ramus of mandible, NCP 216; g) medial view (the broken part on the right corresponds to the symphysis; this specimen shows the sigmoid outline of the tomial crest, which corresponds to the shape of the rostral tomial crests). Posterior part of left ramus of mandible, NCP 217; h) dorsal view (this part shows the two articular surfaces for the quadrate, separated by a very smooth ridge; the retroarticular process and the tip of the medial mandibular process are broken; the arrow indicates the dorsal end of the crista paracoronoidea caudalis). Juvenile right surangular, NCP 218; i) medial view. Juvenile right articular, NCP 219; j) dorsal view. Juvenile right angular, surangular and articular joined, NCP 298; k) dorsal view. The scale bar represents 10 mm.

Fig. 8. Sylviornis *cf.* neocaledoniae. *Part simfisària de mandíbula juvenil, NCP 243; a) norma lateral esquerra; b) norma dorsal; c) norma ventral. Part d'una mandíbula, branca esquerra, recollit per T. H. Worthy* et al.*; d) norma dorsal; e) norma lateral (a d la fletxa gruixada indica la posició del processus mandibularis medialis que a aquest exemplar està romput; a d i e la fletxa prima indica el processus coronoideus; la crista paracoronoidea caudalis no és visible a aquesta mandíbula). Part simfisària de mandíbula adulta, NCP 215, amb una superfície ondulada; f) norma ventral. Part intermitja de branca de mandíbula esquerra, NCP 216; g) norma medial (la part rompuda de la dreta correspon a la símfisi; aquest espècimen mostra el perfil sigmoideu de la cresta tomial, que correspon a la forma de les crestes tomials rostrals). Part posterior de branca de mandíbula esquerra, NCP 217; h) norma dorsal (aquesta part mostra les dues superfícies articulars per al quadrat, separades per una aresta molt suau; el procés retroarticular i la punta del procés mandibular medial estan romputs; la fletxa indica el final dorsal de la crista paracoronoidea caudalis). Surangular juvenil dret, NCP 218; i) norma medial. Articular juvenil dret, NCP 219; j) norma dorsal. Angular juvenil dret, surangular i barra articular junts, NCP 298; k) norma dorsal. L'escala representa 10 mm.*

243, minimal length 64.5 mm, fig. 8, a-c), and that the bone was very thick at the level of the symphysis (NCP 213, minimal depth of the symphysis 18.3 mm). The fragments of mandibular symphysis from adults, particularly NCP 215 (fig. 8, f), show a strongly corrugated ventral surface, with anteroposteriorly oriented ridges. On the fragment of mandibular ramus NCP 216 (fig. 8, g), the dorsal part forms a sharp edge, with a sinuous line that articulates with the external tomial crest of the rostrum. Both internal and external surfaces of this mandibular ramus show a shagreened ornamentation.

The articular part of the mandible (NCP 217, fig. 8, h) shows two articular cotylae for the two mandibular condyles of the quadrate, separated by a smooth ridge. This articulation is not situated in a depression. The medial mandibular process is short and wide, with a pneumatic foramen on its lateral side, ventral to its tip. On the dorsal side of the mandibular ramus, close to the articulation, there is a processus coronoideus and, on the lateral side, a dorsoventrally oriented crista paracoronoidea caudalis (Weber, 1996). This crista has a tubercle at its dorsal part, and is not incurved but quite straight.

The posterior part of a left mandible collected by T. H. Worthy *et al.* (fig. 8, d-e) shows that, in the adult, this area is extremely thick in a mediolateral direction. The retroarticular process of this mandible is very wide, both mediolaterally and anteroposteriorly. The dorsalmost part of this retroarticular process is incompletely preserved but it seems to have a rounded outline, while in the recent megapodes it ends by a dorsally, or dorsoposteriorly oriented point.

In most birds in which both are present, the medial process and the retroarticular process of the mandible are approximately the same size, but in *Sylviornis*, the retroarticular process is much more developed than the medial mandibular one.

The development of the posterior part of the mandible can be correlated with the strong development, both in lateral and posterior directions, of the posterior part of the cranium. There is a strong contrast between the anterior part of the mandible, which forms two cutting blades, and the posterior part which is very thick and massive.

Among the juvenile material there are numerous unfused mandibular bones, such as angulars, articulars, and supraangulars (fig. 8, i-k). This indicates that fusion of the mandibular bones probably occurred late during the development of the animal.

MEASUREMENTS (IN MM)

Adult cranium (NCP 241)

Total length from the lacrimal process to the posteriormost part of the paroccipital process: 100; maximum width at the level of the exoccipitals: 108; maximum dorsoventral height from the top of the cranial vault to the sphenoid, between the rostropterygoid processes: 56.0; minimum width of the frontals at the level of the orbits: 65.6; minimum width of the parietals and squamosals at the level of the temporal fossa: 73.4; width at the level of the craniorostral hinge: 57.0; anteroposterior length from the tubercle situated in the middle of the craniorostral hinge to the occipital condyle: 93.4; anteroposterior length from the same point to the posteriormost part of the paroccipital process: 106.6; anteroposterior length from the same point to the crista nuchalis transversa, in the sagittal plane: 67.0; anteroposterior length of the supraoccipital, from the crista nuchalis transversa to the top of the occipital foramen, in the sagittal plane: 25.0; dorsoventral height of the posterior and lateral part of the cranium, from the top of the crista occipitalis to the base of the paroccipital process: 53.0; internal width of the occipital foramen: 12.0; internal height of the occipital foramen: 16.0; width of the occipital condyle: 12.0; height of the occipital condyle: 9.0; anteroposterior length of the rostropterygoid processes: 16.2 and 16.2; width of the rostropterygoid processes: 7.5 and 7.2

Adult rostrum (NCP 242)

Maximum length from the anterior point of the beak to the articular condyle of the craniorostral hinge: 148.0; dorsoventral height of the rostrum from the top of the articular condyle of the hinge to the posterior angle: ca. 69.0; length from the point of the beak to the posterior angle: ca. 102.0; maximum width between the tips of the two articular condyles: 60.0; length of the bony ornament at its base: 52.0; width of the bony ornament at its base: 41.2; width of the premaxillaries at the level of the external tomial crests: 26.6; width of the rostrum at the level of the posterior angle: 22.2 ; at the level of the articular surfaces for the quadratojugals: 30.0; dorsoventral height from the flattened surface situated at the base of the bony ornament, to the internal tomial crest: 64.0; dorsoventral and anteroposterior diameter of the external naris: 12.5 and 12.0

Mandibles

Anterior parts: see table 1

Cranial parts of mandibles	NCP 213 adult	NCP 243 juvenile	NCP 295 juvenile	NCP 294 juvenile
Length of the almost complete mandibular symphysis	-	-	-	47.8
Length of the mandibular symphysis as preserved	57.0	64.5	54.0	-
Maximum dorsoventral heigth of the complete symphysis	-	16.2	13.6	12.0
Maximum dorsoventral heigth of the symphysis as preserved	18.0	-	-	-

Table 1. *Sylviornis* cf. *neocaledoniae*, Pindai Cave, New Caledonia. Measurements (mm) of the anterior parts of mandible.

Taula 1. Sylviornis *cf.* neocaledoniae, *Pindai Cave, New Caledonia. Mesures (en mm) de les parts anteriors de la mandíbula.*

Posterior part (specimen collected by T. H. Worthy *et al.*): dorsoventral height at the level of the articular surface for the quadrate: 23.0; height from the top of the retroarticular process to the ventralmost part of the mandible: estim. 42.5; anteroposterior length of the retroarticular process at the level of the articular surface for the quadrate: 33.6; mediolateral width of the mandible at the level of the articular surface for the quadrate: estim. 46.0 (based on the specimen collected by T. H. Worthy *et al.* and on NCP 217)

Quadrates, pterygoids, palatines, and quadratojugals
See tables 2 to 5.

JUSTIFICATION FOR THE CREATION OF A NEW FAMILY

The presence of two well-developed basipterygoid processes makes it possible to state that *Sylviornis* belongs to Galliformes or to Anseriformes (Weber, 1993; Dzerzhinsky, 1995; Ericson, 1996; Livezey, 1997), and the presence of palatines with very elongated anterior branches and posterior parts (partes laterales) that are narrow and not wing-like shows that it belongs to Galliformes.

Among the Galliformes, the postcranial skeleton shows more similarities with Megapodiidae than with other families (Poplin *et al.*, 1983; Poplin & Mourer-Chauviré, 1985), but these similarities seem to be symplesiomorphic. The cranial characteristics also present some similarities with Megapodiidae, as for example the slightly developed lacrimal, devoid of orbital process ; the position of the articular surface for the rostropterygoid process at the first third of the pterygoid and not at its anterior end; the presence of well developed alae ethmoidales. The first two characteristics are symplesiomorphies and the third one is variable within the Galliformes (Ericson, 1996).

The creation of a new family is justified by the presence of numerous autapomorphic characteristics in the skull and mandible, characteristics that are indicated in the diagnosis. To our knowledge *Sylviornis* is the only bird to show a true diarthrosis, of ginglymus type, between the skull and the beak, and to show a cranial flexure situated just posterior to the basiperygoid processes.

COMPARISON WITH OTHER EXTINCT GALLIFORM FAMILIES

Three extinct families have been described within the Galliformes, the Gallinuloididae Lucas, 1900, the Quercymegapodiidae Mourer-Chauviré, 1992, and the Paraortygidae Mourer-Chauviré, 1992. These three families display primitive characteristics compared with the recent families of Galliformes (Mourer-Chauviré, 1992; Mayr, 2000; Dyke & Gulas, 2002; Mayr & Weidig, 2004). These characteristics are mainly the presence of a hollow, cup-like, scapular facet on the coracoid, and the absence of a transverse ridge at the beginning of the incisura capitis on the humerus. These characteristics are absent in *Sylviornis* which on the contrary displays the derived character states.

DISCUSSION

It is possible to think that the the ancestor of *Sylviornis* was a galliform comparable in its osteological features to the recent megapodes, which would have reached New Caledonia at an unknown date, and would have evolved there in insular isolation, where it became flightless and acquired its highly derived cranial features. This ancestral form could have reached New Caledonia when it was still

Quadrates	Extremes	Mean	sd	n	V
Dorsoventral heigth from the tip of processus oticus to the ventralmost part of condylus medialis	34.0-38.8	36.15	1.25	35	3.45
Craniocaudal length from the cranial tip of processus orbitalis to the caudal part of processus mandibularis	46.0-51.3	47.90	1.89	9	3.95
Mediolateral width of the top of processus oticus	16.7-20.2	18.35	0.84	35	4.58
Craniocaudal length of the mandibular articular surface	28.0-35.8	30.59	1.71	33	5.59

Table 2. *Sylviornis* cf. *neocaledoniae*, Pindai Cave, New Caledonia. Measurements (mm) of the quadrates.

Taula 2. Sylviornis *cf.* neocaledoniae, *Pindai Cave, New Caledonia. Mesures (en mm) dels quadrats.*

Pterygoids	Extremes	Mean	sd	n	V
Maximum craniocaudal length	31.4-40.8	36.77	2.12	35	5.77
Maximum length of the articular facet for the processus rostropterygoideus	12.4-17.4	14.66	1.28	34	8.73
Width of this articular facet	6.6-8.6	7.66	0.49	34	6.40

Table 3. *Sylviornis* cf. *neocaledoniae*, Pindai Cave, New Caledonia. Measurements (mm) of the pterygoids.

Taula 3. Sylviornis *cf.* neocaledoniae, *Pindai Cave, New Caledonia. Mesures (en mm) dels pterigoides.*

able to fly. Alternatively it may have colonized New Caledonia during the Eocene, via the now submerged Rennell ridge (Balouet, 1984). Olson (1980) has demonstrated that megapodes are able to cross large expanses of seawater and to colonize islands. The recent discoveries of many extinct megapodes in South Pacific islands (Jones *et al.*, 1995; Steadman, 1999) clearly indicates that megapodes were much more widespread in the past, and that their recent distribution is relictual. A large, extinct, form of the genus *Megapodius*, *M. molistructor*, was also present in the Holocene of New Caledonia (Balouet & Olson, 1989).

The oldest representative of the family Megapodiidae, the genus *Ngawupodius*, has been described from the late Oligocene of South Australia (Boles & Ivison, 1999), and it is therefore possible to suppose that a comparable form may have reached New Caledonia at an indeterminate period, between the late Oligocene and the Holocene.

An instance of convergent evolution possibly occurred in the Fiji Islands where Worthy (2000) has described a giant flightless megapode, *Megavitiornis*, from Viti Levu island. In the dimensions of its postcranial skeleton the Pindai *Sylviornis* is on average 25 % larger than *Megavitiornis*, but the head of *Sylviornis* is proportionately much larger, being about twice as large as the estimated length for *Megavitiornis*. In *Megavitiornis* the rostrum is very high, and relatively narrow, but not so narrow as in *Sylviornis*. The associated cranial fragments show that in *Megavitiornis* the craniorostral hinge was unfused, but there was not a true diarthrosis, with two articular condyles and two concave articular surfaces. The nasal shows a robust maxillary process, indicating that it was not completely fused with the maxillary and the premaxillary to form a massive rostrum as in *Sylviornis*. The anterior part of the mandible of *Megavitiornis* also shows convergence with that of *Sylviornis*. It is very high dorsoventrally and very robust, and its symphysis occupies ca. 45 % of the mandibular length. But its posterior part is different. In *Megavitiornis* the processus mandibulare lateralis is a very robust, rounded prominence, and the retroarticular process is prominent, narrow and deep, whereas in *Sylviornis* the mandibular ramus is so thick at its posterior part that the processus mandibulare lateralis is not visible, and the retroarticular process is very long anteroposteriorly, wide at its base, and seems to have a rounded outline at its top. In the postcranial skeleton the main differences between *Megavitiornis* and *Sylviornis* are the shape of the tarsometatarsus, which is proportionally more robust in *Megavitiornis*, and the presence, on one of the two tarsometatarsi described, of a sulcus extensorius connected by a groove to the distal foramen (Worthy, 2000).

In conclusion, *Megavitiornis* shows some convergent evolution with *Sylviornis*, but is less advanced. It is possible to think that several different forms of megapodes, or megapode-like galliforms, colonized the South Pacific islands at different periods of time, and have given rise to somewhat convergent but unrelated forms.

Fused palatines	Extremes	Mean	sd	n	V
Craniocaudal length of the fused part from the cranial point to the pterygoid articulations measured on the dorsal face	24.7-31.8	28.81	2.12	13	7.36
Maximum craniocaudal length from the tip of the branch to the pterygoid articulation	90.5-ca. 98.0	-	-	3	-
Maximum width	17.4-21.9	19.37	1.47	10	7.59
Width of the caudal part (two articular surfaces for the pterygoids measured together)	13.1-21.3	17.00	2.49	13	14.65
Dorsoventral heigth of the articular surfaces for the pterygoids	8.6-11.6	10.25	0.80	13	7.80

Table 4. *Sylviornis* cf. *neocaledoniae*, Pindai Cave, New Caledonia. Measurements (mm) of the fused palatines.

Taula 4. Sylviornis *cf.* neocaledoniae, *Pindai Cave, New Caledonia. Mesures (en mm) dels palatins fusionats.*

Quadratojugals	Extremes	Mean	sd	n	V
Maximum craniocaudal length	84.5-99.4	91.22	3.25	21	3.56
Width of the cranial part	13.0-18.1	14.99	1.42	19	9.47
Heigth of the cranial part (dorsoventral)	5.4-8.0	6.29	0.75	19	11.92
Maximum dorsoventral heigth of the branch	9.6-12.7	11.02	0.83	21	7.53
Width of the branch at the same level	3.9-6.7	5.17	0.66	21	12.77
Maximum craniocaudal length of the articular palette for the quadrate	16.0-19.0	17.76	0.71	21	4.00

Table 5. *Sylviornis* cf. *neocaledoniae*, Pindai Cave, New Caledonia. Measurements (mm) of the quadratojugals.

Taula 5. Sylviornis *cf.* neocaledoniae, *Pindai Cave, New Caledonia. Mesures (en mm) dels quadratojugals.*

DIET OF *SYLVIORNIS*

There is some similarity between the skull of *Sylviornis* and that of the early Tertiary bird *Diatryma* which also shows a narrow, cutting beak, a mobile craniorostral articulation, and a very complex articulation between the quadratojugal and the posterior part of the rostrum (Andors, 1988). Witmer and Rose (1991) have put forward the hypothesis that *Diatryma* was a carnivorous predator but Andors (1988; 1992), using other arguments, has shown that it was vegetarian.

The Australian Dromornithidae, previously considered as ratites, have been studied again by Murray & Megirian (1998) who have shown that, according to their cranial characteristics, they must be classified within the Anseriformes. Some of these Dromornithidae have a very high, narrow beak, ending anteriorly in a hook, and a completely mobile craniorostral articulation, as in *Sylviornis* (Murray & Vickers-Rich, 2004). The mandible was very high dorsoventrally. However, according to Murray & Megirian (1998, p. 78), the rostrum was round-tipped rather than pointed, and the hooked tip differed markedly from the slender, sharply pointed hook in raptors and carrion-eating birds. Their conclusion is that the Dromornithidae were specialized herbivores, able to shear tough plant material. In *Sylviornis* the shape of the rostrum is very pointed and the hooked tip resembles that of raptors, or of birds widely recognized as carnivorous such as the Phorusrhacidae. In posterior view the shape of the cranium, in the Dromornithidae, is very different in its dorsoventral elongation from that of *Sylviornis.*

The Mauritian Dodo, *Raphus cucullatus*, also had a beak ending in a powerful hook. But this hook was mainly formed by the ramphotheca and the bony beak shows a much less pronounced point (Strickland & Melville, 1848). In the Dodo the anterior part of the rostrum is wide and becomes narrower in its middle part. In the Rodrigues Solitaire, *Pezophaps solitaria*, the rostrum is elongated and narrow (Newton & Newton, 1870), but in these two forms, unlike *Sylviornis*, the rostrum is not massive. Its dorsal part consists of a rather thin bony blade formed by the fusion of the processus frontalis of the premaxillary with the processus premaxillaris of the nasal. Ventrally there is a slot-like external naris that is very elongated anteroposteriorly. There is no articulation between the cranium and the rostrum, just a flexion zone. The ventral surface of the rostrum does not show cutting tomial crests. The mandible has narrow and elongated branches and a very short symphysis. It is clear that the diet of *Sylviornis* was different from that of the Raphidae, which were primarily vegetarian.

In the islands devoid of terrestrial mammals, the ecological niche of large herbivores is often filled by large land-tortoises. This is the case for example, in the recent giant tortoises of Aldabra and the Galapagos, and of the recently extinct tortoises of Madagascar and the Mascarenes. In all these forms the masticatory apparatus is not a single cutting blade but a wide triturating surface. The most extreme case is that of the Mascarenian tortoises, which have several ridges, each of them bearing a row of small bony tubercles (Bour, 1979-80).

In the Hawaiian Islands there were no giant land-tortoises and their ecological niche was probably occupied by the flightless ducks called moa-nalos (Olson & James, 1991). In these forms the premaxillaries and the dentaries were very short, massive, and generally presented blunt tooth-like projections.

Most of the cranial characteristics of *Sylviornis* are different from those of the typically vegetarian forms such as the weird anseriforms, the Australian Dromornithidae, the Hawaiian moa-nalos, pigeons in the Raphidae, or the Mascarenian tortoises.

Balouet (1986) proposed the hypothesis that *Sylviornis* was vegetarian and fed on roots and tubercles. This hypothesis was significantly supported by the very high numbers of *Sylviornis* in the fossil sample, which implies that it could not have been a carnivorous predator, hunting and feeding on other large vertebrates. However it is also possible to propose that *Sylviornis* fed on invertebrates. In this case, the available alimentary resources, such as marine organisms or terrestrial gastropods, for example, could have been abundant and varied enough to sustain a large population of this species. We think that the skull of *Sylviornis* has evolved as an adaptation to a particular and highly specialized diet, but it is not possible at this stage to be more precise.

SYLVIORNIS AND THE ORAL TRADITION

Sylviornis was contemporaneous with the first arrival of man in New Caledonia and its disappearance is certainly due to overhunting (Balouet, 1986; 1987). The oral tradition has retained the memory of a vanished bird, called Du (Griscelli, 1976). According to tradition this bird was giant and flightless. It laid a single egg and did not incubate it. This egg took four months to hatch (from November to April). The Du moved along on the ground very rapidly, with its wings spread out. It had a red feathering and a bony ornament on the head. P. Griscelli writes: "It seems that the Du had on its head a kind of bony, solid, casque, in the shape of a star" (1976, p 5, our translation). But the word "Ghi" which designates this ornament should rather be translated as helmet. According to the inhabitants of Houaïlou the Du laid an egg on the top of a lizard sheltered in the hollow of a banyan, then went away, leaving the lizard to incubate it for four months and to break the shell with its jaw. Lastly P. Griscelli states that "tradition attributes great aggressiveness to this bird, in connection with totemic rites and cannibalism" (1976, p. 5, our translation).

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20

PRODROMUS OF VERTEBRATE PALEONTOLOGY AND GEOCHRONOLOGY OF BERMUDA

Storrs L. Olson, David B. Wingate, Paul J. Hearty & Frederick V. Grady

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Resum

Les fluctuacions pleistocèniques del nivell de la mar han estat el primer determinant de la deposició geològica i l'evolució biòtica a Bermuda. L'illa està composta d'arenes carbonatades dipositades sobre el cim erosionat d'un volcà submarí durant el decurs de nivells de la mar elevats dels períodes interglacials. A partir de les arenisques interglaciars s'han obtingut unes poques restes de vertebrats, principalment d'edat pleistocènica mitja. Els intervals glacials estan marcats per sols vermells, derivats principalment de la pols atmosfèrica. Els vertebrats fòssils d'edat glacial no es troben preservats a la superfície i només es coneixen de coves i rebliments de fissures. A Bermuda es coneixen faunes fòssils dels darrers dos episodis glacials, però no dels anteriors. Es coneixen extincions certes o probables de vertebrats correlacionades amb, com a mínim, quatre pujades interglacials del nivell de la mar (estadis isotòpics marins, MIS, 11, 9, 5 i 1). Es revisa la història de la paleontologia de vertebrats a Bermuda i s'allisten i es descriuen breument les localitats de vertebrats fòssils.

Paraules clau: ocells fòssils, extinció pleistocènica, canvi del nivell de la mar.

Summary

Pleistocene sea-level fluctuations were the primary determinant of geological deposition and biotic evolution on Bermuda. The island is composed of carbonate sand deposited on the eroded summit of a submarine volcano during elevated sea-levels of interglacial periods. A few vertebrate remains have been recovered directly from interglacial sandstones, mainly of mid-Pleistocene age. Glacial intervals are marked by red soils derived mainly from atmospheric dust. Vertebrate fossils of glacial age are not preserved at the surface and are known only from caves and fissure fills. Fossil faunas are known on Bermuda from the last two glacial episodes but none of the earlier ones. Certain or probable extinctions of vertebrates are correlated with at least four interglacial rises in sea-level—Marine Isotope Stages (MIS) 11, 9, 5, and 1. The history of vertebrate paleontology on Bermuda is reviewed and fossil vertebrate localities are listed and briefly described.

Keywords: fossil birds, Pleistocene extinction, sea-level change.

INTRODUCTION

Bermuda is an isolated oceanic island situated 1000 km ESE of Cape Hatteras, North Carolina (Fig. 1, inset). Its volcanic core, last active during the Oligocene (Reynolds & Aumento, 1974), was probably subaerial for some of its existence because rare basaltic pebbles and a small percentage of volcanic grains have been found in surface deposits. Apart from the initial volcanic origin of Bermuda, the most important factor affecting the geology of the island has been fluctuating sea-levels during the Pleistocene, with marine carbonate deposition on the platform during interglacial high sea stands. An excellent summary of the Quaternary history of Bermuda may be found in Vacher *et al.* (1995).

The exposed rocks on the island consist almost entirely of biogenic carbonate dunes or "eolianite" (a term coined by Sayles, 1931) formed from comminuted mollusk shells, coral, coralline algae, and foraminifera. These sediments are transported to the shore by waves and currents, and are subsequently blown onto land by strong winds. The eolianites form primarily during interglacial highstands when rises in sea-level flood the Bermuda platform (Bretz, 1960; Land *et al.*, 1967), and during early regression from the highstand position. Thus, eolianites are landward facies of shoreline deposits. During glacial periods of sufficient intensity to bring sea-level below the edge of the platform, the shelf is exposed and biogenic sediment formation ceases because the highest parts of the platform (present-day Bermuda islands) are essentially cut off from eolianite deposition.

During glacial lowstands, red soils develop from oxidation of the underlying limestone and deposition of wind-borne dust coming off of the Sahara Desert (Glaccum & Prospero, 1980; Muhs *et al.*, 1990). These soils redden with age, and become heavily leached while exposed to the elements over tens or hundreds of thousands of years. Thus, they seldom contain identifiable fossils. However, in caves and fissures fossils are protec-

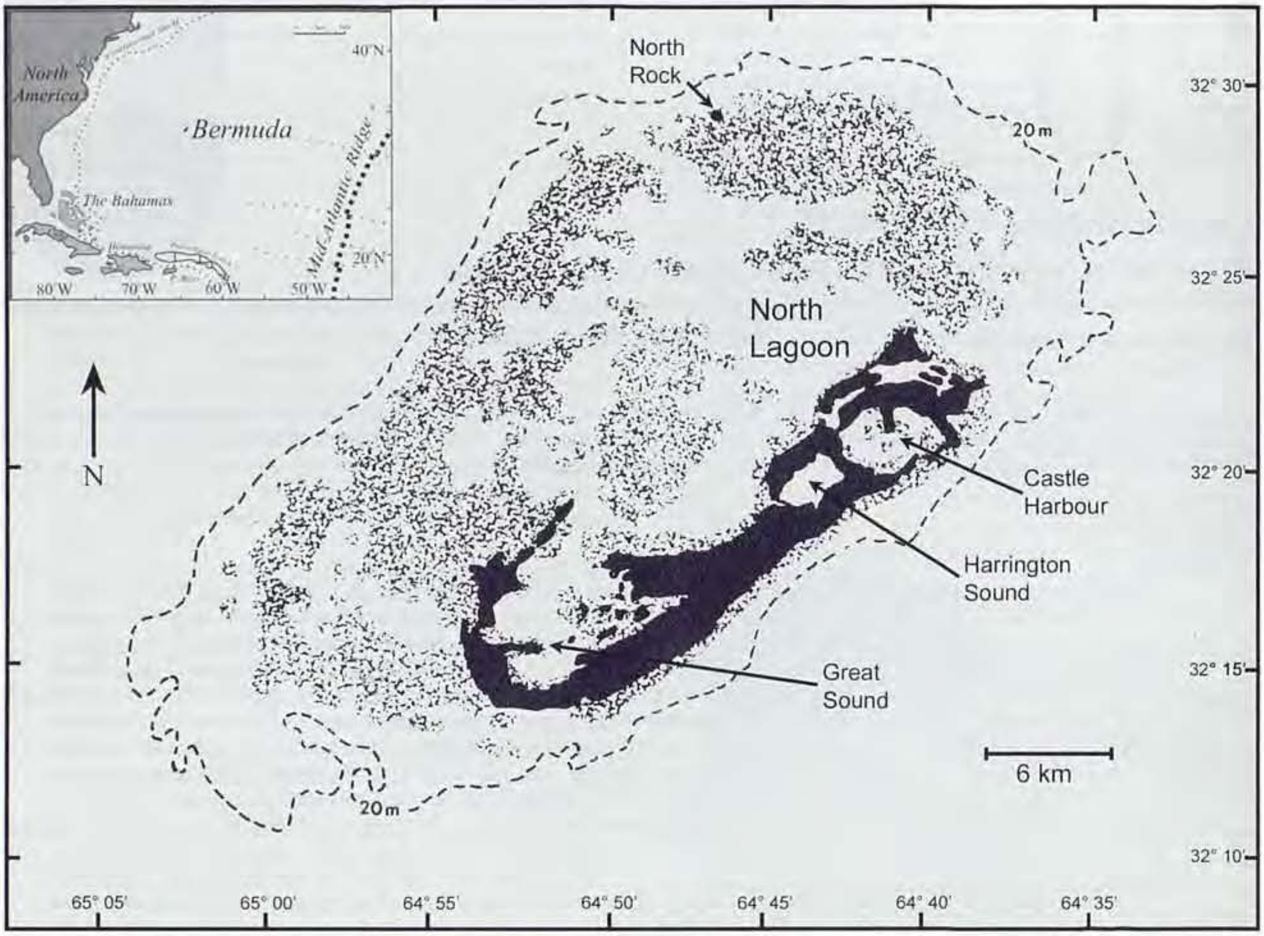


Fig. 1. Map showing present land area of Bermuda (in black) and the extent of reefs and the Bermuda platform (dashed line) that would have been exposed during major glacial episodes (modified from Logan, 1988: 33). Inset: Map showing position of Bermuda relative to the E coast of North America.

Fig. 1. *Mapa on es mostra l'àrea terrestre actual de Bermuda (en negre) i l'extensió dels esculls i la plataforma de Bermuda (línia de punts) que hauria estat exposada durant els episodis glacials principals (modificat a partir de Logan, 1988: 33). Quadre inserit: Mapa on es mostra la posició de Bermuda respecte la costa E de Nord-Amèrica.*

ted from external elements such as sun, wind, and rain, increasing their potential for preservation. Additionally, cave flowstone may also periodically bury fossil deposits, affording even greater protection from degradation. Consequently, nearly all knowledge of faunas of glacial age is derived from subsurface "pitfall" deposits (Hearty *et al.*, 2004).

The majority of fossils from Bermuda that have been extracted from surface deposits are almost entirely of interglacial age, despite the fact that interglacial deposits represent only a fraction (some 10-15%) of the temporal record of Bermuda since the first surface rocks were deposited. By far the greater part of the temporal record of Bermuda is represented by red soils, which rarely contain fossils, thus highlighting the importance of cave and fissure deposits for filling out this important gap in the fossil record.

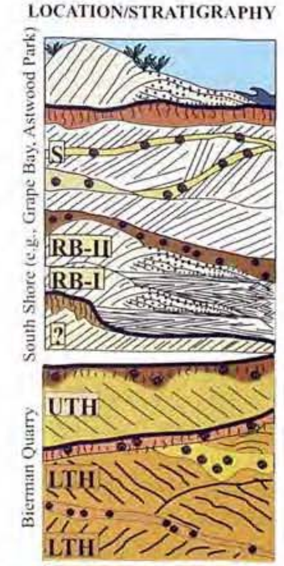
The land area of Bermuda fluctuates greatly between sea-level highstands and lowstands (±100-150 m) (Chappell & Shackleton, 1986). In our current interglacial period, the area of Bermuda is about 56 km^2. This land area would have been significantly reduced at the peak of the last interglacial (MIS 5e) highstand about 120 kya ago when sea level was 6-9 m higher than present (Hearty & Neumann, 2001; Hearty, 2002). During the maximum sea-level rise of the MIS 11 interglacial, ca. 400 kya ago, sea-level was more than 20 m above the present level, reducing the area of Bermuda to less than 20-30% of the island's current area (Olson & Hearty, 2003). In contrast, during maximum glacial lowstands, the entire Bermuda platform would have been exposed, becoming an extensive limestone plateau with an area of about 1000 km^2, nearly two orders of magnitude larger than at present (Fig. 1).

VERTEBRATE CHRONO-STRATIGRAPHY OF BERMUDA

The oldest exposed deposits on Bermuda consist of the highly recrystallized limestone of the Walsingham Formation, cropping out mainly on the SW side of Castle Harbour. The age of the Walsingham Formation has not been radiometrically determined, but it is presumed to be at least 800 kyr old (early Pleistocene) and could possibly be older, as indicated by reversed magnetic polarity and old amino acid racemization and electron spin resonance ages (Hearty & Vacher, 1994). The rocks are primarily eolianite with some weakly-developed intercalated protosols (weak interglacial soils, Vacher & Hearty, 1989), indicating that there was abundant dry land present at the time of deposition. The only terrestrial macrofossils known so far from the Walsingham are two shells of the pulmonate snail *Poecilozonites* (subgenus *Poecilozonites*) recovered from a protosol in Wilkinson Quarry.

Capping the Walsingham Fm is a massive terra rossa soil, referred to as the "Big Red Soil" or BRS (Hearty, 2002), that represents an extended period of island stability in Bermuda's history, when maximum sea-levels were depressed and much of the Bermuda platform emergent. Although sea levels fluctuated during this period, they never rose high enough to initiate carbonate deposition in the area of the present island. This span of almost a half million years (estimated to be from 800 kya to 450 kya—Olson and Wingate 2000) extended from MIS 13 back to MIS 21 (Hearty & Vacher, 1994) or even MIS 26 (Hearty, 2002). Weathering of the Walsingham and deposition of wind-borne dust from the Sahara over this long period of time resulted in the development of a deep karst surface (up to 5 m) mantled by the BRS (Fig. 3). From the available field evidence, it appears that Bermuda island was emergent from much of the early Pleistocene (Walsingham Fm) and early middle Pleistocene (BRS), perhaps for as long as 1 to 1.5 Mya. There can be no doubt that over this long period the biota that must have colonized and evolved would have been more diverse and distinctive than any of those that succeeded it. Unfortunately, because the BRS is heavily leached and no cave or fissure fills of this age have been found, we know nothing at all about the island fauna of this period beyond the assumption that the few terrestrial species known from the Lower Town Hill Formation are probably remnants of a BRS fauna. This extended period of island emergence came to a sudden end during MIS 11, when sea level rose to over 21 m above present (Hearty *et al.*, 1999; Kindler & Hearty, 2001), flooding most of the land area. Eolianites of the Lower Town Hill Formation were deposited during this interglacial.

The earliest fossil vertebrates from Bermuda are those in the Lower Town Hill Formation at Green Island (Olson & Hearty, 2003) that were deposited near present sea-level during interglacial MIS 11, about 400 kya ago. Sea-level continued to rise to more than 21 m above sea-



FORMATION/MB		MIS	Estimated/ Absolute Age (ka)	DESCRIPTION	FOSSIL SITES
Holocene/Recent		1	0-10	✦ Minor coastal deposits with small dunes, marsh sediments, interior soil formation	12; 16-18; 24-26
St. Georges Geosol		2-4	10-70	✦ Reddish brown clayey silt, sparse/rare fossils continued development interior island	8; 9; 18
Southampton Fm		5a/5c	70-105	✦ Extensive weakly-cemented dune complex with intercalated, bifurcating protosols containing abundant invertebrate fossils, primarily land snails; South shore only.	
Hungry Bay Fm*		5c	105	✦ Thin, fine-grained local dunes on South shore	11
Harrington Mb	Rocky Bay Fm	5d	105-118	✦ Thin to locally thick, tan to orange silty soil with abundant land snails and marine fossils at base	
Devonshire Mb Grape Bay Mb*		5e	118-133	✦ Marine and dune facies with fossil mollusks, corals; sea level +2.5 to +6-8 m; exposed along modern shore	
Geosol		6	133-195	✦ Unnamed paleosol at base of last interglacial sequence	8-10; 11
Unnamed Unit*		7	195-235	✦ Isolated, buried dunes of questionable age	
Ord Road Geosol		8	235-300	✦ Reddish brown to orange paleosol	
Upper Town Hill Fm		9	300-330	✦ Extensive eolianites forming core of Bermuda; marine deposits along North Street, Hamilton.	6
Harbour Road Geosol		10	330-370	✦ Clayey red-orange soil with fossil snails	8
Lower Town Hill Fm		11	370-425	✦ Extensive marine and eolian deposits with multiple subdivisions by unconformity and protosols. Fossiliferous marine deposits at +21 m (Government Quarry), +5 to +10 m (Front Street), and +1 to +3 m (Coopers and Green Islands). Multiple zones with abundant avian and land snail fossils.	1-5
Castle Harbour Geosol (aka Big Red Soil)		12-24?	425-900	✦ Deep red clayey soil developed on extensively karstified surface with soil pits extending up to 5 m into host limestone. Fossils absent.	
Walsingham Fm		25-37?	900-1500?	✦ Recrystallized eolianite and marine deposits (St. Georges West); cavernous with extensive speleogenesis and cave fillings with surface materials; faulted with minor displacement and fissures filled with sediments and fossils of various ***younger*** ages.	

Nota Bene: Stratigraphy: Vacher et al. (1989; 1995); Stratigraphy and geochronology: Hearty et al. (1992). Revision of South Shore stratigraphy after Hearty (2002); Isotope ages: Imbrie et al. (1984).

Fig. 2. Composite stratigraphy, nomenclature, correlation with marine isotope stages (MIS), estimated or known ages, description, and source of known fossil deposits from Bermuda. Site numbers refer to the numbering system used in the text. LTH = Lower Town Hill Formation, RB = Rocky Bay Formation, S = Southhampton Formation, UTH = Upper Town Hill Formation, W = Walsingham Formation. * = see Hearty (2002).

Fig. 2. *Estratigrafia composta, nomenclatura, correlació amb els estadis isotòpics marins (MIS), edats estimades o conegudes, descripció, i font dels dipòsits fossilífers coneguts de Bermuda. Els nombres de les localitats corresponen al sistema de numeració emprat al text. LTH = Formació Lower Town Hill, RB = Formació Rocky Bay, S = Formació Southhampton, UTH = Formació Upper Town Hill, W = Formació Walsingham. * = vegeu Hearty (2002).*

Fig. 3. NE corner of Wilkinson Quarry showing the Big Red Soil (BRS) overlying and filling karstic cavities in the recrystallized limestone of the Walsingham Formation. These two units represent more than two-thirds of Bermuda's history, as known from surface rocks, for which there is no vertebrate fossil record. The BRS is capped here by eolianites of the Lower Town Hill Formation (Marine Isotope Stage 11).

Fig. 3. *Cantó NE de la Pedrera de Wilkinson on es mostra la "gran terra vermella" (BRS) que cobreix i reompl les cavitats càrstiques a les calcàries recristal·litzades de la Formació Walsingham. Aquestes dues unitats representen més de dos terços de la història de Bermuda, com se sap a partir de les roques superficials, pels quals no hi ha registre fòssil de vertebrats. La BRS està aquí coberta per eolianites de la Formació Lower Town Hill (estadi isotòpic marí 11).*

level and the small vertebrate faunule known from Calonectris Quarry dates from this inundation (Olson & Hearty, 2003).

We know nothing about the fauna of the succeeding glacial period MIS 10, which would be of extreme interest for determining what vertebrates may have colonized the island during its first expansion following the great MIS 11 inundation.

We know almost as little about the vertebrates of interglacial MIS 9, represented by the Upper Town Hill Fm eolianites. Although snails of this age are known, the only knowledge of vertebrates has come about through the extraordinary discovery of a single fossil tortoise in rocks of this age (see Tortoise Site below). MIS 11 was certainly an extinction event on Bermuda through reduction of land area and alteration of habitat by radical sea-level rise. MIS 9 also probably represents an extinction event if the tortoise is any example.

Following this were two glacial cycles MIS 8 and MIS 6 separated by a less important interglacial MIS 7 that, according to the revised stratigraphy of Hearty (2002), deposited little or no carbonate sand on the present land surface of the island. Thus there may have been a relatively long interval from about 250 kya to 120 kya during which land area may have been sufficiently stable such that the Bermudan biota was not adversely affected. We now know that the so-called "crane fauna" (Olson & Wingate, 2000) dates to glacial period MIS 6 (Hearty *et al.*, 2004) and this fauna may have started to develop as early as MIS 8, though we do not know for certain of any cave or fissure fills dating back to MIS 7 or 8. Deposits of "crane fauna" in association with the large snail *Poecilozonites nelsoni* are known only from fissures in Government and Wilkinson's quarries and possibly Fern Sink and Jane's caves.

The onset of the last interglacial MIS 5e is represented by extensive carbonate deposition and an abundance of the snail *Poecilozonites bermudensis zonatus*. A few fissure fills date to this period, for example Gould's (1969: 511) "Graveyard Fissure" (see Hearty *et al.*, 2004) and a remnant in Convolvulus Cave, but the only deposit of this age with vertebrate remains is the massive talus cone in Admirals Cave (Hearty *et al.*, 2004). MIS 5 was also an extinction event on Bermuda that terminated the "crane fauna," as those species are absent in Admirals Cave with the exception of a few bones of *Rallus ibycus* at the very beginning of the sequence at the onset of MIS 5e.

The last glacial period MIS 4-2, characterized by the "re-appearance" of *P. nelsoni* and the appearance of a large flightless rail *Rallus recessus* (Olson & Wingate, 2001) is well represented in fissure fills in quarries and in Admirals and other caves.

The Holocene interglacial period MIS 1 appears to have caused the disappearance of *Rallus recessus* and at this time *P. nelsoni* was succeeded by *P. bermudensis bermudensis.* Holocene deposits with vertebrates occur in several caves, often as a thin veneer unconformably overlying older sediments. Holocene vertebrates are abundantly represented in the lacustrine sediments dredged from Spittal Pond and sparsely in near-surface deposits on Cockroach Island, Harrington Sound.

Thus although Bermuda has relatively a very good and highly interesting record of fossil vertebrates, there are many gaps and much that we do not know. There is nothing known about glacial age faunas older than MIS 8 and it is not certain that deposits of such age even exist. If they do they will probably only be found by additional quarrying or by underwater exploration.

HISTORY OF VERTEBRATE PALEONTOLOGY ON BERMUDA

The first mention of vertebrate fossils from Bermuda appears to be that of Nelson (1837: 113), who mentioned "birds' bones" found in a cave on Ireland Island (the northern tip of the west end of Bermuda), bones and eggs of birds "in the limestone on the coast of Harrington Sound," and an egg "found in a block of limestone near Hamilton". "Turtle bones," presumably sea turtle "were also procured from the North Bastion [Ireland Island] coral rag, and from the sands at Elbow Bay."

The next mention of vertebrate fossils concerns remains reputed to be of what was then the mysterious "cahow" of early settlers. Until the living bird (*Pterodroma cahow*) was "rediscovered" in 1906 (Nichols & Mowbray, 1916), the identity of this bird was very much in doubt and a considerable amount of speculative literature was devoted to the subject. Verrill (1908) reported on bones and even feathers embedded in a stalactite found in a cave by Louis L. Mowbray, who reported that the bones could be easily distinguished from those of the shearwater *Puffinus obscurus* (= *P. lherminieri*) and must therefore belong to the "Cahow", even though the generic affinity of the latter remained at that point undetermined. The location of the cave, said to have been discovered only a few months before Mowbray's communication of 15 March 1908, was undisclosed. Shufeldt (1916: 626) later reported that Mowbray had collected this material in Crystal Cave in 1907. He also said that Mowbray had collected in Bassett's Cave (see below) a "perfect skull and beak of Strickland's Shearwater (*P. stricklandi*), the specimen being covered with calcite."

Shufeldt (1916, 1922) reported extensively on seabird bones recovered in various Bermuda caves by Edward McGall and Anthony Tall about 1915. No mention is made of the location of these caves apart from the fact that some of them were sea caves in cliffs that had to be reached using ropes—-a description that would perfectly fit caves exposed in the Great Head cliffs of St. David's Island. Most of this material is now in the Carnegie Museum, Pittsburgh, and has been restudied in connection with a revision of Shufeldt's taxonomy (Olson, in press).

Considerable interest once attached to multiple discoveries of fossilized bird eggshell in eolianite deposits of Bermuda (Wood, 1923; Lewis, 1928), although no specific localities were given for any of these. Most of these eggs were about 63 x 38 mm in size (Wood, 1923: 207) and it was speculated that they might be eggs of White-tailed Tropicbird *Phaethon lepturus.* Because of the cliff-nesting habits of tropicbirds, their bones are very rarely preserved in Bermuda or elsewhere (e.g. St. Helena, Olson, 1975), and it would be even more unlikely for their eggs to be preserved. It is far more likely that these were eggs of Cahow *Pterodroma cahow,* formerly the most abundant bird in Bermuda, which nested in burrows and cavities throughout the island. Eggs of the Cahow range from about 56-62 mm long by 41-44 mm in diameter (Wingate in Palmer, 1962, and unpublished data), whereas eggs of Bermuda *Phaethon lepturus* average smaller—-49-58 x 36-41 mm (Lee & Walsch-McGehee, 1998).

Of much greater interest is an egg, deposited in the British Museum (A841a), that Wood (1923: 207) considered likely to be "chelonian" that measured 79 X 48 mm (converted from inches). Data with the specimen indicate that it was presented by W. Young on 14 Oct 1903 and was said to be from the"?Paget limestones" in a "consolidated beach about 40 feet above sea level." Wood (1923: 207) reported that the fossil was "found several feet beneath the deep red, clayey soil that covered the limestone rock in which it was imbedded." What used to be called the Paget Formation is equivalent to aeolianites of the last interglacial (MIS 5). Wood's photograph of the specimen (plate IX, figure 5) shows fairly large pieces of limestone still attached so that analyses of lithology and amino acid racemization should make a more accurate determination of age possible.

Wood's speculation as to the origin of this egg is surely wrong given that sea-turtle eggs are spherical and soft-shelled. The egg is much too small for the Short-tailed Albatross *Phoebastria albatrus,* fossilized eggs of which have been found in Bermuda (Olson and Hearty 2003), but is otherwise much too large for any other seabird known from Bermuda or for the endemic night-heron *Nyctanassa* sp., which was not significantly different in size from the Yellow-crowned Night-heron *N. violacea* (average egg size 51 X 37 mm—-Watts, 1995). Another possibility is that this might be the egg of the endemic crane *Grus latipes* (Wetmore 1960) which is known only from fissure fills that are now thought to date back to two glacial periods ago (MIS 6, Hearty et al. 2004). The measurements of the fossil egg would barely fall within those of the Sandhill Crane *Grus canadensis,* the minimum dimensions of which are 77.4 and 44 mm (Bent 1926: 235). How the egg of a crane would have been incorporated into interglacial eolianites is rather problematic, as sufficient suitable habitat for cranes would probably only have been available during glacial episodes. If the egg is truly that of a crane it would probably date from earliest stages of the last interglacial episode.

Beebe (1935: 190) mentioned and illustrated fossil and "semi-fossil" bones of Cahow from unspecified caves and roadcuts.

In 1956, a fissure that had been opened in Wilkinson Quarry was found to contain bones of extinct birds. More material was collected here in 1958 by Wingate and subsequently an extinct species of duck *Anas pachysceles* and a crane *Baeopteryx* (=*Grus*) *latipes* were described by Wetmore (1960), who also mentioned the presence of undescribed species of rails (Rallidae). Practically simultaneously, several fossiliferous fissures were encountered in Government Quarry and abundant material was recovered here in 1960 by Wingate along with avian paleontologist Pierce Brodkorb of the University of Florida. Brodkorb kept this material, which included excellent representation of 3 new species of rails, in his private collection but despite considerable prodding (e.g. Olson, 1977: 353-354) he never published on any fossils from Bermuda. After his death, the material was incorporated into the paleontological collections of the Florida Museum of Natural History. Information on the morphology and relationships of the largest of the rails was incorporated into a systematic revision (Olson, 1997) prior to the naming of the species as *Rallus recessus* (Olson & Wingate, 2001). Two smaller, and older, species of rails *Rallus ibycus* and *Porzana piercei* (Olson & Wingate, 2000) were also named from the former Brodkorb material.

Meanwhile, Wingate had been accumulating specimens and knowledge of new and potential fossil localities around the island. Olson and Robert F. Baird collected specimens from several of these sites in Jul and Aug 1981. In Aug 1984, Olson and Grady continued collecting, particularly at Green Island and Calonectris Quarry. Olson made additional collections in 1985. Publication on the fossils collected was delayed, however, because of considerable uncertainty regarding the ages of the various fossil deposits. Problems with stratigraphy and chronology of Bermudan vertebrates began to be resolved when Olson and Hearty started collaborative fieldwork with Wingate in Feb and Jul 1999. Olson and Hearty's excavation of Admirals Cave in Oct 2000 provided the Rosetta Stone for understanding the last 120 kya of Bermuda's biotic history (Hearty *et al.*, 2004). They continued to make further refinements and collections, emphasizing the chronology of *Poecilozonites* land snails in Feb 2002. In Nov 2003 Olson, Hearty, and Grady continued fieldwork, making more extensive excavations in Admirals Cave. In Feb 2004, Olson, Grady, and Wingate surveyed almost all the caves and quarries known to have produced fossil vertebrates and in most recovered as much additional material as possible. Olson revisited Fern Sink Cave in April 2004.

The fieldwork and publications to date (Wetmore, 1960; 1962; Olson & Wingate, 2000; 2001; Olson & Hearty, 2003; Hearty *et al.*, 2004; Olson, 2004a,b) have set the stage for a full exposition of the known history of Bermuda's vertebrate biota, including the descriptions of new species. To facilitate future publications we briefly summarize below the general information for all of the fossil vertebrate localities found so far in Bermuda.

FOSSIL VERTEBRATE LOCALITIES OF BERMUDA

Geographical coordinates for most sites, to tenths of a second, were determined by Olson and Grady using a global positioning system (GPS) in Feb 2004. Others are from the United States Board of Geographical Names gazetteer for Bermuda (USBGN 1955). By far the majority of the sites containing significant specimens of fossil vertebrates come from the strip of land forming the northeastern edge of the main island of Bermuda, along the SW shore of Castle Harbour (Figure 4). All sites listed below are in Hamilton Parish unless otherwise indicated. Cave names are from the unpublished Bermuda Cave Survey (1st edition, 22 February 1983) by Thomas M. Iliffe, copies of which have been deposited with the Bermuda Aquarium, Museum and Zoo (BAMZ) and the Bermuda Biological Station for Research.

a) Deposits in Interglacial Eolianites

1. *Green Island.*—-N32°20' W64°39' (USBGN). Also known as Green Rock. Situated just SE of Nonsuch Island at the mouth of Castle Harbour. Many bones of Short-tailed Albatross *Phoebastria albatrus* occur here in rocks of the Lower Town Hill Formation (MIS 11, ca. 400 kya). These represent the remains of a breeding colony and include individuals of all ages from near embryos to adults. The fossils were buried in a back beach storm deposit. The site has been fully described by Olson & Hearty (2003). Most of the specimens were collected in 1984 by Olson and Grady, using a gas-powered rock saw. The only other vertebrate remains found here were a few fish bones (Olson & Hearty, 2003), several bones of the endemic skink *Eumeces longirostris*, and the tip of a rostrum of a Great Auk *Pinguinus impennis* (Olson, 2004a). Recent bones of *Puffinus lherminieri*, which nested here until the mid 20th century but is now extirpated on Bermuda, were collected here by Wingate in 1967.

2. *Cooper's Island.*—- N32°21' W64°39' (USBGN). Fossilized eggs of Short-tailed Albatross *Phoebastria albatrus* have been found on both the north and south sides of the island in a continuation of the same deposits with albatross bones on Green Island (Olson & Hearty, 2003).

3. *Tucker's Bay.*— N32°19'34.3" W64°44'23.7". Fossil eggs of Short-tailed Albatross *Phoebastria albatrus* were collected in the vicinity of Tucker's Bay (specimens labelled Vesey's Bay), referring to the extreme SW corner of Harrington Sound, by Charles Lloyd Tucker in 1936 and subsequently. Three of them are in the collections of BAMZ. Olson and Wingate visited the property in 2004 and took the above GPS reading but very little rock is still exposed. Limestones here are mapped as the Lower Town Hill Formation (Vacher *et al.*, 1989), which would correspond to the age of the albatross deposits in which other eggs were found (Olson & Hearty, 2003). Wingate interviewed Tucker on 27 Oct 1960 at his property on the day after he had found another egg. He related that he had found about 30 eggs there in less than an acre (0.4 hectare) over his lifetime. Wingate's diary records a measurement for one of them as 4 3/8 X 2 7/8 inches (= 111 X 72 mm), a value very close to the mean reported for Short-tailed Albatross by Olson & Hearty (2003).

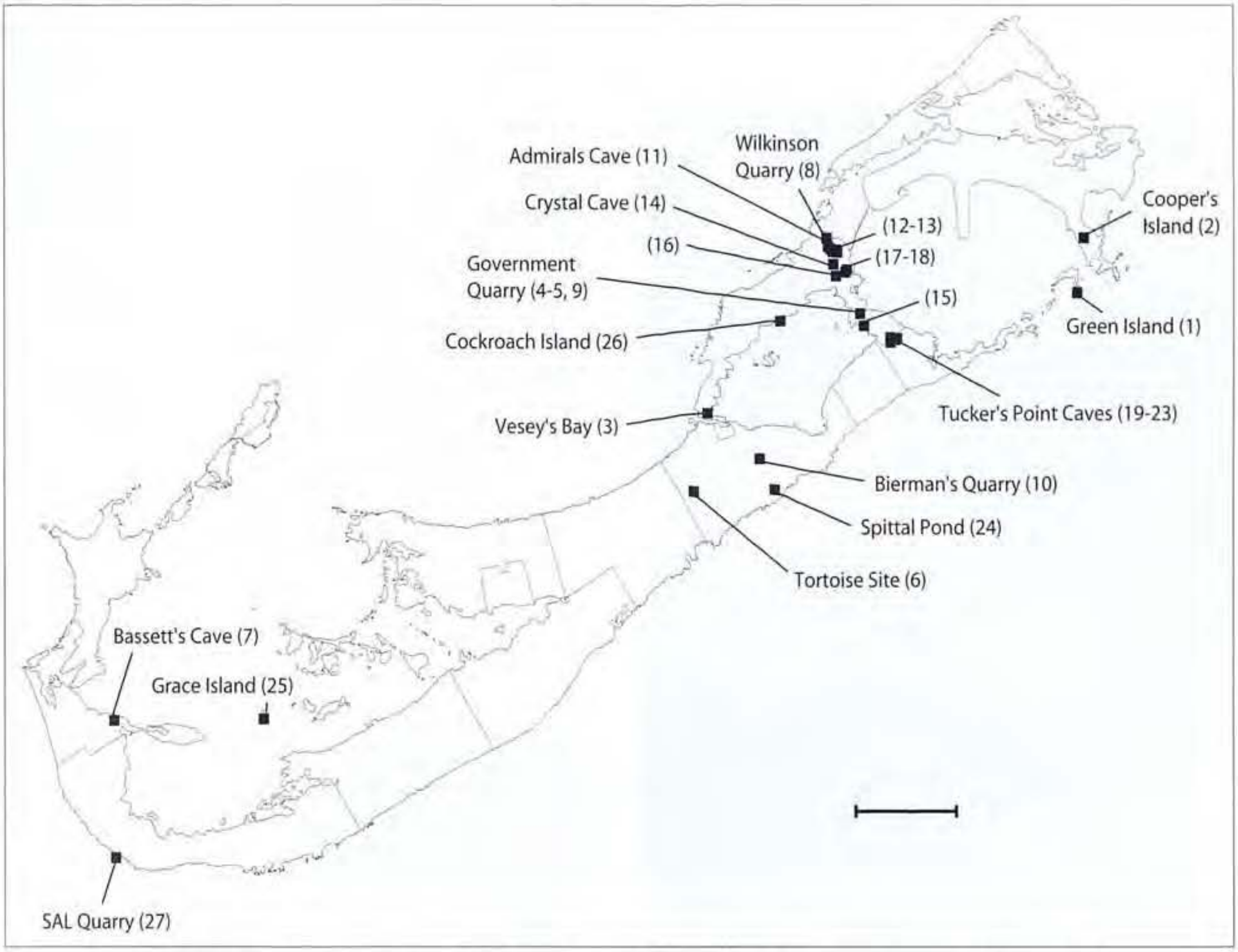


Fig. 4. Map of Bermuda showing known fossil localities. Numbers correspond to the site numbers used in the text. Scale = 2 km.

Fig. 4. Mapa de Bermuda on es mostren les localitats fòssils conegudes. Els nombres corresponen als nombres de les localitats emprats al text.

4. *Calonectris Quarry.*—-N32°20'28.3" W64°42'27.4". Located at the NW extreme of Government Quarry (q.v.), this important site consisted of a beach deposit that formed in a horizontal unconformity between the Walsingham Formation and the overlying Lower Town Hill Formation (Fig. 5). Fossils here consisted mainly of bones of the shearwater *Calonectris diomedea diomedea*, but also included skink, other seabirds, at least 2 species of passerines, and a bat. These were deposited at an elevation of 21.3 m above present sea-level in the maximum rise of interglacial MIS 11, about 400 kya ago (Hearty *et al.*, 1999; Olson & Hearty, 2003), when the land area of Bermuda was at its all-time minimum. Wingate first collected here in Nov 1967, followed by some combination of Olson, Wingate, Grady, and R. Baird in Aug 1981, Aug 1984, and Feb 1985. This site and its fauna will be the subject of a more detailed future publication.

5. *Dead End Cave.*—This is on the SW wall of the northwesternmost extent of Government Quarry probably no more than 10 m directly through the limestone from Calonectris Quarry. It is a sea-cave with deposits of the same age and elevation as Calonectris Quarry (Hearty *et al.*, 1999). It was discovered by Wingate and first investigated by Hearty in 1997 and by Hearty and Olson in Feb 1999. The only vertebrate remains were a few heavily encrusted bones of seabirds.

6. *Tortoise Site.*—- N32°18'40.3" W64°44'36.2". Smiths Parish, 3 Verdmont Valley Close off Verdmont Valley Drive. The holotype of the fossil tortoise *Hesperotestudo bermudae* was collected here in Aug 1991 from a foundation wall that had been excavated in deposits of the Upper Town Hill Formation (Meylan & Sterrer, 2000). This is the only vertebrate fossil yet known from the Upper Town Hill (MIS 9, ca. 310 kya old).

b) Caves and Fissure Fills

7. *Bassett's Cave.*—- Ca. 1 km slightly N of W of the former Tucker's Island (N32°16' W64° 51' U. S Board on Geographic Names [USBGN]) in Sandy's Parish in far western Bermuda. The cave is shown on Vacher *et al.*, (1989) as being in rocks of the Lower Town Hill Formation (MIS 11). Shufeldt (1916: 626) reported that Mowbray had collected in Bassett's Cave a "perfect skull and beak of Strickland's Shearwater (*P. stricklandi*), the specimen being covered with calcite." *Puffinus stricklandi* is a synonym of *P. griseus*, a species unlikely to be found in a cave deposit in Bermuda. The only species of Procellariidae close to this size that has been found as a fossil on Bermuda is *Calonectris diomedea*, known only from Calonectris Quarry in deposits of Lower Town Hill age. Because Bassett's Cave itself would have to be

Fig. 5. The Calonectris Quarry site (at the level of Olson's shoulders) as it appeared in 1981 (it has since been quarried away). Sea level rose to this height (21.3 m above present) during MIS 11. Inset: close-up of the two pockets of Calonectris Quarry excavated in 1981. In both photographs notice the unconformity between the homogeneous limestone of the Walsingham Fm (extending higher on the right) and the overlying, distinctly cross-bedded eolianite of the Lower Town Hill Fm. Dead End Cave is at the same level directly through the wall of the quarry shown here.

Fig. 5. *La localitat de la Pedrera Calonectris (al nivell de les espatlles d'Olson) com es trobava el 1981 (des de llavors la pedrera s'ha continuat explotant). El nivell de la mar va arribar a aquesta altària (21,3 m per damunt de l'actual) durant l'estadi isotòpic marí 11. Quadre inserit: visió de prop de dues borses de la Pedrera Calonectris excavades el 1981. A les dues fotografies es nota la disconformitat entre les calcàries homogènies de la Formació Walsingham (que s'estenen més adalt a la dreta) i la clara laminació encreuada de les eolianites de la Formació Lower Town Hill que s'hi sobreposa. La cova Dead End es troba al mateix nivell directament a través de la paret de la pedrera que es mostra aquí.*

younger than this, the identity of the procellariid skull that Mowbray found here becomes highly problematic. Most likely it was the skull of a Cahow made to seem larger by its encrustation of flowstone. Bassett's Cave was massively polluted with aviation fuel and heavy metals from a U. S. military installation prior to 1995 (Kent, 2004) and we made no attempt to explore it for fossils.

8. *Wilkinson Quarry.*— Located on the S shore of the NW corner of Castle Harbour, the quarry now extends landward nearly as far as Admirals Cave. Several fissures of different ages exposed in this quarry have yielded important fossils of vertebrates and snails.

Original fissure.— This is the site of the original fossil material studied by Wetmore (1960) from which he named *Baeopteryx* (=*Grus*) *latipes* and *Anas pachysceles*. This fauna also contained the rails *Rallus ibycus* and *Porzana piercei* that were described later (Olson & Wingate, 2000). The first fossil birds collected here were obtained by David Nicol in 1956, and more extensive material was obtained in 1958 by Wingate, all of which is now in the National Museum of Natural History, Smithsonian Institution, Washington (USNM). This early material came from a fissure in the NE part of the quarry in the vicinity of site UWQ 8 (see below).

Site UWQ 1. N32°21'08.9" W64°42'52.2". On 15 Feb 1999, Olson and Hearty found that a large fissure in Lower Town Hill (MIS 11) limestone about 6-8 m deep and ca. 0.5 m wide at the widest point had been exposed in the middle of the E side of the quarry (Fig. 6). This was filled with reddish-brown (5-7.5YR 3.5/4 Munsell, 1994) soil and contained abundant shells of *Poecilozonites nelsoni* and bones of *Rallus recessus*, as well as those of other species of birds. On 17 Feb Olson and Wingate removed about 0.5 m^3 of sediment from this fissure that was later processed to recover small bones and snails. This fissure was determined to be of last glacial age: 29,510 ±210 ^{14}C yr BP (Hearty *et al.*, 2004).

Site UWQ 8. N32°21'13.9" W64°42'53.2". This smaller fissure (Fig. 7), in the Walsingham Formation, was found on the N side of the quarry by Olson and Hearty on 10 Nov 2003 and collected by them and Grady on several subsequent days. It was mostly open at the top and was then blocked by a slanting piece of flowstone. Beneath this was a column of red soil the main portion of which was about 95 cm high by 45 cm wide, with a narrow pocket extending about 65 cm higher on one side. Rock rubble and flowstone effectively divided the main sediment accumulation into upper and lower units. This sediment contained heavily mineralized shells of land snails and a few bones of a rail and passerine birds. Beneath the sediment was an opening ca. 40 cm high completely rimmed with flowstone and with small stalactites pendant from the ceiling. These had a U/Th date of 55.2 ± 0.9 ka. The bottom of this opening was a thick layer of pure yellowish calcite flowstone at the same level as the present floor of the quarry. This had a U/Th date of 62.9 ± 1.5 ka. We were able to break through this to reach a small amount of additional red soil with remains of snails. Thus this deposit appears to have formed during the last glacial period MIS 4 but is considerably older than UWQ 1.

9. *Government Quarry.*—Bermuda's largest quarry occupies much of the SE portion of the isthmus between Harrington Sound and Castle Harbor. The main part of the quarry is just to the E of Calonectris Quarry, which was in the westernmost portion of the larger quarry. Over the years many caves and fissures were opened here, most of which have since been quarried away, although their approximate location has been determined by reference to the 1960 topographical survey map. With the exception of Calonectris Quarry and Dead End Cave, these contain deposits dating from the last glacial (MIS 4), the last interglacial (MIS 5), and the preceding glacial period (MIS 6 or possibly MIS 8-6). Specimens from these deposits have been given the following 6 label designations.

Crane Crevice.—-SE face of Government Quarry. Material collected in 1960 by Wingate and Pierce Brodkorb in USNM and Florida Museum of Natural History (UF). The presence of *Anas pachyscelus, Grus latipes*, and *Rallus ibycus* indicate deposition no younger than glacial MIS 6, although this fauna could possibly have existed from MIS 8 through 6. Material in USNM collected by Howard Wilson labeled "South Face fissure fill" is probably the same as Crane Crevice. This includes bones of seabirds, a dove, a small rail, and passerines but no certain index species to suggest the age of deposition.

Rail Cave.—-W face of S half of quarry. Material collected in 1960 by Wingate and Pierce Brodkorb in USNM and UF. The presence of *Rallus recessus* indicates deposition during the last glacial period MIS 4. Specimens are marked as coming from "lowest level" and "upper shelf". The lowest level was very clearly an original solution tube created by a former underground stream, the only such feature found so far during subaerial cave exploration on Bermuda, as secondary roof collapse has destroyed or buried the original solution features in other caves. All of the bones were found in mud-filled swirl pits on the floor of the cave and one fully articulated skeleton of *Rallus recessus* was found here cemented in place by a patina of flowstone (Fig. 8).

Finch Cave.—-S face of S half of Government Quarry about 100 m W of Crane Crevice. Material in USNM collected by Wingate. Named for the presence of abundant remains of an as yet undescribed endemic species of towhee *Pipilo*, many of which are heavily encrusted with calcite. The presence of some bones apparently referable to *Rallus ibycus* suggests that this deposit was contemporaneous with the "Crane Fauna" of Olson & Wingate (2000).

Wilson's Cave.—-Material at UF is so labeled. Additional specimens in USNM collected by Howard Wilson and labeled "Southeast Face fissure fill" indicating the SE face of Government Quarry is believed to be from the same site. This includes bones of passerines and a bat.

Fissure fill, upper level, Government Quarry.—-Material in USNM was collected in August 1981 by Robert Baird, with a second batch dated 19 August. Estimated to be 12 to 15 ka, based on calibrated amino acid ratios from *Poecilozonites nelsoni*. Contains skink, seabirds, rail, dove, and passerines.

1985 Fissure, Government Quarry.—-E end of S working face. Vertical fissure with red soil and snails and bones. Material in USNM was collected by Olson 15 Feb 1985. Estimated to be 12 to 15 ka, based on calibrated amino acid ratios from *Poecilozonites nelsoni*, which is corroborated by a humerus of *Rallus recessus*. There are also two bones of a small heron, possibly *Butorides*.

10. *Biermans Quarry*.— N32°19'00.5" W64°43'45.3". Located in Smiths Parish, south of Harrington Sound, this quarry is in rocks of the Upper Town Hill and Lower Town Hill formations (MIS 9 and 11, respectively), rather than in the older Walsingham Formation being mined at Wilkinson and Government quarries. On the currently disused NE wall of the quarry (coordinates above) there is a well-developed red soil between the two formations that probably represents the MIS 10 glacial period, but unfortunately this contains no identifiable fossils. We have not seen any crevices or fissures in this quarry, and although it has produced important collections of land snails, only one collection of vertebrate remains has so far been found. A small lot of bird bones at USNM collected by Patricia Corrado for a school project and later obtained by Wingate was defintely collected in Biermans Quarry, where Corrado's father worked, but the exact locality was never determined. This collection consists of bones of *Anas pachysceles* and *Rallus ibycus*, species that occurred during glacial period MIS 6 (and perhaps in MIS 7-8).

11. *Admirals Cave*.—-Entrance N32°21'07.4" W64°42'50.6"; the current opening in the area of the talus cone is at N32°21'05.6" W64°42'48.6", which as calculated by GPS would be 80 m SE (137°) of the entrance. This is the most important fossil site in Bermuda (Hearty et al., 2004), containing a massive talus cone of beautifully stratified sediment and fossils with nearly continuous deposition over the past 120 kya (Fig. 9). The position of the talus cone in the cave has been well mapped by Iliffe (2003) and the stratigraphy and chronology documented

Fig. 6. E wall of Wilkinson Quarry, site UWQ 1. The red soil of the fissure fill dates back to the height of the last glaciation and contains abundant shells of *Poecilozonites nelsoni* and bones of the extinct flightless rail *Rallus recessus*, as well as other birds.

Fig. 6. *Paret E de la Pedrera Wilkinson, localitat UWQ 1. La terra vermella del reblit del crull data del punt alt de la darrera glaciació i conté escopinyes abundants de* Poecilozonites nelsoni *i ossos del rascló avolador extingit* Rallus recessus, *i d'altres ocells.*

in detail by Hearty et al., (2004). Fossils were collected here desultorily in the 1980s. Serious excavation of a test trench and small bulk samples of sediment was undertaken by Olson and Hearty in Oct 2000. Olson, Hearty, and Grady extended this trench in Nov 2003, taking out larger bulk samples for screening elsewhere amounting to perhaps a little over one cubic meter. Olson and Grady obtained additional fossils here in Feb 2004.

West wall red talus, Admirals Cave.—High up on the west wall of the main chamber in Admirals Cave is a thick talus slope of red soil ca. 4.5 m from top to bottom and 4.7 m wide at the base. It is 30-40 cm deep at the sides and deeper toward the middle. On the map in Iliffe (2003: 219) it is in the small chamber just north of the one labelled "Chamber of Innocence." Excavations made 14 and 16 Nov 2003 by Olson and Grady yielded abundant remains of land crab, some charcoal, and very few bones. Shells of *Poecilozonites bermudensis* were uncommon in the upper portions, those of *P. nelsoni* were occasional at mid-level and more common at the bottom. Thus it appears, despite the absence of any distinct strata in the soil, that deposition here probably represents mid- to late Holocene unconformably overlying sediments of the last glacial maximum such as observed in Walsingham Sink Cave.

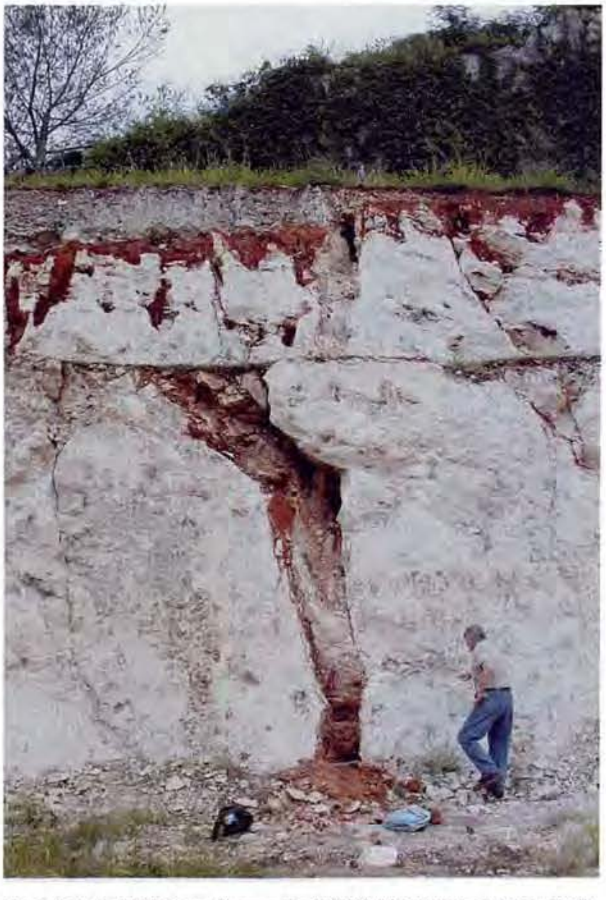


Fig. 7. N wall of Wilkinson Quarry, site UWQ 8. This fissure contains shells of *Poecilozonites* that must be older than MIS 6 and may be the oldest fissure filling yet found on the island. A few bones of an extinct rail similar to *Rallus ibycus* and passerine birds were collected here in 2003.

Fig. 7. *Paret N de la Pedrera Wilkinson, localitat UWQ 8. Aquest crull conté copinyes de* Poecilozonites *que indiquen que ha de ser més primerenc que l'estadi isotòpic marí 6, i pot ser el reompliment més primerenc trobat a l'illa. El 2003 es varen recollir aquí uns pocs ossos d'un rascló similar a* Rallus ibycus.

12. *Convolvulus Cave.*—Entrance N32°21'06.5" W64°42'45.8"; position approximately over SE talus slope N32°21'05.4" W64°42'45.0". By GPS calculation the SE talus slope would be 40 m approximately SSE (148°) of the entrance. This cave is near the entrance to the present Grotto Bay Hotel and has also been known as Bourne's Quarry Cave and Grotto Cave (Hearty et al., 2004: fig. 2) but the name Convolvulus Cave has been in use at least since 1873 when visited and photographed by scientists of the Challenger Expedition (Wyville Thompson, 1878: 302). There are two or three perimeter entrances that all eventually open into a large sinkhole formed by complete collapse of the former cave roof. On the SE wall of this sink may be seen a patch of thick veneer of indurated red soil packed with myriad shells of *Poecilozonites bermudensis zonatus* indicative of a soil accumulation during the last interglacial (MIS 5) that has now mostly been removed, presumably by roof collapse and erosion. The cave system continues off to the SE ending in a chamber with a long sloping cone of red soil talus.

Bones were collected from this cave by Wingate in 1961, and from the surface of the lower part of the SE red talus slope on 29 Aug 1981 by Olson, Wingate, and Robert Baird. Olson and Grady sampled extensively here on 10 Feb (with Wingate) and on 11 and 14 Feb 2004. Bones came from 3 areas: a small cave chamber (Toad Pocket) off the shallow sink at the entrance to the cave; a deposit of red soil encountered just before emerging into the large sink opening at mid-cave; and the SE talus cone.

The SE talus of red soil is a triangular slope about 4 m long and fanning out to about 4 m wide at the bottom, the soil having come in through another small entrance that now appears to be blocked. The cone was well stratified at least in the upper portions. A section ca. 1.5 m from the apex consisted of 3 cm of granular, almost pebbly, soil the bottom 1 cm of which was paler in color. Beneath this was 4-5 cm of similar soil, also lighter in color at the bottom. Beneath this was a 5-6 cm layer of darker soil with masses of large pieces of charcoal and abundant shells of land snails, including *P. b. bermudensis*. This overlay 2 cm of fine soil of lighter color, which in turn lay above 10 cm of very granular red soil with abundant snail shells and fragments but much less charcoal. Below this was a thick layer of undetermined depth of sterile granular red soil. Bird bones were scarce in the two levels with abundant snail shells. Taxa of birds recovered from Convolvulus Cave include seabirds, *Aegolius* sp., Picidae, and various passerines.

13. *Sibley's Cave.*—N32°21'06.7" W64°42'46.4". Shown as Old Muddy Cave in Hearty et al. (2004: fig. 2). This is a high, relatively narrow passageway that descends rather steeply but ends in rubble without going to the water table. It contained only small patches of dry sediment here and there. Loose soil in the uppermost one of these, in a bowl-like depression about a meter across, was nearly entirely removed by Olson and Grady and washed elsewhere in an unsuccessful attempt to find more bone that might go with a complete cranium of the endemic night-heron *Nyctanassa* found here. Two

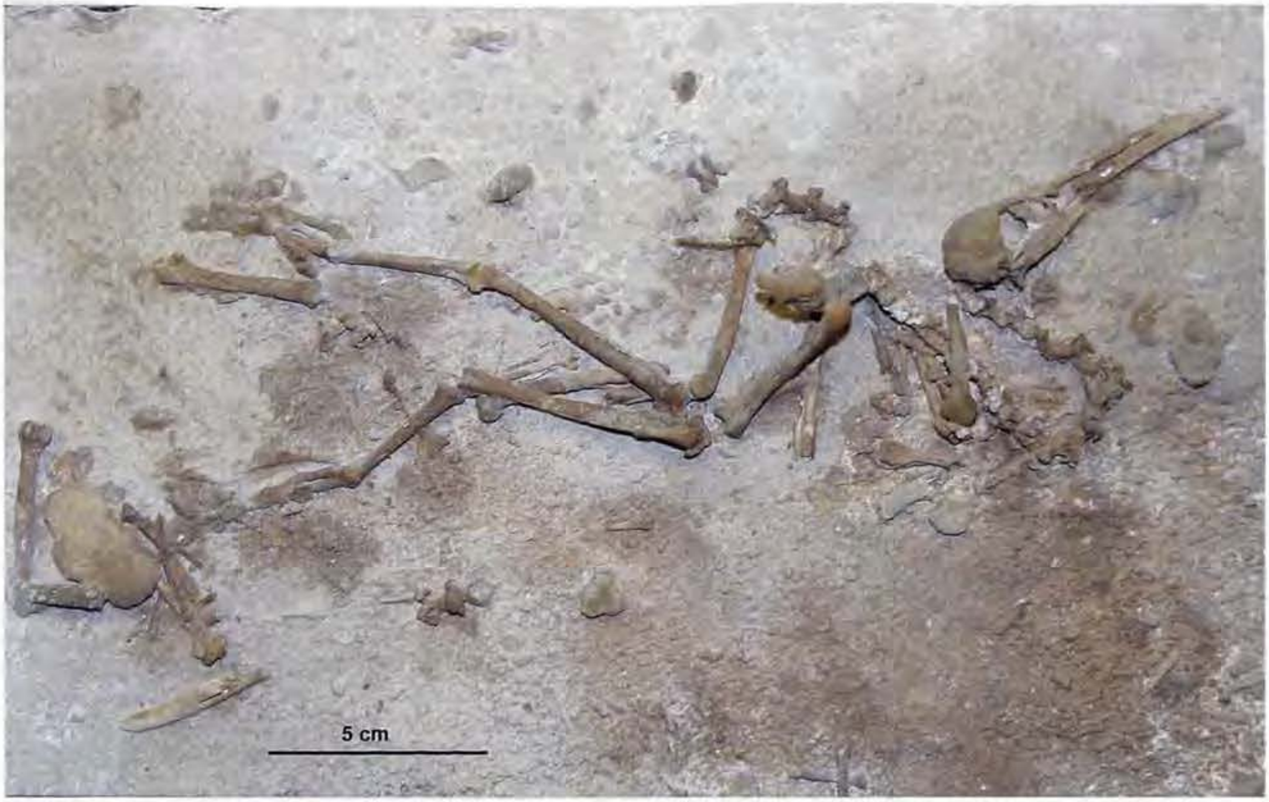


Fig. 8. Associated incomplete skeleton of *Rallus recessus* (BAMZ 2000 190 001) covered with flowstone, from Rail Cave, Government Quarry.

Fig. 8. Esquelet incomplet associat de Rallus recessus *(BAMZ 2000 190 001) cobert per una colada, provinent de la cova Rail, Pedrera Government.*

bones of a hawk were found in the lower sediments. Material in USNM was collected by surface picking by Olson, Wingate, T. Illife and R. Baird on 19 Aug 1981; sediments were excavated and more bones collected by Olson and Grady on 12-14 Feb 2004.

14. *Crystal Cave.*—-Entrance N32°20'58.1" W64°42'48.1". Now a highly commercialized cave system that we have not investigated, this is where L. L. Mowbray obtained a number of the seabird bones studied later by Shufeldt (1916; 1922). In the USNM collections there is a complete mandible of *Aegolius* sp. labelled "Crystal Cave bone deposits" that was collected by the naturalist William Beebe in 1930. In 1935, the specimen was forwarded by Robert Cushman Murphy to Alexander Wetmore who decided he could not distinguish it from *Aegolius acadicus.*

15. *Devil's Sinkhole.*—-N32°20'20.9" W64°42'24.5". Located less than 10 m from Harrington Sound Road, just W of Government Quarry, the entrance is a relatively small opening in the Lower Town Hill Formation that drops precipitously over 12 m, so that access was only by means of two extension ladders lashed together, leading to a large cavern with large boulders of roof fall. Very well-preserved bird bones, often partial or nearly complete associated skeletons, occurred here in the interstices of boulders, usually in deep pockets of yellowish-white disintegrated limestone. Specimens were collected in August 1981 by Robert Baird, assisted later by Olson and Wingate; and again by Baird in January 1982 The avifauna consisted almost entirely of many individuals of *Pterodroma cahow* and *Puffinus parvus,* but also included one partial associated skeleton of the endemic night heron *Nyctanassa* sp.

16. *Fern Sink Cave.*—-Also known as Grand Canyon Cave (Hearty et al., 2004: fig. 5). Ca. 200 m NE of N32°20'50.9" W64°42'46.0". This cave system is entered through a great fault cleft in the Walsingham limestone that extends to the water table. In the subterranean part, on the SW side there is an extensive, steeply inclined, deposit of red soil talus. Parts of this have experienced sheetwash that has created occasional erosional cavities in places. The deposits consist of a thin surface veneer of Holocene sediments and fossils, as evidenced by shells typical of modern-type *Poecilozonites bermudensis* along with bird bones, overlying a glacial soil as indicated by the presence of shells of *P. nelsoni.* Most of the bird bones from here appear to belong to an undescribed species of small gallinule (*Gallinula*). These fossils occur below a zone about 5 cm thick of sterile, apparently leached sediment. The above-mentioned erosional cavities are in the glacial-age soil but may be lined with well-embedded shells of *P. bermudensis* from the overlying Holocene. Because of the sheetwash, the unconformity here is probably an erosional one that has removed the early Holocene, although the deposits in Walsingham Sink Cave and the W wall red talus of Admirals Cave suggest that the glacial/Holocene transition may have been a period of little deposition anyway. Charcoal from the lower level containing gallinule bones gave a radiocarbon date of 20,080 ± 110 ybp (Beta 192239).

Fossils were collected from the surface on 24 Feb 1979 by Wingate and T. Iliffe and mainly from the surface on 13 Feb 2002 by Olson, Hearty, and Wingate. On 11 Feb 2004 Olson and Grady collected surface samples and dug into the underlying glacial-age level in which fossils were rather heavily encrusted with calcite, as opposed to the Holocene bones, which were relatively clean. Olson collected additional samples here on 30 Apr and 3 May 2004. In addition to bones of seabirds, passerines, and the presumed gallinule, were two bones of the endemic night heron *Nyctanassa* sp., a tarsometatarus of *Aegolius*, and a partial tibiotarsus of a hawk.

17. *Walsingham Cave.*—Main entrance N32°20'54.7" W64°42'37.7". This was once a popular recreational cave, with a relatively deep pool of blue water open to the light at the entrance with concrete steps for bathers. By leaving the path by the pool and going NE over a boulder field one passes another entrance called Bee Pit Cave on the cave survey although it is completely continuous with Walsingham Cave. This leads to a separate chamber leading back down to water. On the map in Richards (2003: 215) this is the slope indicated above the isolated pool shown in the passageway going off to the SW of the main chamber. Here on 17 Feb 2004 Olson and Grady excavated bones, mainly of seabirds, from a talus cone of red soil containing shells of *Poecilozonites bermudensis* but no *P. nelsoni*, hence the whole deposit is probably of Holocene age. A few bones labeled Walsingham Cave were collected by surface picking on 14 Aug 1981 by Robert Baird and Paul Cooper. We are not certain that this is the same cave as called Walsingham here and as this small sample contained one bone each of a hawk (Accipitridae) and a crow (*Corvus*), neither of which taxa were encountered by Olson and Grady, it seems quite possible that a different cave is involved.

18. *Walsingham Sink Cave*: N32°20'53.3" W64°42'39.0". The entrance is approximately 50-60 m NE ofWalsingham Cave. This is a high, narrow cleft in a limestone escarpment that shortly beyond the entrance bends sharply to the right (NE), descends steeply to the water table, and continues on to open into a sinkhole to the NE. Olson and Grady collected here on 15 Feb 2004. Fossils occurred in two discrete deposits of red soil. The first was at the entrance, still in the light zone. The second was a talus cone deep in the cave about 2 m above the water table, and appeared to have come in through a separate small entrance. Both deposits contained shells of *Poecilozonites bermudensis* and *P. nelsoni*, and in the lower one it was clear that the *P. bermudensis* occurred only in a thin surface veneer of loose soil lying above a deeper, more consolidated, darker sediment with well-encrusted shells of *P. nelsoni* and at least one bone of *Rallus recessus*. So, as with the sediments in the W wall red talus in Admirals Cave, there appears to have been an unconformity here perhaps equivalent to units "w" through "z" in Admirals Cave (Hearty *et al.*, 2004). Apparent lack of deposition during that period resulted in late Holocene sediments being laid down directly on those probably dating back to near the last glacial maximum. It appears that the interval between deposition of abundant *P. nelsoni* at glacial maximum and deposition of abundant *P. bermudensis* in the latter part of the Holocene may have been a time when sedimentation ceased in many caves.

c) Tuckers Point Caves

The following 5 sites are all located near the SW shore of Castle Harbour on the grounds of the present Tuckers Point golf club.

19. *Church Cave.*—N32°20'13.4" W64°41'59.1". A large, high-ceilinged cavern containing a substantial lake and with large boulders of roof-fall at the entrance among which Wingate obtained a few bones of seabirds and the rostrum of a crow *Corvus* sp. in May 1974. The latter may be modern. Olson, Hearty, and Wingate entered here briefly on 13 Feb 2002 but found nothing more of interest.

20. *Jane's Cave.*—N32°20'11.1W64°42'04.0". On the S side of Paynter's Hill. A steep cave with two major chambers near the entrance. On 17 Feb 2004 Grady and Olson encountered a very few bones in a patch of thin sediment between the two chambers. In another chamber off to the N, not visited by Olson and Grady, Wingate obtained various bird bones in January 1975. These were labelled "Prettybone Cave" but Wingate's notes indicate that this is the same as Jane's Cave. The bones include a confusing assortment of rails suggesting perhaps that deposits here may be diachronic.

21. *Zephyr Cave.*—N32°20'12.7" W64°42'00.5". A small, shallow opening practically in the fairway of the golf course. Grady and Olson excavated a few bones on 17 Feb 2004.

22. *Terrapin Cave.*—N32°20'14.0" W64°42'04.3". Apparently not named on the cave inventory. Terrapin Cave is Wingate's designation because of finding remains of an individual of the possibly introduced (see Davenport *et al.*, in press) terrapin *Malaclemmys* here. The cave is located at the base of a limestone escarpment on the S side of Paynter's Hill. A few bones of *Puffinus parvus* were collected here by Wingate on 23 Jan 1974. Olson and Wingate visited the cave on 12 Feb 2004 and found that the entrance led to a steep drop requiring climbing gear or a ladder and no more bones were encountered.

23. *Tropicbird Cave.*—Wingate's designation. The labels with specimens indicate that this cave was also on Paynter's Hill and Wingate's diary entry for 23 Jun 1974 includes a map showing that it is on the north slope of the hill close adjacent to the south side of the golf course fairway. Bones include those of *Pterodroma cahow, Puffinus parvus*, an associated skeleton of *Phaethon lepturus*, various rails, and passerines.

d) Miscellaneous Sites

24. *Spittal Pond.*— N32°18' W64°43' (USBGN). This relatively large pond, located on the south shore in Smiths Parish, would only have begun to fill when sea level approached its present level about 5000 years ago. It is the focal point of Bermuda's largest nature reserve, as the pond is an important resting and feeding area for transient waterbirds. In Jun/Jul 1979, the pond was dredged to improve waterfowl habitat and the spoil from this dredging was dumped along the S side of the pond. Vertebrate remains, mostly those of non-resident waterbirds, were collected from this spoil by Wingate in Jul/Aug 1979 and throughout the subsequent year. More were collected by R. F. Baird in 1981. There was also evi-

dence of a midden accumulation, probably a European camp site just prior to, or after British settlement because of the discovery of a human femur belonging to a male Caucasian, as well as bones of pigs and cattle, fish bones, West Indian Top Shell *Cittarium pica*, and other edible mollusks. The spoil is now entirely vegetated, precluding the recovery of further fossil material.

25. *Grace Island.*——N32°16' W64°49' (USBGN) in Great Sound. Bones of *Pterodroma cahow*, and *Phaethon lepturus* were collected by Wingate, Jun 1972, from two small sink holes in Walsingham Formation.

26. *Cockroach Island.*—-N32°20' W64°43' (USBGN for Abbots Cliff) In Harrington Sound, base of Abbott's Cliff. Bones of *Pterodroma cahow, Puffinus lherminieri/parvus*, and *Phaethon lepturus* were collected by Wingate in Nov 1958. These remains were identified by Wetmore (1962: 15) who reported that they "were dug from about 4 cubic feet of sandy soil and rubble, some of them from near the surface where they were among roots of plants." The bones were thought to be Recent in age. They were collected with shells of *Poecilozonites bermudensis*, which we now know to indicate Holocene age.

25. *SAL Quarry.*—-Southampton Parish, a sand quarry in the Southampton Formation on the coastline south of "Landmark", ca. 300-400 m SE of West Whale Bay (N32°15' W64°52' USBGN). Various lots of bones of *Pterodroma cahow* found embedded in the sand along with abundant charcoal. Collected by Wingate 9 April 1979, Olson and R. F. Baird on 30 Aug 1981, and by Baird in Jan 1982.

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Fig. 9. Excavation at the base of the immense talus cone inside Admirals Cave. Nearly 120,000 years of continuous deposition is preserved here.

Fig. 9. Excavació a la base del talús immens a l'interior de la cova Admirals. Aquí es conserven prop de 120.000 anys de deposició contínua.

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FOOD HABITS OF *"PRAEMEGACEROS" CAZIOTI* (DEPÉRET, 1897) FROM DRAGONARA CAVE (NW SARDINIA, ITALY)

INFERRED FROM CRANIAL MORPHOLOGY AND DENTAL WEAR

Maria Rita PALOMBO

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Resum

S'ha estudiat l'adaptació alimentària de *"Praemegaceros" cazioti* (Depéret, 1897), en base a la rica mostra trobada als dipòsits del Pleistocè tardà de la cova de Dragonara (nord-oest de Sardenya, Itàlia). Amb aquest objecte, s'han pres en consideració els trets cranials, així com el gradient de desgast d'abrasió – atrició (mesodesgast), i els efectes produïts a l'esmalt dentari per les partícules contingudes als vegetals, per l'acidesa i/o duresa del menjar i per la força i direcció dels moviments mandibulars (microdesgast).

Els resultats de les anàlisis qualitatives i quantitatives són consistents amb una adaptació alimentària a una dieta mixta, tal com també ho són algunes característiques cranio-dentàries: en particular, el morro, més aviat quadrat, les grans àrees d'inserció del *musculus masseter*, el desenvolupament de la prominència massetèrica sobre el M^1, la profunditat i altura del *corpus* i *ramus* a l'*angulus mandibulae*, la superfície d'inserció reduïda del *musculus temporalis* a la mandíbula i les dents hipsodontes. Els resultats de la nostra anàlisi suggereixen que el cèrvid de la Cova Dragonara era un animal de dieta mixta, que va incrementar el consum d'herba en comparació amb el seu possible ancestre.

Paraules clau: *"Praemegaceros" cazioti*, Pleistocè tardà, Sardenya, morfologia cranio-dentària, microdesgast dentari, mesodesgast, adaptacions alimentàries.

Abstract

The dietary adaptation of *"Praemegaceros" cazioti* (Depéret, 1897) has been investigated on the basis of on the rich sample found in the Late Pleistocene deposits in Dragonara Cave (north-western Sardinia, Italy). To this end, we have taken into consideration cranial features as well as the abrasion-attrition wear gradient (mesowear) and the defects produced on tooth enamel by the particles contained in vegetables, by the acidity and/or hardness of food and by the strength and direction of jaw movements (microwears).

Results of qualitative and quantitative analyses of microwears are consistent with mixed-feeder dietary adaptation, as are some cranio-dental features: in particular the rather square muzzle, the large insertion areas of *musculus masseter*, the developed masseteric prominence above M^1; the depth and height of *corpus* and *ramus* at *angulus mandibulae*; the reduced insertion surface of *musculus temporalis* on the jaw and hypsodont teeth. Results of our analyses suggest that the cervid from Dragonara Cave was a mixed-feeder, increasing the consumption of grass as compared to its possible ancestor.

Keywords: *"Praemegaceros" cazioti*, Late Pleistocene, Sardinia, cranio-dental morphology, dental microwear, mesowear, dietary adaptation.

INTRODUCTION

Several morphological features of the herbivore skull, mandible and dentition can be correlated with dietary adaptations and used in estimating the feeding ecology of extinct taxa (e.g., Solounias & Dawson-Saunders, 1988; Janis, 1988; Solounias *et al.*, 1988; Solounias & Moelleken, 1993a,b; Janis, 1995; Caloi & Palombo, 1996; MacFadden & Shockey, 1997; Pérez-Barbería & Gordon, 1999; MacFadden, 2000; Pérez-Barbería & Gordon, 2001; Pérez-Barbería *et al.*, 2001; Williams & Kay, 2001; Mendoza *et al.*, 2002; Kaiser & Solounias, 2003; Mainland, 2003, and references therein).

As indicators of herbivore feeding behaviour, we can analyse cranio-dental morphology (see Mendoza *et al.*, 2002, and references therein), skull foramina (Solounias & Moelleken, 1999), the relative height of crown and the morphology of the occlusal surface of chewing teeth, which depend on combined attrition-abrasion actions (see Kaiser & Solounias, 2003, and references therein), the enamel scars produced during mastication by tooth-food and tooth-tooth contact (e.g., Resenberg, 1978; Solounias & Hayek, 1993; Solounias *et al.*, 2000; Solounias & Semprebon, 2002; Mainland, 1997; 2003; Teaford, 1988; 1991; 1994; Hayek *et al.*, 1991; Maas, 1991; Solounias & Moelleken, 1992; Palombo *et al.*, 2005).

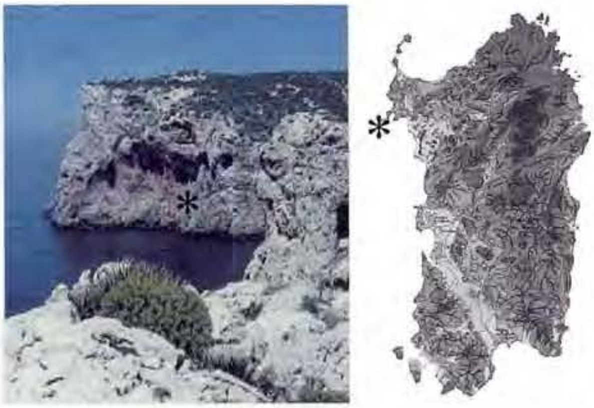

Fig. 1. Localisation of Dragonara Cave (Alghero, North-Western Sardinia).

Fig. 1. Localització de la cova Dragonara (L'Alguer, nord-oest de Sardenya).

Such features are obviously functionally constrained by the "baup-plane" inherited from the ancestor, as four main combined factors (phylogeny, morphogenetic structure, biological function, and environment), lead to the overall constructional morphology of each organism.

Moreover, it is worth noting that many ungulates are also opportunistic, and their diets can vary according to place or season or, sometimes, only occasionally. Though three main dietary classes (browser, grazer, mixed feeder) were generally considered, the type of food and lifestyle spectrum between typical grazer and browser is extremely varied, as highlighted by the heterogeneous feeding behaviour shown by so-called mixed feeders (see Kaiser & Solounias, 2003).

Deer, generally regarded as brachyodont herbivores inhabiting woodlands, are actually rather adaptable animals able to live in different environments (Geist, 1999). Among extant and Pleistocene cervids, many are mixed feeders, alternating seasonally, regionally or occasionally between browse and grass, though the feeding spectrum is extremely vast.

For instance, *Capreolus capreolus, Alces alces* and *Odocoileus virginianus,* are typical browsers; *Dama dama, Axis axis, Cervus canadensis, Rangifer tarandus* and species of the genus *Rusa* are feeders on fruit and foliage (trees and shrubs) as well as fresh-grasses, alternating their food according to the season, or even occasionally (meal-by-meal); *Elaphurus davidianus* and *Cervus albirostris* seems to be deer whose diet most resembles that of not strictly grazers (Hofmann, 1989; Cornelius *et al.*, 1999; Geist, 1999; Fortelius & Solounias, 2000; Cransac *et al.*, 2001; Stewart *et al.*, 2002), whereas the European *Cervus elaphus* feeds on the most available resources in its inhabited area (Groot Bruinderink & Hazebrock, 1995). Moreover, the feeding aptitude can change in particular environmental conditions, depending on the vegetation cover or the occurrence of unusual free ecological niches.

Accordingly, a multiple analytical approach (craniodental morphofunctional analysis, qualitative and quantitative studies of effects produced on tooth enamel during mastication) seems to be the most appropriate way to study the dietary preference of extinct mammals, especially in the case of the problematic group of deer. Research on the dietary adaptation of *"Praemegaceros" caziotі*[1] is of great interest, since this cervid is the only large herbivore existing in Sardinia during the Middle and Late Pleistocene. Consequently, *"P." caziotі* did not have any competitor for niche occupation and resource partitioning in Sardinia, whereas in Corsica, during the Middle Pleistocene, it had to compete with *C. elaphus rossii,* thus far not recorded in Sardinia (Pereira, 2001).

In the post-Tyrrhenian deposits of Dragonara Cave, more than 800 remains belonging to *"P." caziotі,* carefully described by Caloi & Malatesta (1974), were found. A preliminary analysis of the morpho-functional features of skull, mandible and *autopodium* (carpus, tarsus, metapodials and phalanges, Caloi & Palombo, 1991), as well as limb proportions, showed that the cervid from Dragonara Cave shared some cranial morphologies with grazers and was capable of agile, fast locomotion on prevalently hard and uneven ground (Caloi & Palombo, 1995; 1996).

In this paper, a multiple analytical approach is adopted in order to compare cranio-dental morphology with dental micro- and mesowear, using a large sample; this enables us to create support for further studies devoted to better defining the ecological niche of *"P." caziotі* from Sardinia and Corsica.

MATERIAL AND METHODS

We have examined the skulls, mandibles (Plate 1) and upper and lower teeth uncovered in the "post-Tyrrhenian" deposits filling the Dragonara Cave (Caloi & Malatesta, 1974) (Fig. 1). The specimens are currently kept at the "Museo di Paleontologia" at "La Sapienza" University in Rome (MPUR).

As far as craniodental morphology is concerned, we have analysed extant and fossil species as listed in the appendix.

Microwear analysis (see below) was done on casts of the enamel cusp of M^2 paracone. Analytical methods were adapted from those described by Solounias & Moelleken (1992) and Solounias & Semprebon (2002), for SEM and stereomicroscopic analysis respectively.

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[1] It is worth noting that Joleaud (1914) proposed the name *Megaceroides,* as *Cervus* subgenus, with the type species *"Cervus" algericus,* for a fragmentary maxillary: subsequently, Arambourg (1932, 1938) ascribed a skull from the Late Pleistocene of Algeria and Morocco to this species. Mean similarities in skull characters between specimens from the Magreb and the megalocerine from Europe, first pointed out by Azzaroli (1952), have subsequently been widely debated (see e.g. Hadjoudis, 1990; Azzaroli & Mazza, 1992; Abbazzi, 2004; van der Made & Palombo, in press). All in all, it seems more correct to maintain the name *Megaceroides* only for the North African species. Nevertheless, the problem concerning the nomenclature of the genera referring to the tribu Megacerini is still unresolved. Assuming that the species ascribed to the so-called "*verticornis*" group and those to the "*giganteus*" group belong to two distinct lineages, what is the correct generic name to choose among those used thus far for the giant deer belonging to the "*verticornis*" group? The name "*Praemegaceros*", though not formally correct (see e.g. Azzaroli, 1979; Caloi & Palombo, 1996), was frequently employed, whereas other names, such as "*Ortogonoceros*" or "*Psekupsoceros*", have not been *de facto* widely utilised in more recent times. For this reason, to avoid additional confusion, we provisionally use the generic name "*Praemegaceros*" for European megalocerine as well as, of course, for the Sardinian and Corsican ones.

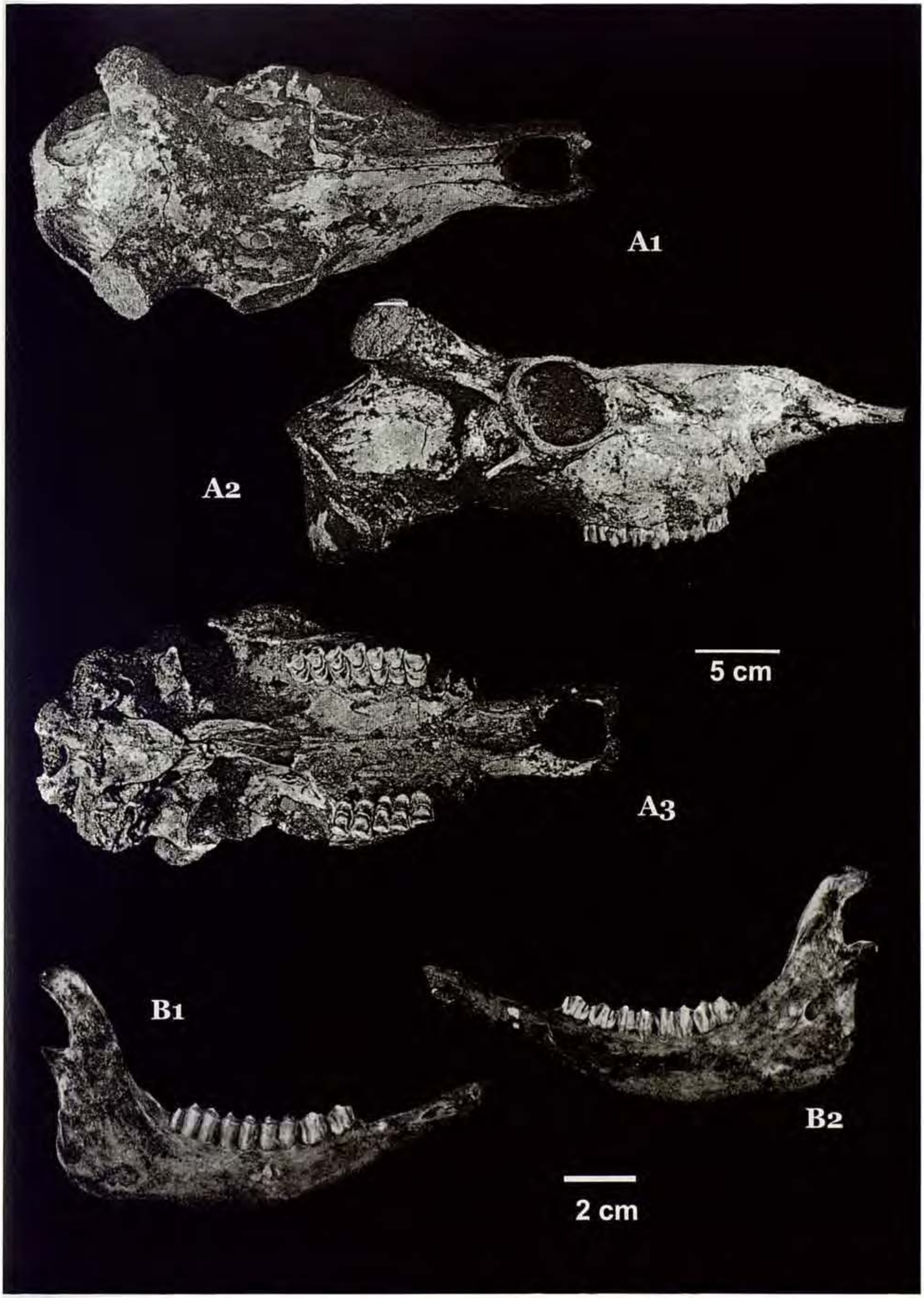

Plate 1. *"Praemegaceros" cazioti*, Dragonara Cave. Late Middle Pleistocene:
A) skull (MPUR/V s.n.) in dorsal (1), lateral (2), ventral (2) view.
B) mandible (MPUR/V 1/235) in lingual (1) and buccal (2) view.

Làmina 1. "Praemegaceros" cazioti, *cova Dragonara. Pleistocè Mitjà Tardà:*
A) crani (MPUR/V s.n.) en visió dorsal (1), lateral (2), i ventral (2).
B) mandíbula (MPUR/V 1/235) en visió lingual (1) i bucal (2).

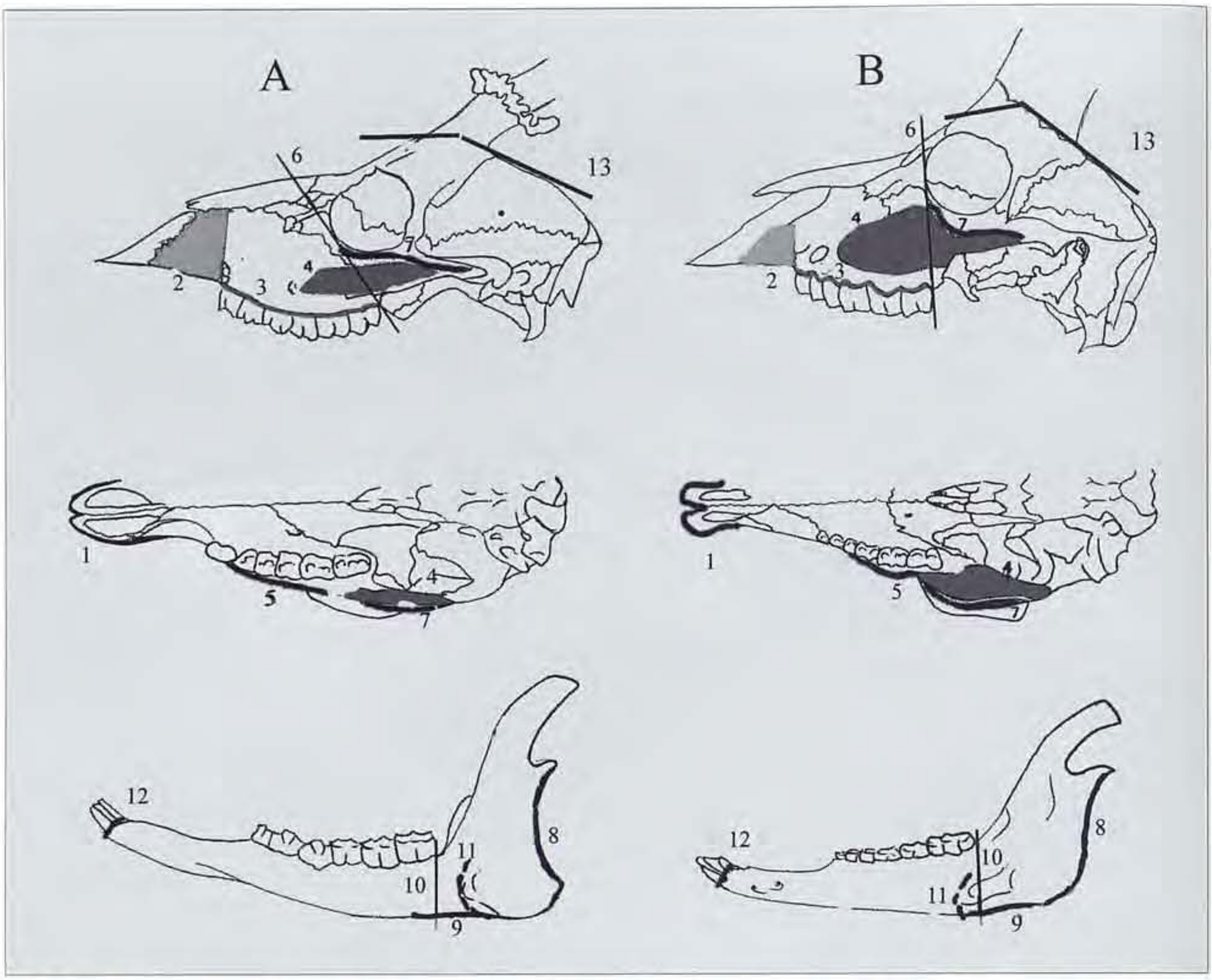

Fig. 2. Scheme of the main morphological features connected with masticatory modalities showed by a browser (A = *Capreolus capreolus*) and a mixed-feeder (B = *Capra hircus*) ruminants: 1 = shape and extent of the rostral premaxillary portion; 2 = development of the maxillary area anterior to P^2; 3 = shape of the alveolar margin; 4 = origin of the *m. masseter;* 5 = development of the *tuberculus faccialis;* 6 = position of the orbit; 7 = origin of the *m. zygomatico-mandibularis*; 8 = posterior part of *ramus mandibulae;* 9 = thickness of the *corpus mandibulae* between the *angulus mandibulae* and the *impressio vasculosa*; 10 = increase in height of the *corpus mandibulae* from P_2 to M_3; 11 = front extension of the *m. masseter* termination; 12 = alveolar line of incisive; 13 = Braincase angle; mt = moment arms of *temporalis* muscle; mm = moment arms of *masseter* muscle.

Fig. 2. *Esquema dels trets morfològics principals relacionats amb les modalitats masticatòries presentades per un remugant brostejador (A =* Capreolus capreolus*) i per un de dieta mixta (B =* Capra hircus*). 1, forma i extensió de la part premaxil·lar rostral; 2, desenvolupament de l'àrea maxil·lar anterior al P^2; 3, forma de la vorera alveolar; 4, origen del* musculus masseter*; 5, desenvolupament del* tuberculus faccialis*; 6, posició de l'òrbita; 7, origen del* m. zygomatico-mandibularis*; 8, part posterior del* ramus mandibulae*; 9, gruixa del* corpus mandibulae *entre l'*angulus mandibulae *i la* impressio vasculosa*; 10, increment en altura del* corpus mandibulae *des del P_2 al M_3; 11, extensió frontal de la terminació del* m. masseter*; 12, línia alveolar de la incisiva; 13, angle de la caixa craniana; mt, moment del m. temporalis; mm = moment del muscle masseter.*

The casts were first examined at 35x magnification using an Olympus stereomicroscope. Then, the casts, spatter-coated with 200 angstroms of gold, were analysed using a Cambridge Stereoscan 250. Photomicrographs were taken at 20 x, 35x, 200x and 500x magnification. The 20 x photomicrographs were taken in order to better check the region and orientation of the less magnified photomicrographs. The 35x photomicrographs were used for comparison with the images obtained with the light stereomicroscope. Both 200x and 500x photomicrographs were used for analysis in order to contrast results at different magnifications. Quantitative analysis was made using the Microwear 4.0 software programme, provided by Ungar (2001).

Mesowear analysis (see below) was performed according to the methodology proposed by Kaiser (2003). Analysis is focused on the buccal cutting edges of the enamel surfaces (paracone/ metacon), following methods proposed by Kaiser (2003) and Franz-Odendaal & Kaiser (2003). Moreover, according to our personal observation, as far as *"P." cazioti* is concerned, there are not significant differences between mesowear data resulting from the analysis of upper and lower last four (P^4-M^3) teeth. Consequently, also P_4-M_3 were considered, as well as upper ones, following the "four positions" method proposed by Kaiser (2003). We considered the following variables: occlusal relief, high or low (height of cusp divided by tooth length, respectively > or < 0,1) and cusp shape, defined as sharp, round and blunt, in decreasing order of facet development (Kaiser, 2003; Kaiser & Solounias, 2003).

CRANIO-DENTAL MORPHOLOGY

The characters tested are mainly those discussed by Solounias *et al.* (1988), Solounias & Dawson-Saunders (1988), Solounias & Moelleken (1993a,b), Solounias *et al.* (1995), MacFadden & Shockey (1997), Mendoza *et al.* (2002) for ruminants in general and adapted by Caloi & Palombo (1996), Croitor (1999; 2001) and Valli & Palombo (in press) specifically to cervids.

The most significant cranial features correlated with dietary preferences in ruminants, and valid for the fossil deer too, can be restricted to muzzle shape, the extension of the origin and insertion area of *masseter* muscle (on skull and mandible respectively), the shape and the depth of *angulus mandibulae*, the shape of the posterior outline of the vertical *ramus mandibulae* (Fig. 2).

Indeed, the outline of distal premaxillary bones and of the mandibular symphysial region are good indicators of the 'cropping mechanism', since the more selective feeding- browsing cervids (such as *C. capreolus*) have narrow muzzles and more pointed premaxillary outlines, whereas in mixed feeders (such as *D. dama*) the muzzle shows a squarer outline, like in grazers, allowing the most effective cutting of grasses growing in clusters on the ground.

Furthermore, the larger the origin and insertion areas of the *masseter* (*pars superficialis* and *profunda*) muscle, the more powerful chewing is. In addition, a long *masseter* muscle moment arm suggests powerful biting (see e.g. Vizcaíno & Bargo, 1998; Vizcaíno *et al.*, 1998). The shape of *angulus mandibulae* and the depth and height of the vertical *ramus* are also affected by the extension of insertion areas of the *masseter* (*pars superficialis* and *profunda*), *zygomaticomandibularis* and *pterigoideus* muscles. Cervids feeding on grasses, such as *E. davidianus*, have a deeper *angulus mandibulae* region; the condylus is in a higher position and articular surface is rather symmetrical and horizontal, as in grazers (Croitor, 1999; 2001). Conversely, the insertion of the *temporalis* muscle is wider in browser than in mixed- feeder cervids (Caloi & Palombo, 1995).

Some other cranial features may represent a useful tool in the attempt to detect deer feeding, but have to be employed more cautiously. For instance: 1) grazers have a more highly-developed masseteric prominence above the M^1, due to a stronger tendon of the *masseter superficialis* muscle than in browsers; nevertheless, *C. capreolus* shows relatively enlarged maxillary bones above M^1; 2) due to the larger origin of the *masseter* muscle on the maxillary bone of grazers, the orbit is usually positioned above M^2 in browsers, whereas it starts above M^3 or further back in grazers; nevertheless, in cervids, the orbit position is quite variable, also depending on structural characteristics; 3) Solounias *et al.* (1988) and Solounias & Dawson-Saunders (1988) consider a reduced area of maxillary bones in front of P^2 as a grazer feature; among cervids, the shape of this area appears quite uniform, and ecomorphological variations seem to be of little relevance; 4) the *corpus mandibulae* is usually larger and deeper in grazers due to the presence of hypsodont molars, though in cervids the increase in crow height seems does not significantly change the shape of the *corpus mandiblulae*; 4) it has been observed that grazers have equal or sub-equal size incisors, whereas in browsers the size differs, and the first incisor is more or less larger than the third (Gordon & Ilius, 1988; Janis & Ehrhardt, 1988); however, this feature is not evident in cervids and, moreover, the incisors of fossil taxa are rarely recorded; 5) sub-equal size incisors of grazers are usually combined with straight incisor arcades; cervids generally show a more or less rounded incisor arcade; moreover, this feature is also usually difficult to evaluate in fossils; 6) the high glenoid fossa (above the occlusal plane) and higher vertical *ramus mandibulae* of ruminant browsers have comparatively longer premolar tooth rows than grazers.

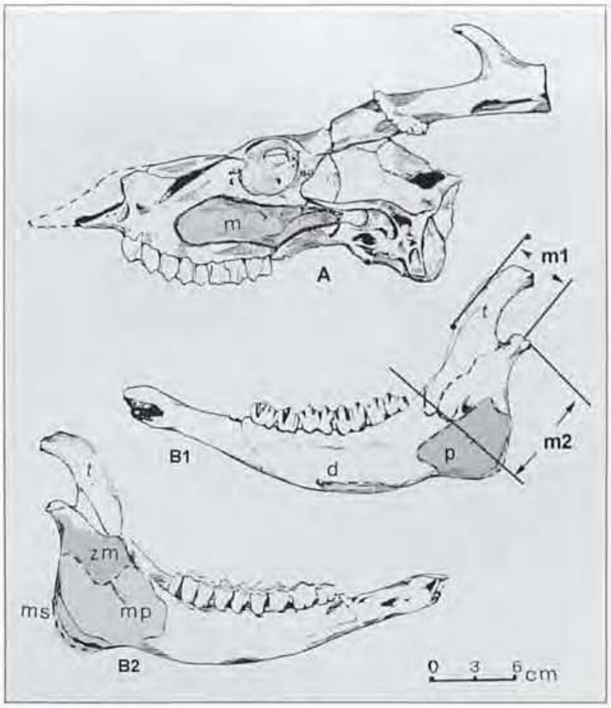

Fig. 3. *"Praemegaceros" caziotí*: skull (MPUR/V 1/1) and mandible (MPUR/V 1/235). Insertion areas of masticator muscles: d = *m. digastricus*; m = *pars profunda* and *pars superior* of *m. masseter*; mp = *pars profunda* of *m. masseter*; ms = *pars supeficialis* of *m. masseter*; p = *m. pterygoideus medialis*; t = *m. temporalis*; zm = *m. zygomatico-mandibularis.*

Fig. 3. "Praemegaceros" cazioti*: crani (MPUR/V 1/1) i mandíbula (MPUR/V 1/235). Àrees d'inserció dels músculs mandibulars: d* = m. digastricus*; m* = pars profunda *i* pars superior *del* m. masseter*; mp* = pars profunda *del* m. masseter*; ms* = pars superficialis *del* m. masseter*; p* = m. pterygoideus medialis*; t* = m. temporalis*; zm* = m. zygomatico-mandibularis.

Other features, recognised as being distinctive from those of grazers, such as a narrow braincase angle and larger skull length in relation to body size (Mendoza *et al.*, 2002), cannot be taken into consideration when analysing insular specimens, because a larger skull, as well as the relative variation in skull/ brain case proportion, are features characterising most endemic insular mammals (Azzaroli, 1982; Palombo, 2001; Köhler & Moyà-Solà, 2003, 2004).

Furthermore, as is widely known, ungulates that feed on abrasive grasses with high silicophytolith contents have higher hypsodonty values than leaf-eating

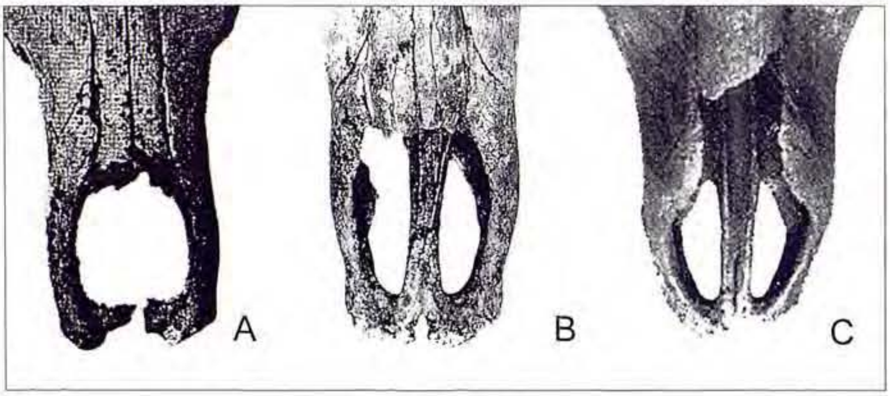

Fig. 4 . Premaxillary shape in A) *"Praemegaceros" cazioti* (MPUR/V1/1), B) *"Praemegaceros" obscurus* (late Villafranchian, Cava Liberatori-Tuscany, adapted from Abbazzi, 1995), C) *Megaloceros giganteus* (Holocene, Ireland, Museo Agenzia Nazionale per l'Ambiente, Roma).

Fig. 4. Forma del premaxil·lar a: A) "Praemegaceros" cazioti *(MPUR/V1/1), B)* "Praemegaceros" obscurus *(Villafranquià tardà, Cava Liberatori-Toscàna, adaptat de Abbazzi, 1995), C)* Megaloceros giganteus *(Holocè, Irlanda, Museo Agenzia Nazionale per l'Ambiente, Roma).*

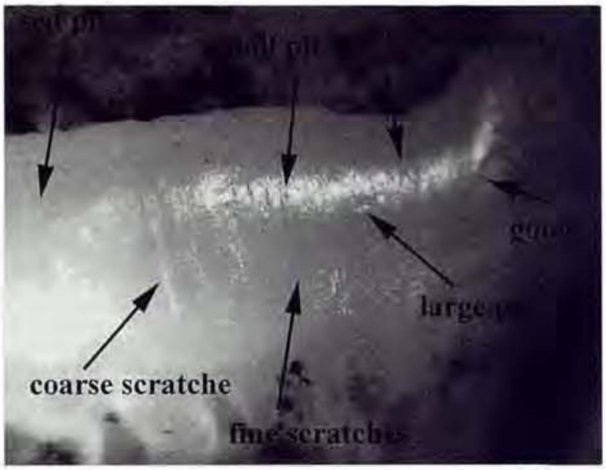

Fig. 5. *"Praemegaceros" cazioti*: second (lingual) enamel band of the paracone of a right M^2 (MPUR/V1/115). Microwear scars fotographed using stereomicroscope (magnification 40x).

Fig. 5. "Praemegaceros" cazioti*: segona (lingual) capa d'esmalt del paraconus d'un M^2 dret (MPUR/V1/115). Marques de microdesgast fotografiades amb un estereomicroscopi (40x).*

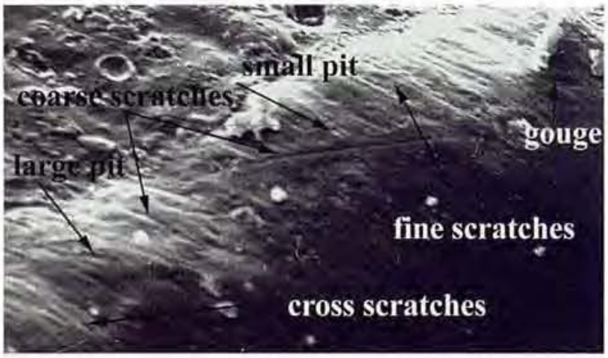

Fig. 6. *"Praemegaceros" cazioti:* M^2 (MPUR/V 1/116). SEM photomicrograph (magnification 60 x) of second enamel band of the paracone showing pits (large and small), scratches (coarse, crossed and fine), and gouges.

Fig. 6. "Praemegaceros" cazioti*: M^2 (MPUR/V 1/116). Microfotografia amb el SEM (60 x) de la segona capa d'esmalt del paraconus mostrant forats (grans i petits), ratllades (grolleres, creuades i fines), i clots.*

browsers (van Vale, 1960; Janis, 1988; Solounias & Dawson- Saunders, 1988; Jernvall & Fortelius, 2002). The criteria for assigning species to the three hypsodonty classes (brachydont, mesodont and hypsodonty) generally used for herbivores are based on the ratio of height to length of the second or third molar (upper or lower). The relative tooth crown height (hypsodonty index) is less than 0.8 for brachydont, 0.8–1.2 for mesodont and more than 1.2 for hypsodonty teeth. Although the hypsodonty index and diet are not strictly correlated (see e.g. Kaiser *et al.*, 2000; Fortelius *et al.*, 2002), an increase in dental crown height in populations belonging to the same species or genus might be regarded as an ecomorphological response to a change in diet.

As far as cervids are concerned, it is also more difficult to interpret the meaning of variations in the premolar/ molar length ratio (ruminant browsers have comparatively longer premolar tooth rows than grazers, Mendoza *et al.*, 2002) due to the evolutionary significance sometimes assumed by the increasing size of premolars in deer (Heintz, 1970).

In light of all this, the cranium of the Dragonara cervid (Fig. 3) shows some morphological features that, to a varying degree, are similar to those characterising mixed-feeder ruminants, whose feeding also includes some fresh-grasses, as well as drier herbs. Accordingly, the Dragonara cervid, like ruminant mixed-feeders, is similar to grazers in the following: having a square muzzle; a rough, large origin area of *musculus masseter;* a reduced insertion area of *musculus temporalis* on the jaw; a high, deep *corpus mandibulae* behind M3; a round outline of *angulus mandibulae* and little concave posterior outlines of *ramus verticalis;* moreover, the facial tubercle above M^1 is quite well developed, the orbit starting above M3; the glenoid fossa is high with respect to the occlusal plane; the teeth are hypsodont (Fig. 3; Plate 1). It is worth noting that among giant continental deer, *"P." obscurus* has quite an enlarged distal portion of premaxillary bones, even if less than in *"P." cazioti*, whereas the muzzle's shape of *Megaloceros giganteus*, as well as of *Eucladoceros*, is similar to that of browsers (Fig. 4).

MICROWEAR

Microwear analytical methods were developed at the end of the 1970s in an attempt to define dietary adaptation on the basis of scars produced during chewing on enamel occlusal surface by tooth /food (abrasion) and tooth/tooth (attrition) interaction. Differences in microwear patterning and formation processes depend on the physical properties of food (acidity, hardness, particles contained) and the strength and direction of jaw movements (magnitude and direction of chewing forces) affecting microwear patterns, notably their shape, size, distribution and density. Due to the very short time turnover (formation/obliteration) of wear patterns, microwear can provide information on the nature of the last few meals of the examined individual (Solounias *et al.*, 1994; Teaford & Oyen, 1989). Nevertheless, this rapid change can constitute a power point in research on extinct species: in this case, we can avoid the bias of short time occasional feeding and evaluate average dietary preferences over the course of time.

According to their microwear patterns and feeding preferences, artiodactyls were grouped in the following categories: 1) browsers, including: typical browsers (feeding mainly on foliage, ligneous plants) characterised by a high percentage of pits and few longitudinal, often crossed scratches; fruit/seed browsers, having a high number of coarse scratches and large pits; 2) grazers (eating more exclusively grasses), characterised by a high percentage of striation, especially fine parallel scratches; 3) mixed feeders (having a diet including a mixture of ligneous plants and grasses, with seasonal and/or spatial variation), with a more variable pattern; and, in addition, 4) fruit-seed browsers; 5) bark, coarse stem and leaf feeders, such as elephants, 6), rooters, such as some suids (Solounias & Semprebon, 2002).

Microscopic scars, analysed using light microscopy (35-40X) (Fig. 5) and at SEM (200X and 500X) on the second band of M^2 paracone (Fig. 6), can be arranged into three main categories: i) striations or scratches (linear depression whose length is always greater than its breadth; coarse scratches have a large bottom, fine scratches are thinner and straighter); ii) pits, large" or "small" (depressions whose length and breadth are approximately equal); iii) gouges (microwear scars larger and deeper than pits, with irregular edges) (Gordon, 1982, 1988; Solounias & Semprebon, 2002; Palombo, unpublished data) (Fig. 6).

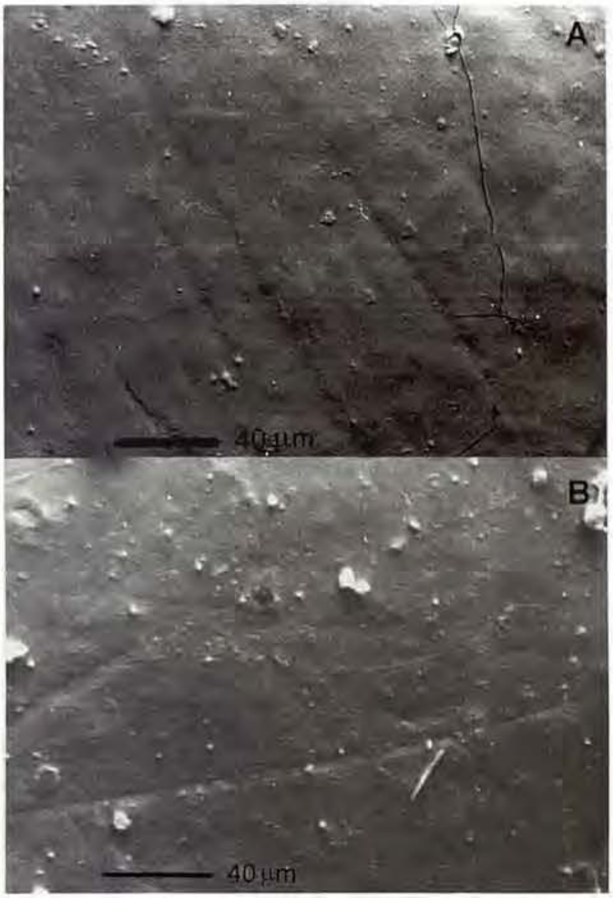

Fig. 7. *"Praemegaceros" cazioti*: SEM photomicrographs (magnification 500 x) of second enamel band of the paracone, 7a) M^2 (MPUR/V1/237) - the photomicrograph shows some parallel coarse stratches, several large pits quite abrasion that caused the polished feature of the enamel surface; 7b) M^2 (MPUR/V 1/123) - the photomicrograph shows both coarse scratches and fine crossed scratches, some times crossed, several pits and two gouges are also present.

Fig. 7. "Praemegaceros" cazioti*: microfotografies amb el SEM (500 x) de la segona capa d'esmalt del paraconus: 7a) M^2 (MPUR/V1/237) – la microfotografia mostra algunes ratllades grolleres paral·leles, alguns forats grans bastant desgastats degut al poliment de la superficie de l'esmalt; 7b) M^2 (MPUR/V 1/123) – la microfotografia mostra tant ratllades grolleres com fines, de vegades creuades, i també hi ha alguns forats i dos clots.*

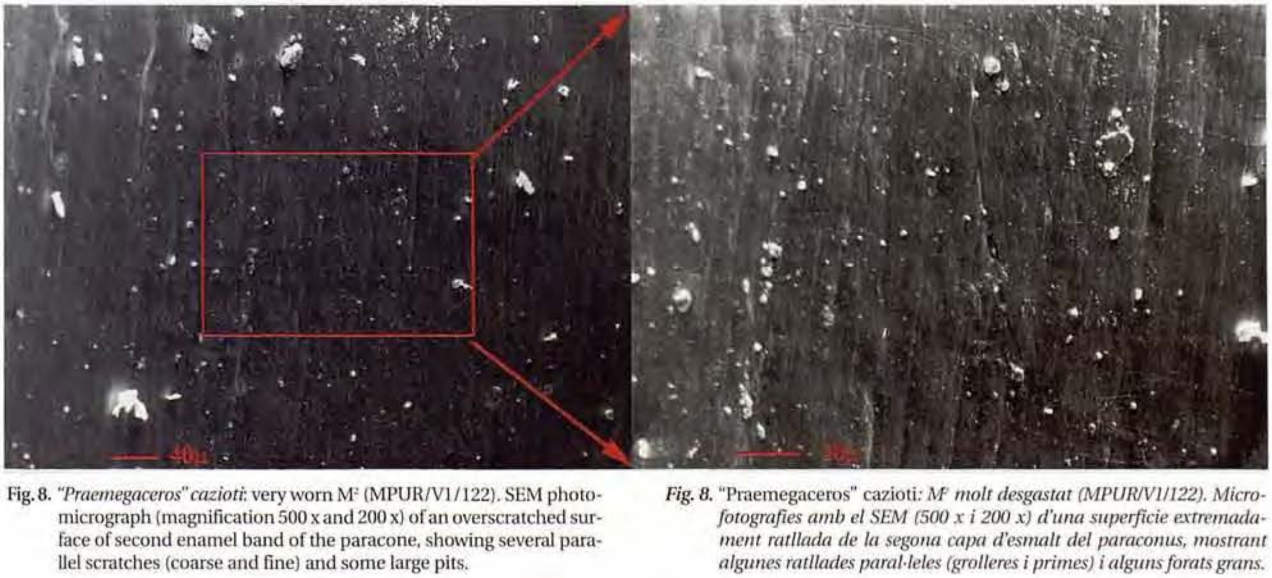

Fig. 8. *"Praemegaceros" cazioti*: very worn M^2 (MPUR/V1/122). SEM photomicrograph (magnification 500 x and 200 x) of an overscratched surface of second enamel band of the paracone, showing several parallel scratches (coarse and fine) and some large pits.

Fig. 8. "Praemegaceros" cazioti*: M^2 molt desgastat (MPUR/V1/122). Microfotografies amb el SEM (500 x i 200 x) d'una superficie extremadament ratllada de la segona capa d'esmalt del paraconus, mostrant algunes ratllades paral·leles (grolleres i primes) i alguns forats grans.*

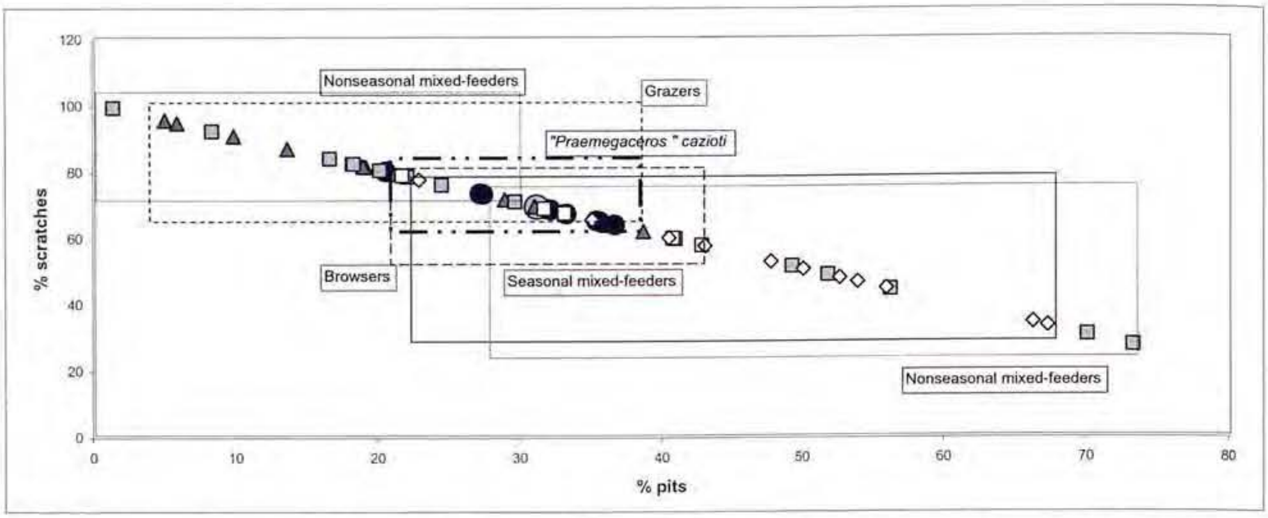

Fig. 9. Percentage of pits versus percentage of scratches for *"Praemegaceros" cazioti* and extant herbivores (average number of pits and scratches of extant species from Solounias & Semprebon, 2002).

Fig. 9. Percentatge de forats respecte el percentatge de ratllades per a "Praemegaceros" cazioti *i diversos herbivors vivents (nombre promig de forats i ratllades de les espècies vivents, a partir de Solounias & Semprebon, 2002).*

The microwear pattern shown by the cervid from Dragonara Cave (Fig. 7, 8) is characterised by a high percentage of scratches (Fig. 9) and, consequently, a low density of pits (Fig. 10), similar to those of extant "high scratch" mixed-feeder cervids such as *Axis axis* and *Cervus canadensis*, having average scratch numbers at the grazing end of the scratch range (Solounias & Semprebon, 2002). However, the average density of scratches is inferior to that of extant grazers. Accordingly, *"P." cazioti* from Dragonara is clearly distinct from browsers, and can be situated in the seasonal mixed-feeder group.

MESOWEAR

Dietary adaptation of fossil herbivores, or better certain kinds of wear, can also be inferred using the mesowear method (Fortelius & Solounias, 2000; Kaiser *et al.*, 2000; Kaiser & Solounias, 2003; Kaiser, 2003)

This method, already described in terms of facet development by Butler (1952) and Janis (1990), was considered by Fortelius & Solounias (2000) as a proxy to illustrate the average diet of a particular species living in a

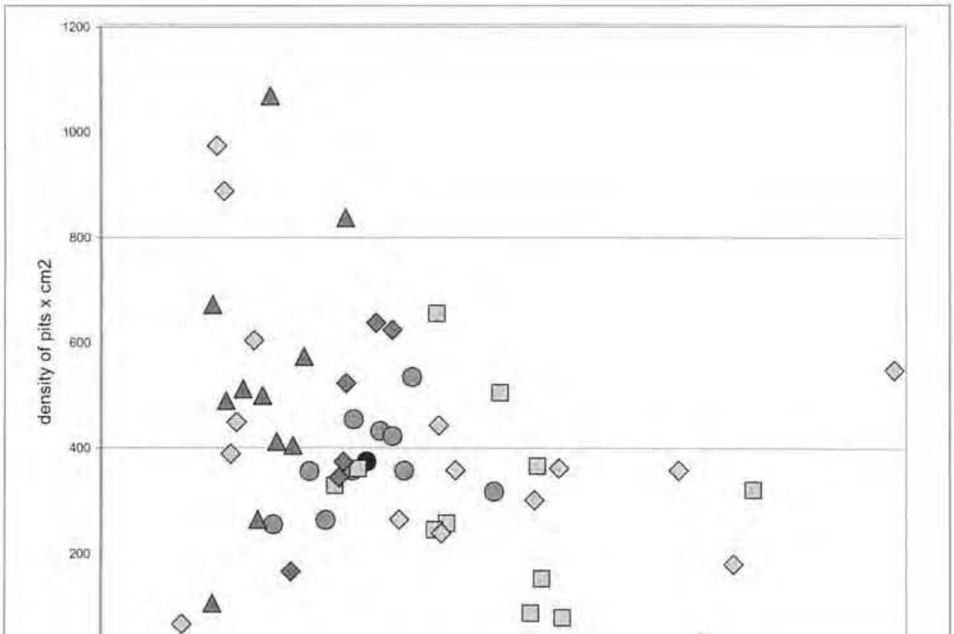

Fig. 10. Density of pits versus density of scratches for *"Praemegaceros" cazioti* and extant herbivores (average density of pits and scratches of extant species from Solounias & Semprebon, 2002).

Fig. 10. Densitat de forats respecte la densitat de ratllades per a "Praemegaceros" cazioti *i diversos herbivors vivents (nombre promig de forats i ratllades de les espècies vivents, a partir de Solounias & Semprebon, 2002).*

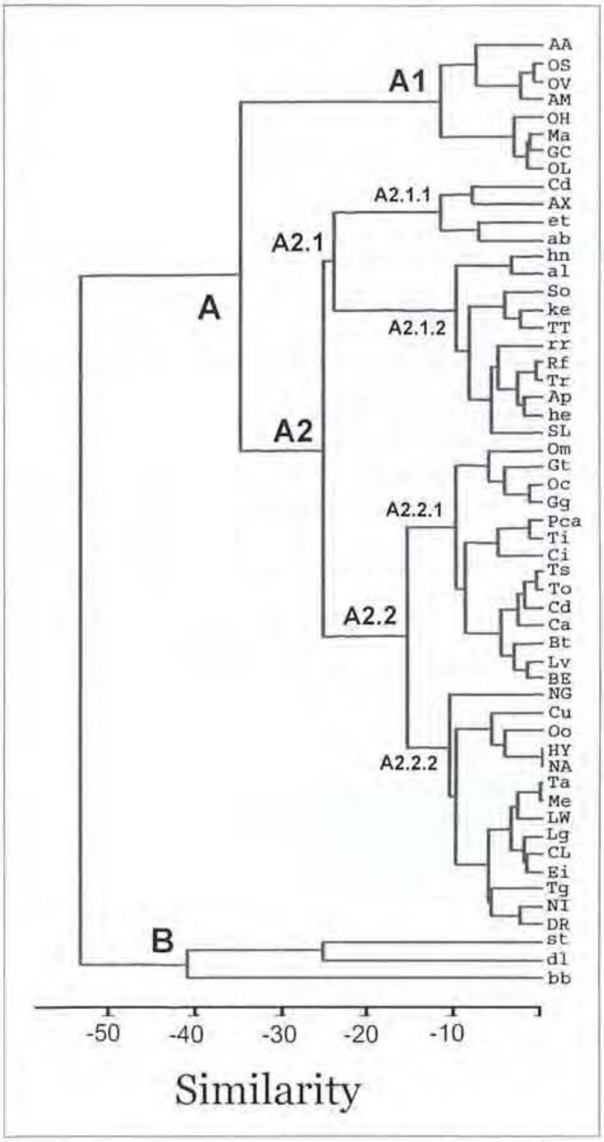

Fig. 11. Hierarchical cluster diagram based on recent cervid (data from Kaiser, 2003). The mesowear variables considered for cluster analysis (normalized Euclidean distance, NED) are: percent high occlusal relief, percent sharp cusps and percent blunt cusps.
Browser (upper case): AA *Alces alces*; BE *Boocercus euryceros*; EI *Ammodorcas clarkei*; GC *Giraffa camelopardalis*; LW *Litocranius talleri*; OH *Odocoileus hemionus* ; OJ *Okapia johnstoni*; OL *Capreolus capreolus* ; OV *Odocoileus virginianus*; TT *Tragelaphus strepsiceros*
Grazers (small case): ab *Alcelaphus buselaphus*; al *Alcelaphus lichtensteinii*; bb *Bison* bison; ct *Connochaetes*; dl *Damaliscus lunatus*; he *Hippotragus equines*; hn *Hippotragus niger*; ke *Kobus ellipsiprymnus*; rr *Redunca redunca*;
Mixed feeders (capital first): Ap *Axis porcinus*; Ax *Axis axis*; Bt *Budorcas taxicolor*; Ca *Capricornis sumatraensis*; Cc *Cervus canadensis*; Cd *Cervus duvauceli*; Ci *Capra ibex*; Cl *Camelus dromedarius*; Ru *Rusa unicolor*; Gg *Gazella granti*; Gt *Gazella thomsoni*; Lg *Lama lama*; Lv *Lama vicugna*; Ma *Antidorcas marsupialis*; Me *Aepyceros melampus*;
Oc *Ovis canadensis*; Om *Ovibos moschatus*; Oo *Ourebia ourebi*; Rf *Redunca fulvorufula*; Sc *Syncerus caffer*; St *Saiga tartarica*; Ta *Tragelaphus angas*; Ti *Tragelaphus imberbis*; To *Taurotragus oryx*; Tq *Tetracerus quadricornis*; Tr *Boselaphus tragocamelus*; Ts *Tragelaphus scriptus*; Pr.c *"Praemegaceros" cazioti*, Dragonara Cave

Fig. 11. *Diagrama d'agrupacions jeràrquiques basat en cèrvids recents (dades de Kaiser, 2003). Les variables de mesodesgast considerades per a l'anàlisi d'agrupaments (distància euclidea normalitzada, NED) són: percentatge de relleu oclussal alt, percentatge de cúspides agudes i percentatge de cúspides polides.*
Brostejadors (amb majúscules): AA Alces alces; *BE* Boocercus euryceros; *EI* Ammodorcas clarkei; *GC* Giraffa camelopardalis; *LW* Litocranius talleri; *OH* Odocoileus hemionus ; *OJ* Okapia johnstoni; *OL* Capreolus capreolus ; *OV* Odocoileus virginianus; *TT* Tragelaphus strepsiceros
Pastadors (amb minúscules): ab Alcelaphus buselaphus; *al* Alcelaphus lichtensteinii; *bb* Bison bison; *ct* Connochaetes; *dl* Damaliscus lunatus; *he* Hippotragus equines; *hn* Hippotragus niger; *ke* Kobus ellipsiprymnus; *rr* Redunca redunca.
Dieta mixta (amb la primera lletra majúscula): Ap Axis porcinus; *Ax* Axis axis; *Bt* Budorcas taxicolor; *Ca* Capricornis sumatraensis; *Cc* Cervus canadensis; *Cd* Cervus duvauceli; *Ci* Capra ibex; *Cl* Camelus dromedarius; *Ru* Rusa unicolor; *Gg* Gazella granti; *Gt* Gazella thomsoni; *Lg* Lama lama; *Lv* Lama vicugna; *Ma* Antidorcas marsupialis; *Me* Aepyceros melampus; *Oc* Ovis canadensis; *Om* Ovibos moschatus; *Oo* Ourebia ourebi; *Rf* Redunca fulvorufula; *Sc* Syncerus caffer; *St* Saiga tartarica; *Ta* Tragelaphus angas; *Ti* Tragelaphus imberbis; *To* Taurotragus oryx; *Tq* Tetracerus quadricornis; *Tr* Boselaphus tragocamelus; *Ts* Tragelaphus scriptus; *Pr.c* "Praemegaceros" cazioti, *cova Dragonara.*

particular time and environment, because this feature can provide an intermediate level of information, between hypsodont, reflecting long-term adaptation, and microwear, providing direct information regarding the nature of individual feeding.

Mesowear analysis is based on the degree of facet development on the occlusal surfaces of teeth. The development of tooth cusps depends on the relative amounts of attritive and abrasive wear of tooth-to-tooth contact (attrition) over food-to-tooth contact (abrasion). The more attrition prevails, the higher the tooth cusp relief (difference in height between cusp tips and inter cusp valleys), as lower occlusal stress permits higher occlusal relief.

According to Fortelius & Solounias (2000), apices were characterized as sharp, rounded, or blunt (in decreasing order of facet development), and the valleys between them either high or low. Four main groups have been recognised, ranging from abrasion-dominated to attrition-dominated and corresponding to the following trophic categories: grazers, graze-dominated mixed feeders, browse-dominated mixed feeders, and browsers.

The cusps of *"P." cazioti* from Dragonara Cave show a prevalently sharp shape, as seen in the buccal projection of the more or less worn teeth examined, confirming that attrition produced by tooth-on-tooth contact predominates, as usually observed in cervids, whereas the abrasion produced by food becomes more evident only on strongly worn molars. For example, the metacone of some M^2 belonging to senile individuals (MPUR/V 1/126) maintains a smooth cusp, confirming that a precise occlusion between the upper and lower teeth is maintained until the very latest wear stages. Moreover, this observation confirms what was already observed by Fortelius & Solounias (2000). "The ontogenetic changes that take place in the occlusal configuration are minor, or else restricted to very early and very late wear stages".

A cluster analysis in which mesowear features of *"P." cazioti* from Dragonara Cave have been compared with some extant ruminants (53 species among cervids, bovids, giraffids and camelids, data from Fortelius & Solounias, 2000) shows quite good resolution in dividing selected extant ruminants according to their dietary adaptation (Fig. 11). Indeed, we can recognize the major

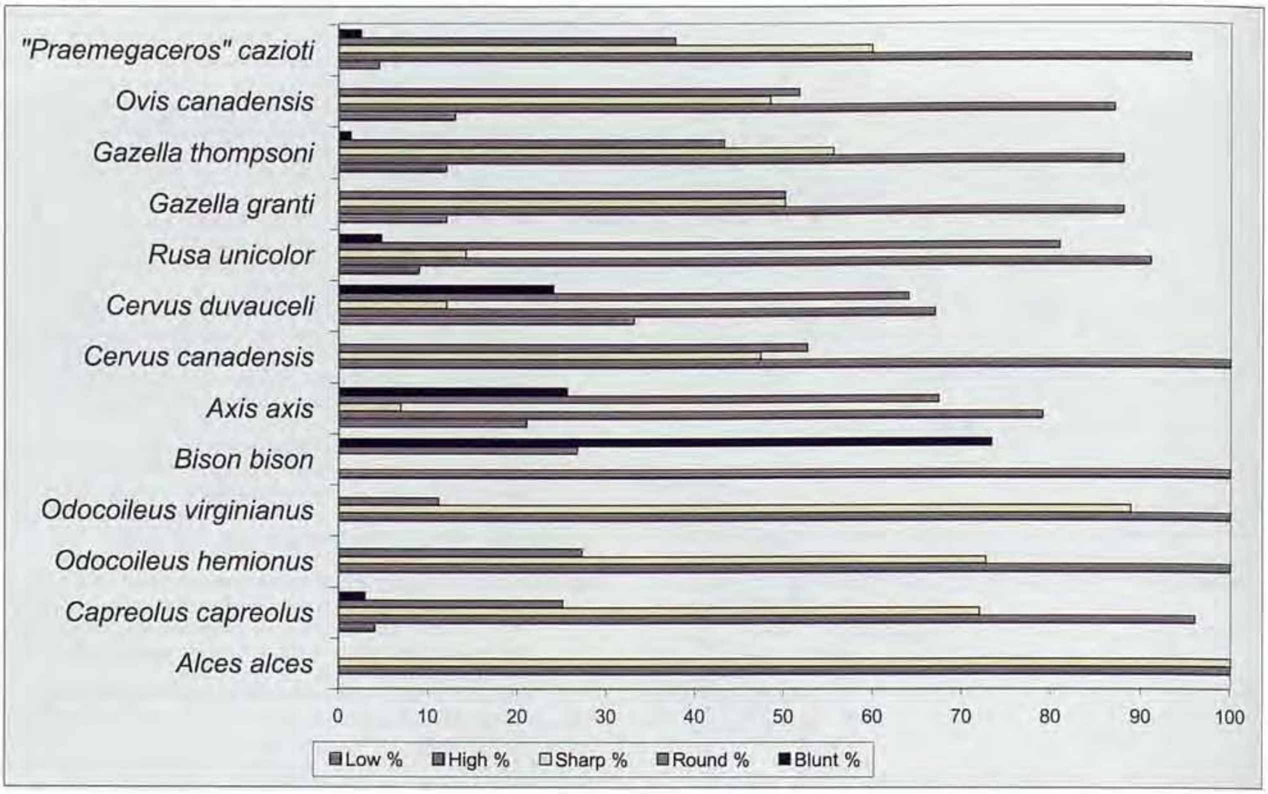

Fig. 12. Comparative histograms of mesowear variables based on "on tooth method". Data of extant species from Fortelius & Solounias (2000).

Fig. 12. Histogrames comparatius de variables de mesodesgast basades al "mètode sobre les dents". Dades de les espècies vivents, a partir de Fortelius & Solounias (2000).

clusters of typical grazers (A1) and of browsers and mixed-feeders (A2). Within the latter, we find the groups that include either mainly browsers (A2.1), or mixed-feeders (A2.2), the second divided into mixed versus grazer-feeders (A2.2.2) and more typical mixed-feeders (A2.2.1). *"P." cazioti* also falls among the latter, together with species such as *Gazella granti*, *G. thomsoni* and *Ovis canadensis* (see also Fig. 12), which are seasonal-regional mixed feeders, eating leaves but also grass and roughage, as often occurs among taxa regarded as representative of the "browsing-grazing transitional phase" (as far as microwear is concerned, see Solounias & Semprebon, 2000).

Taking all this into consideration, the mesowear method seems to be a less discriminatory tool in the attempt to detect minor differences in food exploitation, especially within a group where mixed-feeders are prevalent, as is the case with cervids.

REMARKS

Although in cervids, as well in each phylogenetic group, cranio-dental structure, morphology and proportions are constrained by their own evolutionary history, adaptation to a given trophic niche can involve some morphological skull and mandible features allowing optimal exploitation of feeding resources.

The skull and mandible of *"P." cazioti* from Dragonara show some features that, to a varying degree, are comparable to those of grazers: essentially, a square muzzle; rough, large origin area of *m. masseter*; non- hollow posterior border of vertical *ramus mandibulae*. Some other features are more frequent in mixed-feeders that eat large amounts of grasses. Cranium morphology suggests that the diet of the Dragonara cervid possibly included a larger amount of grasses than that of its hypothetical continental ancestor.

The microwear pattern agrees with cranium data. Dental microwear analysis of *"P." cazioti* from the Dragonara Cave enabled us to qualify it as a seasonal-mixed feeder, like some extant fallow deer characterised by similar pit density. However, its diet seems to have contained more gramineae, being presumably composed of harder vegetation than that of extant fallow deer species, even if sometimes it may have occasionally included ligneous plants and fruit, possibly during the milder months of the year. This could be connected with the contrasting seasonal conditions characterising Sardinia during the Late Pleistocene.

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APPENDIX

Examined taxa: *Moschus moschiferus* Linnaeus 1758, *Muntiacus muntjak* (Zimmermann 1780) *Cervus elaphus* Linnaeus 1758; *Cervus albirostris* Pzevalski 1883; *Cervus canadensis* Exleben 1777; *Cervus duvaucelli* Cuvier 1823; *Capreolus capreolus* (Linnaeus 1758); *Dama dama* (Linnaeus 1758); *Dama clactoniana* (Falconer 1868) *Alces alces* (Linnaeus 1758); *Rusa unicolor* (Kerr 1792); *Rusa timorensis* (Blainville 1822); *Odocoileus virginianus* (Zimmermann 1780); *Odocoileus hemionus* (Rafinesque 1817, *Axis axis* (Exleben 1777); *Elaphurus davidianus* Milne Edwards 1899; *Rangifer tarandus* (Linnaeus 1758; *Megaloceros giganteus* Blumenbach 1803; *"Praemegaceros" obscurus* (Azzaroli, 1953*)*, *Eucladoceros senesensis* Heintz 1970.

The specimens are kept at the following Institutions: Natural History Museum, London; Natuurmuseum, Rotterdam; Museum National d'Histoire Naturelle, Paris, Istitute de Paléontologie Humaine, Paris; Laboratoire départimental de Préhistoire du Lazaret, Nice; Naturhistorischen Museum, Basel; Museo di Scienze Naturali "La Specola", Firenze; Museo di geologia e Paleontologia, Firenze; Museo di Anatomia comparata, "La Sapienza" University of Rome; Museo di Paleontologia and Dipartimento di Scienze della Terra, "La Sapienza" University of Rome; Museo Civico di Zoologia, Rome; Istituto Italiano di Paleontologia Umana, Roma; Museo Preistorico Etnografico Pigorini, Roma.

22

THE ENDEMIC ELEPHANTS FROM SARDINIA: AN UNSOLVED PROBLEM

Maria Rita PALOMBO, Sergio GINESU, Rita Teresa MELIS & Stefania SIAS

PALOMBO, M.R., GINESU, S., MELIS, R.T. & SIAS, S. 2005. The endemic elephants from Sardinia: an unsolved problem. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 245-254.

Resum

Mammuthus lamarmorae (Major, 1883) (= *M. lamarmorai*, d'acord amb el ICZN 2000) fou identificat en base a restes molt escasses: alguns ossos tarsians, carpians i llargs obtinguts als dipòsits de la darrera edat glacial que afloren a Fontana Morimenta (Gonnesa, sud-oest de Sardenya); alguns molars aïllats descoberts a les bretxes post-tirrenianes (posteriors al MIS 5e) de Tramariglio (l'Alguer), a una bretxa pre-tirreniana (pre-MIS 5e, MIS 6?) que aflora a San Giovanni in Sinis (Oristano, Sardenya occidental) i a uns dipòsits al·luvials del Pleistocè Mitjà tardà que omplen la conca de Campu Giavesu (nord-oest de Sardenya, Sassari). En base a l'evidència morfològica i biomètrica, sembla possible que a Sardenya visquessin dos elefants endèmics de diferent mida. Degut a la incertesa amb les edats dels espècimens més grans, no es pot descartar la suposició que els elefants assolissin Sardenya en més d'una onada migratòria, talment com ja s'ha confirmat per a Sicília i Creta.

Paraules clau. Elefants endèmics, Pleistocè, Sardenya.

Abstract

Mammuthus lamarmorae (Major, 1883) (= *M. lamarmorai* according to ICZN 2000) was identified on the basis of very scanty remains: some tarsal, carpal and long bones, recovered from the last glacial deposits cropping out at Fontana Morimenta (Gonnesa, southwestern Sardinia); some isolated molars discovered in post-Tyrrhenian (post-MIS 5e) breccias at Tramariglio (Alghero), in a pre-Tyrrhenian (pre-MI substage 5e, ?MIS 6) beach deposit cropping out at S. Giovanni in Sinis (Oristano, western Sardinia) and in late Middle Pleistocene alluvial deposits filling the Campu Giavesu Basin (north-western Sardinia, Sassari). On the basis of morphological and biometric evidence, it seems possible that two endemic elephants of different size existed in Sardinia. Due to incertitude regarding the age of larger specimens, the supposition that mainland elephants reached Sardinia in more than one migration wave, as already affirmed for Sicily and Crete, cannot be completely ruled out.

Key Words. **Endemic elephants, Pleistocene, Sardinia.**

INTRODUCTION

During the Pleistocene, endemic elephants, descending from the Middle and Late Pleistocene continental *Elephas (Palaeoloxodon) antiquus* Falconer & Cautley, 1847, were quite common in unbalanced faunas on several eastern and western Mediterranean islands (Tilos, Crete, Cyprus, Sicily and Malta), whereas dwarfed taxa belonging to *Mammuthus* have been recorded only in Crete [*Mammuthus creticus* (Bate, 1907)] and Sardinia. Elephant remains were first discovered in Sardinia at the end of the XIXth century, when some tarsal, carpal and long bones were recovered from Late Pleistocene deposits near the village of Gonnesa (south-western Sardinia). On the basis of these bones, first reported by Acconci (1881) as similar in size to *"Elephas melitensis"*, Major (1883) described the new species "*Elephas lamarmorae*", without providing any illustration.

Later, during the second half of the 20th century, two molars were discovered respectively in post-Tyrrhenian (post-MIS 5e) breccias at Tramariglio (Alghero; Malatesta, 1954a) and in pre-Tyrrhenian (pre-MIS 5, ?MIS 6) beach deposits at S. Giovanni in Sinis (Ambrosetti, 1972; Melis *et al.*, 2001). More recently, we have had the opportunity to examine two specimens (one fragment and one complete last upper molar) collected at the beginning of the last century in alluvial deposits cropping out at Campu Giavesu (Sassari; Palombo *et al.*, 2003; Fig. 1).

The aim of this paper is to illustrate the elephant remains thus far recorded in Sardinia, to provide synthetic information on their stratigraphic context and to highlight the complexity of understanding the colonisation and evolutionary processes of Sardinian elephant populations.

FONTANA MORIMENTA

At the end of the 19th century, several bones of a small-size adult elephant were found in the area surrounding the village of Gonnesa. As reported by Acconci (1881), the bones, partially connected anatomi-

Fig. 1. A map of Sardinia showing localities where elephant remains have been discovered: 1 = Fontana Morimenta; 2 = Tramariglio; 3 = San Giovanni in Sinis; 4 = Campo Giavesu.

Fig. 1. *Mapa de Sardenya amb les localitats on s'han trobat restes d'elefants. 1 = Fontana Morimenta; 2 = Tramariglio; 3 = San Giovanni in Sinis; 4 = Campo Giavesu.*

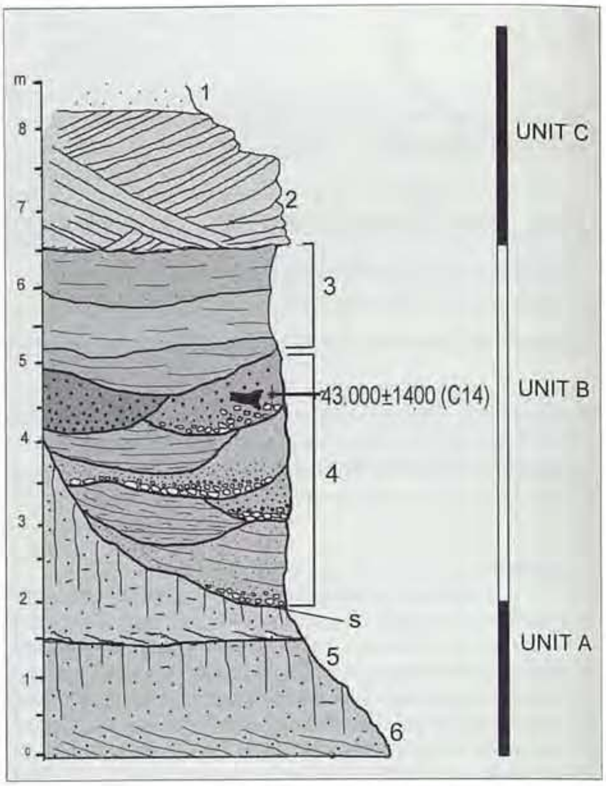

Fig.2. Gonnesa section.1: eolian sediments (Olocene); 2: eolianites (MIS 2); 3: alluvial deposits (parallel bedding MIS 3); 4: alluvial deposits (cross bedding MIS 3); 5: paleosol (MI substage5e); 6: eolianites (MIS 6); S: erosional surface (MIS 4).

Fig. 2. *Tall de Gonnesa. 1: sediments eòlics (Holocè); 2: eolianites (MIS 2); 3: dipòsits al·luvials (sedimentació paral·lela MIS 3); 4: dipòsits al·luvials (sedimentació creuada MIS 3); 5: paleosol (MI substage5e); 6: eolianites (MIS 6); S: superfície erosiva (MIS 4).*

cally, belonged to a skeleton found during railway construction. See Major (1883): "Dagegen nähert sich der sardische Zwerg am meisten – natürlich nicht in den Dimensionen, sondern die Cohnformation der Gelenkflachen, der Fußknochen – dem die Riesen der Gattung, dem *E. meridionalis* unserer Pliocäns...". Consequently, the English palaeontologist ascribed them to a new species, *"E. lamarmorae"*. Later, several authors either regarded *"E. lamarmorae"* as a valid species, belonging to the "*Palaeoloxodon*" genus (Osborn, 1942) or, more frequently, attributed the specimens to *Elephas mnaidriensis* or to *Elephas melitensis*, considering the Sardinian elephant very similar in size and morphology to specimens from Malta and Sicily (de Stefani, 1891; Novarese, 1913; Caterini, 1923; Joleaud, 1926; Vaufrey, 1929; Comaschi Caria, 1965). Unfortunately, at present, we have no certain information on the deposit containing the elephant remains, even if, in the course of time, the samples have always been recorded as belonging to "eolian" deposits. Indeed, strongly cemented, cross-bedded eolianites crop up at Fontana Morimenta. Consequently, it was generally believed that the elephant remains were found in these deposits. Nevertheless, in keeping with the taphonomic features of the acropodium bones preserved at the Naturhischen Museum in Bale, it seems quite improbable that the skeleton was buried in the strongly-cemented sediments; accordingly, the hypothesis that the remains were uncovered in alluvial sediments cannot be completely ruled out.

Geological Setting

During the Quaternary, the Gonnesa Basin was affected by eolian processes, producing dunes extending several kilometres inland. Orrù & Ulzega (1982,1986) recognized several generations of dunes along the coast. The authors attributed the oldest eolian deposits, called the "*Funtana Morimenta Formation*", to the Middle Pleistocene. Indeed, along the *Plage e Mesu* beach, a Tyrrhenian conglomerate (MI substage5e) lies on the erosional surface cutting the eolianites. A second eolian complex, well-cemented and with cross bedding, crops out in the valley of Riu Cabroila (Orrù & Ulzega, 1986). The complex has been attributed to the post-Tyrrhenian, and *Mammuthus lamarmorai* remains have thus far been thought to belong to these eolianites.

Nevertheless, about 200 metres south of the supposed discovery spot, a long stratigraphic sequence (about

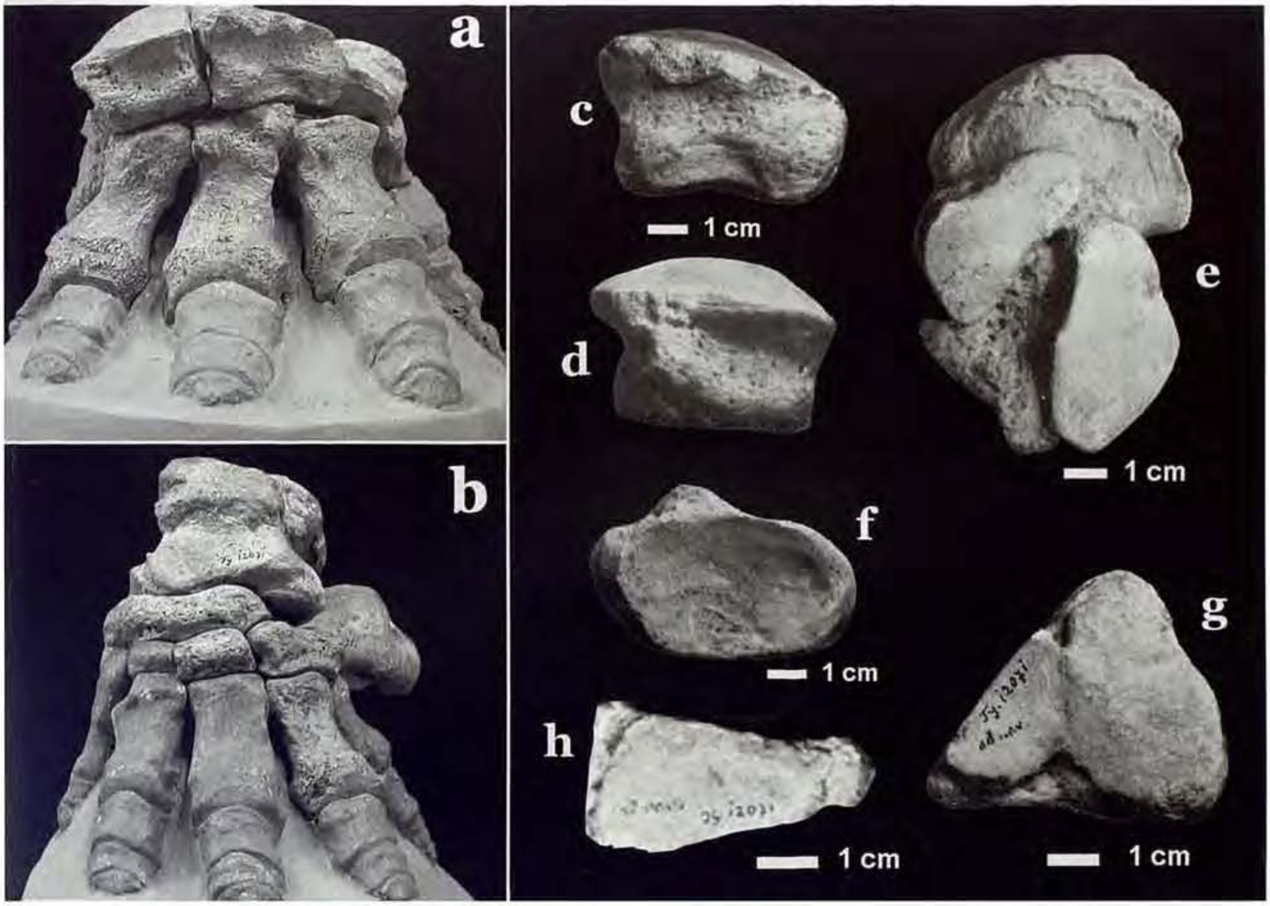

Fig. 3. *Mammuthus lamarmorai* (Major, 1883); Fontana Morinentu (Gonnesa, Western Sardinia), Late Pleistocene. Anterior (a) and posterior (b) footh (Naturhistorische Museum, Bale), uncinatum in anterior-dorsal view (c), magnum in anterior-dorsal view (d), calcaneum in anterior view (e), navicular in dorsal view (f), cuboid in dorsal view (g) , ectocuneiform in dorsal view (h).

Fig. 3. Mammuthus lamarmorai *(Major, 1883); Fontana Morinentu (Gonnesa, Western Sardinia), Pleistocè superior. Peu anterior (a) i posterior (b) (Naturhistorische Museum, Bale), uncinatum en norma anterior-dorsal (c), magnum en norma anterior-dorsal (d), calcaneum en norma anterior (e), navicular en norma dorsal (f), cuboid en norma dorsal (g) , ectocuneiform en norma dorsal (h).*

20 m), including eolian and alluvial deposits, has been exposed in a sand quarry (Melis *et al.*, 2002). Three units have been distinguished from bottom to top (Fig. 2): 1) Unit A is made up of eolian cross-bedded deposits (at the bottom) overlaid by a palaeosol cut by an erosional surface, on top of which eolian sandy deposits and red soil lie. The microstucture of soils indicates climatic evolution towards more arid conditions. A deep incision separates Unit A from the superimposed Unit B. 2) Unit B corresponds to about 6 m of gravely, sandy and clayey alluvium, deposited by a braided stream system. 3) Unit C is made up of about 7-8 m of eolian cross-bedded deposits and by yellowish-red soil, documenting the occurrence of a more or less Mediterranean, seasonally contrasting climate (Duchaufour, 1983). At the top of the section, well-cemented eolianites crop out, and the old railway is still visible.

An absolute age of 43,000 ± 1400 BP obtained for charcoal remains found in the alluvial deposit (Melis *et al.*, 2002), as well as sedimentological and mineralogical data, enable us to hypothesise that: 1) Unit A sediments deposited during MIS 6 (eolianits), MI substage 5e (soil occurring at the top of this unit) and MI substage 5d (eolian sediments and rubified soil); 2) the deep incision, separating Unit A from Unit B, probably testifies to erosional processes taking place during MIS 4; 3) the alluvial deposits of Unit B filled the small valley during MIS 3, under wet climatic conditions; 4) the eolian deposits, calcrete and paleosols on top of the alluvium could be respectively connected with the MIS 2 and the Early Holocene.

Elephant remains (Fig. 3)

The carpal of the second range of the Fontana Morimenta elephant, in particular the magnum and uncinatum (Fig.3 c,d), are higher than they are wide, more similar to those of *M. meridionalis* than to those of *E. antiquus*. In detail, on the magnum the articular facet for the trapezoid is divided, the articular surface for the lunatum and navicular is quite narrow and elongated and the articular surface for the second metacarpal is reduced. Moreover, on the uncinatum, the articular surface for the fourth metacarpal is concave. All these features resemble *M. meridionalis* carpal bones. As far as the tarsal bones are concerned, the navicular (Fig. 3 f) is considerably extended latero-medially and the articular surface for the astragalus is oval and notably concave; on the

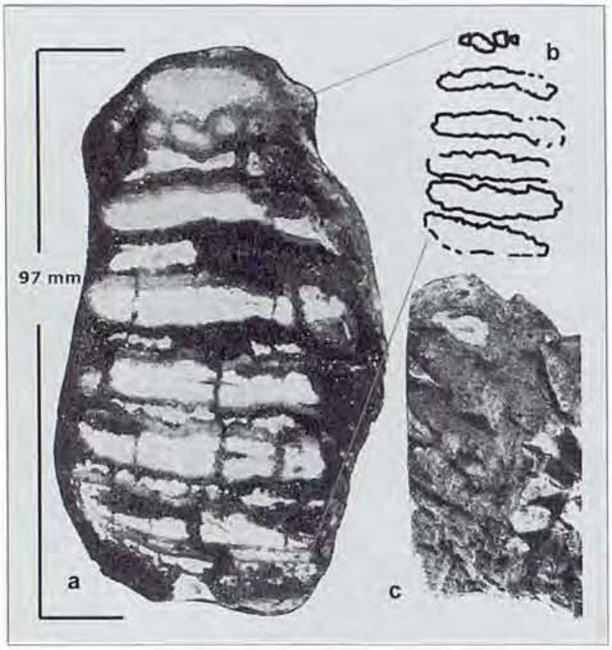

Fig. 4. *Mammuthus lamarmorai* (Major, 1883); Tramariglio, ? late Pleistocene. Right ?M^1 in occlusal (a, b) and labial (c) view.

Fig. 4. Mammuthus lamarmorai *(Major, 1883); Tramariglio, Pleistocè superior?, ?M^1 dret, en normes oclusiva (a, b) i labial (c).*

cudoid (Fig. 3 g), the extension and proportions of the articular surfaces for the calcaneum and navicular are more similar to *Mammuthus* than to *E. antiquus* tarsal bones; the ectocuneiform (Fig. 3 h) is narrower than in *E. antiquus*, extending much further towards the back than in *M. meridionalis* too, and it seems to articulate only with the third metatarsal, not with the fourth.

Moreover, the astragalus is very wide, almost completely impending over the fourth metatarsal. This corresponds to the considerable extension of the articular portion of the calcaneum (Fig. 3 c), in which the tuber is greatly extended transversely, providing a large attachment surface for the *gastrocnemius* and *soleus* muscles. The lower external profile of the calcaneum is greatly expanded.

In addition, carpals and tarsal bones seem to be arranged in a weakly-arcuated way. The structure provided better support for the body on the ground and better thrust in movements. All things considered, the limb posture of the Fontana Morimenta elephant might be quite different from that of continental taxa, adapted either to clear forest or more open environments. The Sardinian elephant possibly moved quite fast, even on rough terrain.

Furthermore, on the basis of the maximal length of the humerus (450 mm, according to Acconci, 1881), the Fontana Morimenta elephant was about 130-135 cm tall at the shoulder. This size exceeds the variability ranges of both *Mammuthus exilis* and *Elephas falconeri*, is notably less than the size hypothesised for *E. mnaidriensis* and parallels the size of elephants from Tilos (Palombo, 2004). It is worth noting that the smallest dwarfed elephants (Sicily, Crete, Tilos, the Santa Rosa islands) generally characterised strongly oligotypic faunas, where elephants were the only large mammals (Palombo, 2004). Conversely, among impoverished and unbalanced Sardinian Middle and Late Pleistocene faunas, a middle-sized cervid, *"Paraemegaceros" cazioti*, also occurred.

TRAMARIGLIO

Geological Setting

The coastal area between Capo Caccia and Punta Giglio (north-western Sardinia) is characterised by high calcareous cliffs, broken by small bays. Recent studies (Antonioli *et al.*, 1998a,b; Fara *et al.*, 1998), have pointed out the presence of a continuous beach deposit, with inserted eolian deposits, attributed to isotopic stage 5e, previously identified by Malatesta (1954b) in the Punta Negra and Dragonara sections. The eolian deposits have consequently been attributed both to a previous cold stage and to one following the 5e isotopic stage (Antonioli *et al.*, 1998a; Fara *et al.*, 1998).

In the stretch of coast between Punta del Dental and Torre di Tramariglio, on the eastern side of the Capo Caccia headland, strips of Quaternary deposits, prevalently breccias (Malatesta, 1954a), are placed against the calcareous Mesozoic cliffs. Five metres above sea level, a shoreline furrow with date mussel holes is evident. According to Malatesta (1970), the breccias must thus originate, at least in part, from a period preceding the sea level attributed to isotopic stage 5e (Antonioli *et al.*, 1998a).

Near the beach in tiny Tramariglio Bay, calcareous breccias cover the Tyrrhenian conglomerate and are interspersed by a horizon of red soil with mammalian remains (Malatesta, 1954a). On top of the breccias, which in some places extend down to sea level, lie eolian sandstones (?MIS 2). The latter also outcrop under the Tramariglio Tower and are the source of the tooth reported by Malatesta (1954a).

Elephant remains (Fig. 4)

An elephant molar (?M^1) was recovered from post-Tyrrhenian breccia at Tramariglio (Alghero; Malatesta, 1954a). Malatesta (1954a) supposed the molar to be nearly complete, since the first root supports three plates; the dimensions do not contradict this hypothesis. Unfortunately, the molar is not available at present. According to Malatesta's pictures (1954a, fig.1,2), some tooth features, such as thick, quite simple enamel and low lamellar frequency, paralleled those of some quite advanced *M. meridionalis* specimens. Nonetheless, we have to take into account both: 1) the reduced size of the Tramariglio specimen (smaller molars have more closely-spaced plates, Lister & Joysey, 1992) and 2) the fact that endemic elephants, relative to the decrease in tooth size, reduced the number of laminae, whereas the enamel became thicker and less pleated. Consequently, enamel thickness and lamellar frequency, the variables most frequently used in tracing elephant evolution, have to be used with care when analysing dwarfed elephants, especially when studying isolated teeth, as in this case.

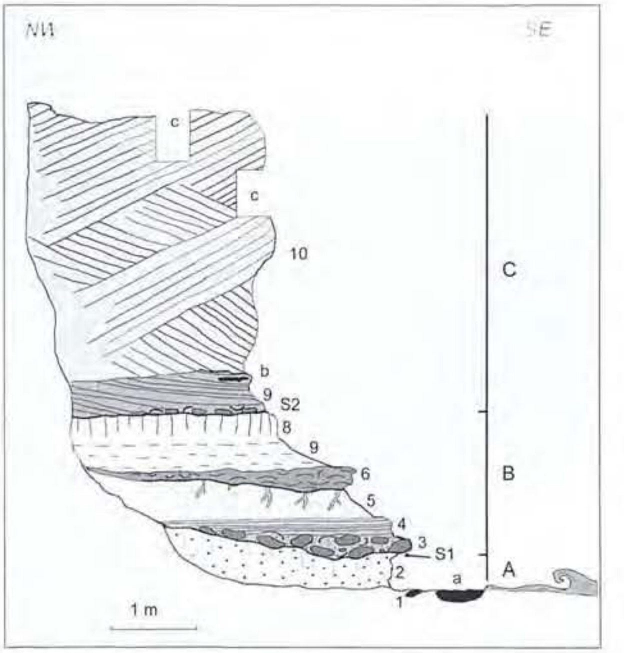

Fig.5. San Giovanni section. 1: calcrete; 2: palaeosol developed on beach sediments rich in *Helicoda* remains; 3 conglomerate containing pebbles from the erosion of the underlying level as well as basal pebbles; 4: beach sediments; 5: palaesols with rhizoliths; 6: marine deposits rich in *Mytilus* and *Ostrea* shells (MI substage 5e); 7: lagoonal deposits with *Limnea*; 8: calcrete; 9: beach deposits, overlying a conglomerate with remains of *Ostrea* shells; 10: dunes: a: Elephant molar; b: cervid remains; S1 and S2 erosional surfaces.A, B, C: sequences.

*Fig.5. Tall de San Giovanni. 1: calcreta; 2: palaeosol ric en restes d'*Helicoda *desenvolupat sobre sediments de platja; 3: conglomerat amb còdols procedents de l'erosió del nivell inferior al igual que còdols de basalt; 4: sediments de platja; 5: palaesols amb rizocrecions; 6: dipòsits marins rics en copinyes de* Mytilus *i* Ostrea *(MI subestadi 5e); 7: dipòsits de llacuna amb* Limnea; *8: calcreta; 9: dipòsits de platja, cobrint un conglomerat amb restes de copinyes d'*Ostrea*; 10: dunes; a: molar d'elefant; b: restes de cèrvid; S1 i S2 superficies erosives. A, B, C: seqüències.*

SAN GIOVANNI IN SINIS

Geological Setting

In the southern Sinis Peninsula (western Sardinian coast), late Middle Pleistocene marine and continental deposits crop out near the village of San Giovanni (Fig. 1). Rather complex stratigraphic successions appear over approx. 1 km in a quickly-retreating cliff, and several papers have been devoted to clarifying them (Maxia & Pecorini, 1968; Ambrosetti, 1972; Caloi *et al., 1980*; Ulzega *et al., 1980*; Ulzega & Ozer, 1982; Ulzega & Hearty, 1986; Carboni & Lecca, 1985; Dudaud *et al*., 1991; Kindler *et al*., 1997). In 1968, Maxia and Pecorini reported an elephant tooth, found in the calcrete level at the bottom of the sequence. The molar was then extensively described by Ambrosetti (1972) as belonging to post-Tyrrhenian levels.

According to our recent studies, three different sequences can be detected, from bottom to top, (Fig. 5): 1) Sequence A, sloping towards the southeast and characterised by calcrete overlaid by a pedogenised sandy deposit, rich in Helicidae and bioclastic fragments (benthic foraminifers, echinoids and red algae). 2) Erosional surface (S1) that truncates sequence A. 3) sequence B, lying on the erosional surface, consisting of: polygenic conglomerate, containing fragments reworked from an underlying eroded level, and basalt pebbles; cross-bedding beach sands, on which a palaeosol with rhyzoliths has developed; calcarenite with tightly-packed *Mytilus* and *Ostrea* shells; lagoonal deposits with *Limnea*. 4) Erosional surface (S2). 5) sequence C, which includes: a thin conglomerate with fragments of the underlying *Mytilus* level; beach low-angle cross-bedding sandy deposits, including rare remains of *"P." cazioti*; cross-bedded dune deposits. Ulzega & Hearty (1986), proposed an age of 90 ±15 ka (MIS substage 5c) for the *Mytilus* deposit (Sequence B). On the other hand, Duvaud *et al.* (1991) and Kindler *et al.* (1997) hypothesised that sequence A deposits could be earlier than MI substage 5e.

Studying the San Giovanni stratigraphic section confirms that, as already suggested by previous studies, the layer in which the elephant molar was found could be assigned to the pre-Tyrrhenian age (pre-MIS 5). The remains were buried within sandy beach sediments,

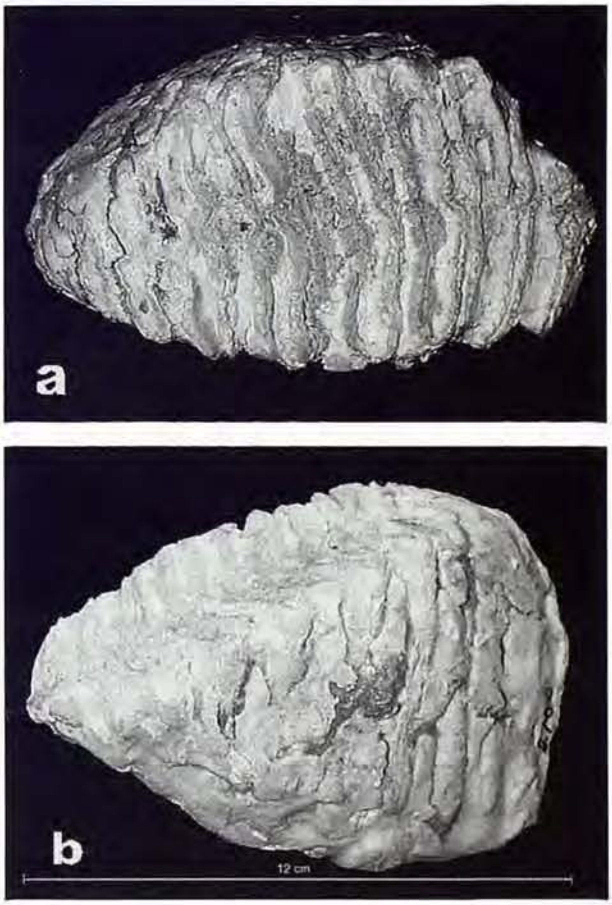

Fig.6. San Giovanni in Sinis (Western Sardinia), latest Middle Pleistocene. Right upper molar, in occlusal (above) and buccal (below) view. Approximately, x000 of natural size.

Fig.6. San Giovanni in Sinis (Sardenya occidental), Pleistocè Mitjà darrer. Molar dret superior en vista oclusiva (a dalt) i bucal (a sota). Aproximadament, x000 de la mida natural.

Fig. 7. Campo Giavesu landscape.

Fig. 7. Paisatge de Campo Giavesu.

affected by pedogenesis during a period of low sea level. Later, a calcrete developed under arid climatic conditions (?MIS 6). Furthermore, an increase in rainfall led to an erosive phase that truncated the soil overlying the calcrete. Marine transgression and deposition of "Tyrrhenian" (MI substage 5e) sediments followed, underlying the deposits containing the elephant molar.

Elephant Molar (Fig. 6)

The most important of the elephant remains discovered in the sixties by Prof. Giuseppe Pecorini is a well-preserved upper molar later described by Ambrosetti (1972). Ambrosetti considered it an M^3, although the gradually decreasing height typical of an M^3 elephant is not evident; moreover, the proportion of short and wide occlusal surfaces (greatest distal length =130 mm, functional (occlusal) length = 116 mm, greatest lingual breadth = 69 mm; functional (occlusal) breadth = 5.5 mm; height 90+ mm) is quite unusual for a penultimate *Mammuthus* tooth. On the other hand, there is no clear evidence of pressure from a posterior tooth; consequently, the hypothesis that the tooth is actually an M^2 of anomalous proportions cannot be definitively ruled out. The tooth is almost totally consumed by wear: of the 11 laminae, 9 are in use; the shape of the tooth suggests loss through wear of some other laminae at the front. The morphology of the molar, showing an oval- shaped occlusal surface, undulated enamel loops, and regularly folded enamel, suggests its attribution to the *Mammuthus* genus.

Enamel thickness (e = 1.8), average lamellar frequency (F = 8) and hypsodonty (HI = about 1,55) are consistent with this attribution. As far as the evolutionary degree of the San Giovanni tooth is concerned, we have to remember, as mentioned above, that in continental taxa, size reduction increases lamellar frequency (Lister & Joysey, 1992), whereas, in endemic elephant teeth, the number of laminae decreased and the enamel became thicker and less pleated with respect to their mainland ancestors. All things considered, on the basis of enamel thickness and lamellar frequency, the *M. lamarmorai* from San Giovanni in Sinis seems to be later than the Early Middle Pleistocene *Mammuthus trogontheri* (Pohlig, 1885). Nevertheless, due to the absence of any other remains, this hypothesis has not yet been fully substantiated.

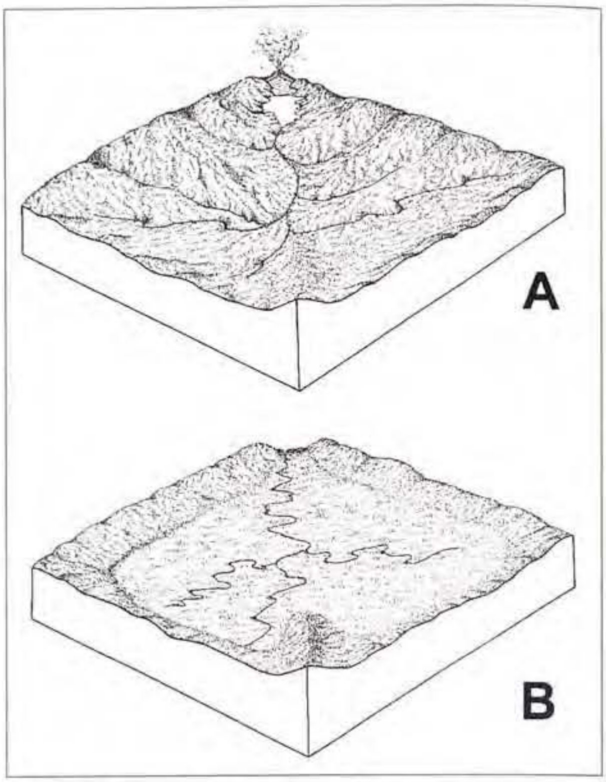

Fig 8. Blok diagrams showing geomorphological evolution of Campo Giavesu area

Fig 8. Diagrames de blocs que mostren l'evolució geomorfològica de l'àrea de Campo Giavesu.

CAMPO GIAVESU

Geological Setting

The geomorphological evolution of the Campu Giavesu area (Fig. 7) was greatly influenced by the Pleistocenic volcanic activity starting around 0.8 My (K/Ar date by Beccaluva *et al.*, 1981) and ending around 0.1 My (Ar/Ar date, cfr. Sias, 2002). At the beginning of the Middle Pleistocene, basaltic lava flows invaded the inner parts of the south-western basin of the Coghinas River, producing an important alluvial episode due to the obstruction of fluvial patterns. This phase was followed, for a short period, by drainage reorganization. Then, the activity of the Austidu volcano produced complete fossilization of the main river (Rio Mannu di Mores; Sias, 2002). This condition gave rise to a progressive over-alluvial process along the drainage network. In the same way, M.Annaru-M.Poddighe volcanic activity (dated 0.2 My,

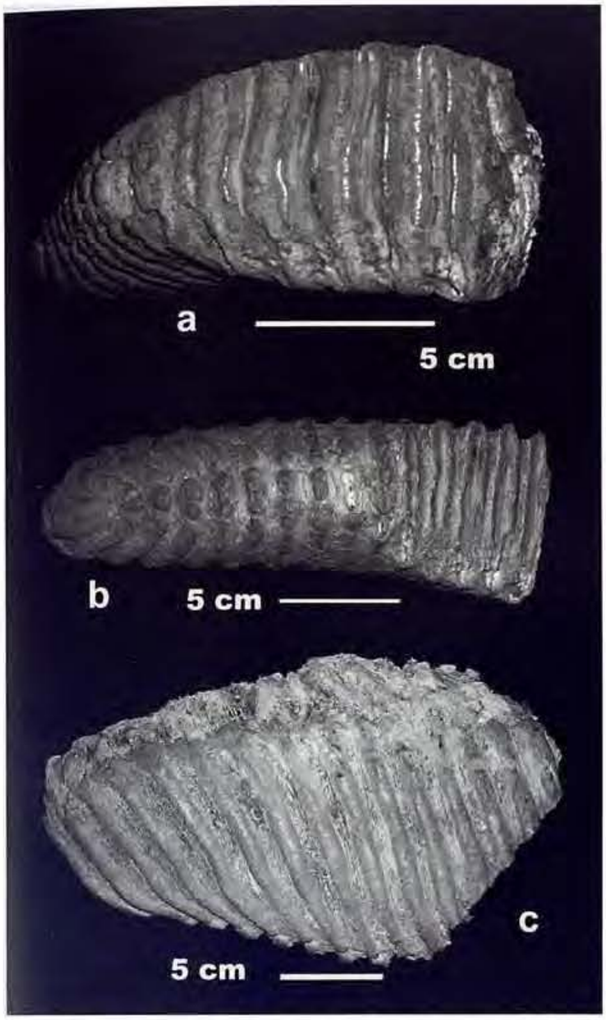

Fig. 9. Campu Giavesu (North-Western Sardinia), late Middle Pleistocene. Last right upper molar in occlusal (a), occlusal/posterior (b) and labial (c).

Fig. 9. Campu Giavesu (Sardenya nord-occidental), Pleistocè Mitjà darrer. Darrer molar superior dret en norma oclusiva (a), oclusiva/posterior (b) i labial (c).

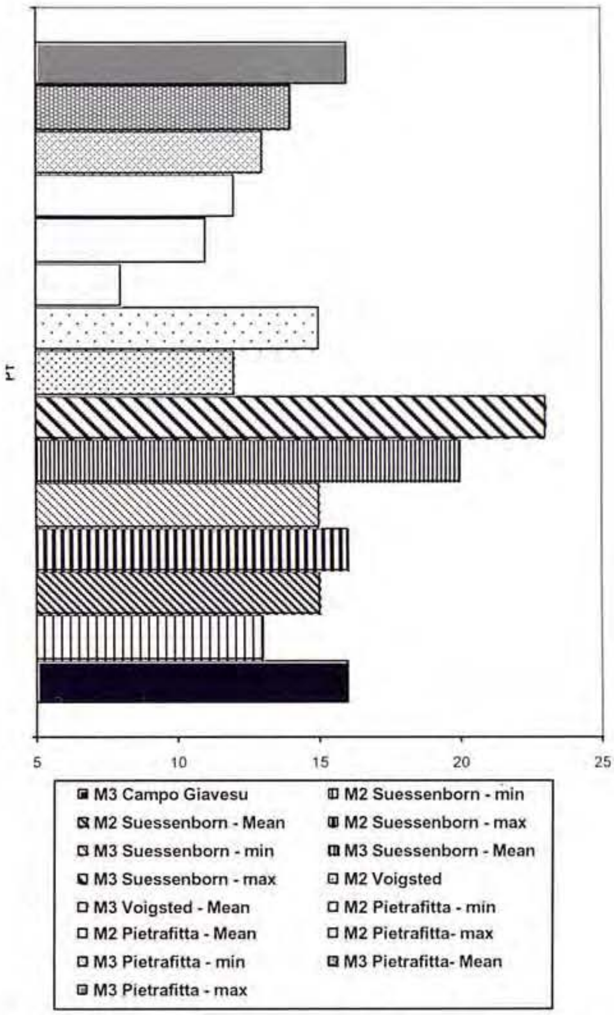

Fig. 10. Scatter diagram comparing plate number (Pf) of Campu Giavesu molar with the range of variability of M^2 and M^3 belonging to some important European samples of the late Early Pleistocene *Mammuthus meridionalis* and the Middle Pleistocene *Mammuthus trogontherii*.

Fig. 10. Diagrama de dispersió on es compara el nombre de plaques (Pf) del molar de Campu Giavesu amb l'espectre de variació dels M^2 i M^3 d'algunes mostres europees de Mammuthus meridionalis *del Pleistocè primerenc darrer i de* Mammuthus trogontherii *del Pleistocè Mitjà.*

K/Ar method, Beccaluva *et al.*, 1981) constrained the geomorphological evolution of the Campu Giavesu Plain: first, lava flows blocked river drainage and later, colluvial sediments filled the valley (Fig. 8). During the Upper Pleistocene, clayey sediments produced by alteration of the piroclastic rocks cropping out around the basin border deposited over the whole valley. The filling-up of the Campu Giavesu Plain was completed in about 0.2 My, giving rise to a complex drainage network (Fig. 8). Elephant remains were buried in sediments deposited in the marshland environment formed after M. Annaru volcanic activity.

Elephant molars (Fig. 9)

The samples recorded from Giavesu consist of a nearly-complete upper molar and a fragment of a very worn one, belonging to two different individuals. The complete specimen is a last upper molar, as indicated by the lack of any evidence of pressure by a posterior tooth and by the typical reduced height of posterior plates. The tooth has 15.5 plates (the anterior part of the molar is broken; consequently, only the posterior side of the first plate is present) including talon, the first seven in use. The three anterior plates apparently belong to the same root. The molar shows an elongated shape; its maximum length is 225 mm, the height of the first unworn plate 129 mm. The occlusal surface is ovoid, quite narrow, with a maximum width of 76.5 mm. The length and number of plates fall within the variability range for the "primitive" *Mammuthus trogontherii* M^2 (e.g. the teeth from Süssenborn, Guenther, 1969), whereas average enamel thickness is slightly greater and teeth are less hypsodont. Furthermore, according to Lister & Sher (2001), the laminae of the last upper molar range number from 16 to 22 in *M. trogontherii* and from 20 to 26 in *M. primigenius.*

On the other hand, the last upper molar of *Mammuthus trogontherii* representatives is usually larger, whereas the M^3 belonging to small specimens of

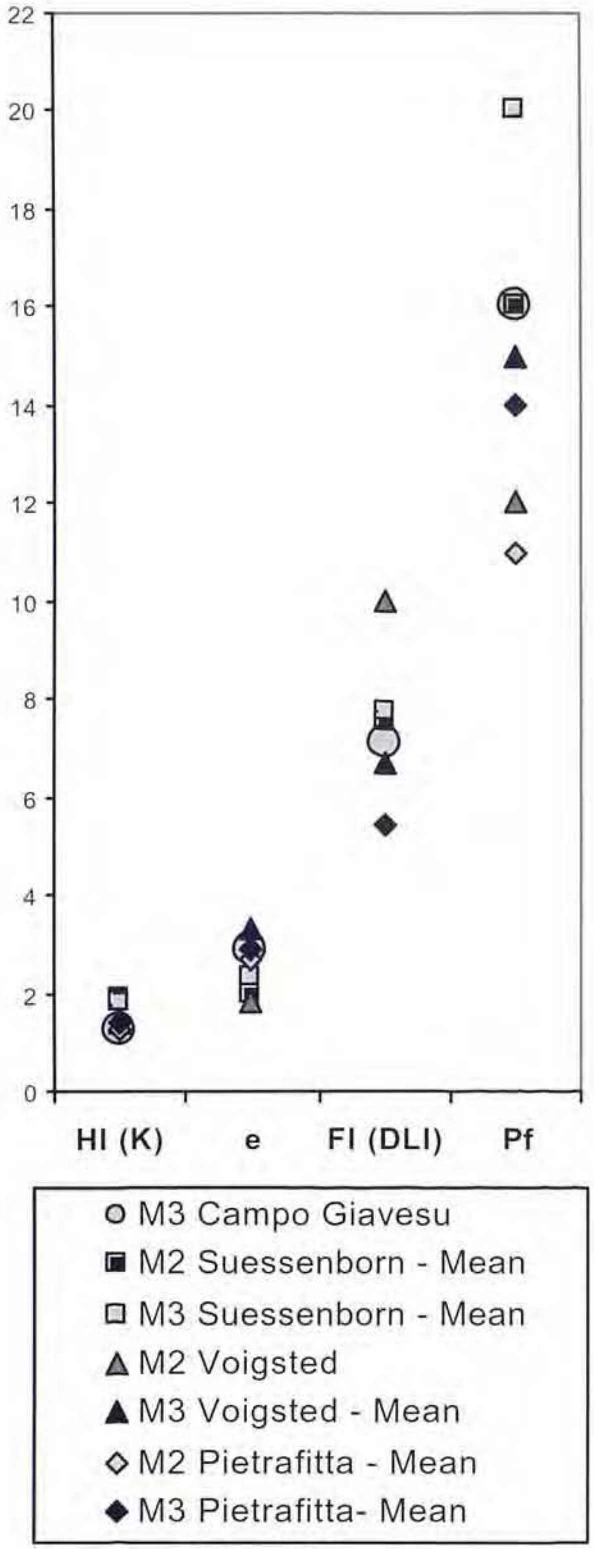

Fig. 11. Values of number of plates (Pf), hypsodonty index (HI), frequency index (DHI) and enamel thickness (e) of Campu Giavesu molar compared with the range of variability of M^2 and M^3 belonging to some important European samples of the late Early Pleistocene *Mammuthus meridionalis* and the Middle Pleistocene *Mammuthus trogontherii.*

Fig. 11. Valors dels nombres de plaques (Pf), índex d'hipsodòncia (HI), índex de freqüència (DHI) i gruixa de l'esmalt (e) del molar de Campu Giavesu en comparació amb l'espectre de variació dels M^2 i M^3 d'algunes mostres europees de Mammuthus meridionalis *del Pleistocè primerenc darrer i de* Mammuthus trogontherii *del Pleistocè Mitjà.*

Mammuthus primigenius (e.g., some teeth from Predemostí, Musil, 1968) displays more advanced features and more plates. Compared with the above-described molar from San Giovanni in Sinis, the occlusal surface of the tooth from Giave shows almost oval, non-undulated enamel loops, regularly but less densely plicated, and a greater average enamel thickness and lower lamellar index. Nevertheless, it differs from the *Mammuthus meridionalis* of the Italian late Early Pleistocene basically in the larger number of plates and higher frequency index (Figs. 10, 11).

All things considered, according to enamel thickness, hypsodonty index, lamellar frequency and enamel loop morphology, the M^3 from Giavesu appears more archaic than the specimen from San Giovanni in Sinis. Moreover, the molar from Giavesu belongs to a *Mammuthus* that is less reduced in size.

DISCUSSION

In the past few decades, several authors have emphasized the role played by different factors in explaining evolutionary patterns in isolated areas, especially changes in body size. For example, as in unbalanced insular faunas large terrestrial predators have not been recorded, the lack of their selection pressure was considered one of the most important factors in explaining insular dwarfing (see e.g. Thaler, 1973; Sondaar, 1977; Lomolino, 1985). Other authors have considered the host-island surface (e.g.Heaney, 1978; Burness *et al.*, 2001), some behavioural features such as territoriality (Case, 1978), feeding specialization (Lawlor, 1982) or trophic requirements, and the metabolic rate (e.g. Damuth, 1993; Demetrius, 2000; Burness *et al.*, 2001, and references therein) to be extremely important. Others have pointed to the impact of genetic segregation and endogamy (Malatesta, 1986) or reduction in the area, population density, overgrazing (Theodorou, 1988) or overcrowding (Roth, 1990). Accordingly, numerous hypotheses have been formulated to explain such body size modification; nevertheless, to date, no model seems to adequately explain the problems related to the origin and evolution of insular species (e.g., Foster, 1964; MacArthur & Wilson, 1967; Diamond & May, 1976; Alcover *et al.*, 1981, and references therein; Azzaroli, 1982; Lomolino, 1985; Malatesta, 1986; Caloi & Palombo, 1989, and references therein; Wilson, 1992; Lister, 1994; Sondaar *et al.*, 1996; Burness *et al.*, 2001; Roth, 2001; Poulakakis *et al.*, 2002). The process is the result of the interaction of several factors, whose dynamics vary from island to island or even on the same island at different times, as demonstrated by modification patterns in the Pleistocene elephant from Mediterranean islands (e.g., Crete, Sicily, Tilos; Palombo, 2004). Indeed, dwarfed elephant populations are especially appropriate subjects for such a study. On every island, each colonisation phase was generally followed by dwarfing processes: the same island and the same ancestor subsequently gave rise to endemic taxa of varying size. Moreover, it is worth noting that most dwarfed taxa (e.g. Sicilian *E. falconeri*) occurred in faunas where no other large mammals emerged, whereas the largest-sized taxa occurred in more diversified faunas (e.g. Sicilian *E. mnaidriensis* or Crete *E. "creutzburgi"*). Based on these observations, it appears that in an insular environment and in the absence of competition factors, large herbivores reached the minimum body size depending on their baup plane, in accordance with the niche available on the island, changing metabolic rate an trophic requirements. In addition, body size could also have been affected by occasional dispersal from the mainland to a nearby island, possibly by crossing a narrow stretch of water; that event could have led to periodic genetic contact (genetic introgression) and could have stunted the dwarfing process (see Palombo, 2004 and reference therein).

Taking all this into consideration, we could hypothesise that Sardinian elephants had to be quite large, due to the occurrence on the Island of endemic middle–sized cervids. Nonetheless, explaining the apparently different sizes of elephant remains found thus far in Sardinia is not a simple task.

In keeping with the scantiness of elephant remains, are we authorized to suppose that in Sardinia elephant population density was very low and the process of size reduction quite slow?

Supposing a possible difference in age, could we hypothesize that the larger and more archaic molars from Campu Giavesu belong to a direct ancestor of the elephant from San Giovanni in Sinis?

In addition, body size could also be affected by occasional dispersal from the mainland to a nearby island, possibly by crossing a narrow expanse of water. That event could lead to periodic genetic contact (genetic introgression) and could stunt the dwarfing process, or lead to the presence of species as large as the mainland equivalents, even on relatively small islands. Consequently, taking only size into consideration, we cannot exclude that the Campu Giavesu elephant might have reached the island in successive migration waves. Nevertheless, such a hypothesis disagrees with the morphological features shown by the Campu Giavesu and, possibly, by the Late Pleistocene molar from Tramariglio.

CONCLUSION

On the basis of the available evidence, it is likely that at least two endemic elephants of different size occurred in Sardinia. If stratigraphic evidence demonstrates that the Sardinian medium-sized elephant is actually older than the smaller *M. lamarmorai* specimen from San Giovanni in Sinis, the hypothesis that the Campu Giavesu and San Giovanni in Sinis specimens might represent different stages in a progressive size reduction trend can be formulated.

Moreover, the occurrence of elephant remains in Middle Pleistocene deposits allows one to hypothesise that the ancestor of the endemic elephants from Sardinia (an advanced representative of *Mammuthus meridionalis* or an archaic *Mammuthus trogontherii)* reached the island during the Early - Middle Pleistocene transition, when a noticeable drop in sea level reduced the distance between Sardinia-Corsica and continental coasts. Nevertheless, due to the scarcity of data, this hypothesis still has to be fully substantiated. Moreover, the supposition that mainland elephants reached Sardinia during several migration waves, as already stated for Sicily and Crete, cannot be ruled out.

A systematic review and a substantial increase in stratigraphic and biochronological data are needed to better understand the highly-complex colonisation of the island of Sardinia. Solving standing problems will further contribute to a more complete understanding of the process of elephant dwarfing, testing the hypothetical models proposed to date.

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ELEPHAS FALCONERI FROM SPINAGALLO CAVE (SOUTH-EASTERN SICILY, HYBLEAN PLATEAU, SIRACUSA):

A PRELIMINARY REPORT ON BRAIN TO BODY WEIGHT COMPARISON.

Maria Rita PALOMBO & Caterina GIOVINAZZO

PALOMBO, M.R. & GIOVINAZZO, C. 2005. *Elephas falconeri* from Spinagallo Cave (South-Eastern Sicily, Hyblean Plateau, Siracusa): a preliminary report on brain to body weight comparison. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 255-264.

Resum

El crani d'*Elephas* (*Palaeoloxodon*) *falconeri* Busk 1867 de la cova de Spinagallo (Pleistocè Mitjà, sud-est de Sicília, Itàlia) forneix l'evidència de que la mida relativa del cervell d'aquest elefant va augmentar significativament degut a les condicions d'aïllament. El pes del cervell de l'espècie continental *Elephas* (*Palaeoloxodon*) *antiquus* Falconer & Cautley, 1847, del Pleistocè mitjà tardà d'Itàlia, correspon a devers 1/600 del seu pes corporal, mentre que als exemplars nans adults procedents de la cova de Spinagallo aquesta proporció és de 1/60. El canvi significatiu en les proporcions del cervell a *Elephas falconeri* està relacionat amb la necessitat de mantenir un volum mínim del cervell funcional, fins i tot quan el crani es redueix molt. A més, són particularment evidents característiques pedomòrfiques a la forma del crani d'*Elephas falconeri*, semblant al crani d'exemplars juvenils d'elefants vivents i extingits, especialment als que pertanyen als gèneres *Elephas* i *Loxodonta*.

S'ha estimat la massa corporal d'elefants nans i continentals en base a noves equacions basades en l'alçària a la creu i la circumferència de les potes, comprovades als elefants vivents. L'adult d'*Elephas falconeri* hauria d'haver tingut una alçària màxima a la creu de devers 120 cm i un pes de devers 150 kg , amb valors devers el 70% inferiors en l'altària i devers el 98,4% en pes en comparació amb les alçàries i pesos promig estimades per als espècimens italians d'*Elephas antiquus*.

Paraules clau: *Elephas falconeri*, mida corporal, mida del cervell, Pleistocè Mitjà, Sicília, Itàlia.

Abstract

The skull of *Elephas* (*Palaeoloxodon*) *falconeri* Busk, 1867 from Spinagallo Cave (Middle Pleistocene; south-eastern Sicily, Italy) provides evidence that the brain of this dwarf elephant significantly increased in relative size as a result of its geographic isolation. Indeed, the brain weight of continental *Elephas (Palaeoloxodon) antiquus* Falconer & Cautley, 1847, from the late Middle Pleistocene of Italy, corresponded to about 1/1600 of its body weight, whereas for the adult dwarf specimens from Spinagallo Cave, this ratio was about 1/60. The significant change in brain proportions in *Elephas falconeri* was linked to the need to maintain minimal functional brain volume, even when the skull was greatly reduced in dimensions. Moreover, paedomorphic features are particularly evident in *Elephas falconeri* skull shape, similar to the skull of juvenile specimens of extant and fossil elephants, especially those belonging to the *Elephas* and *Loxodonta* genera.

We have estimated the body mass of dwarfed and continental elephants on the basis of new equations based upon shoulder height and pad circumference and tested on living elephants. On the basis of our results, the adult *Elephas falconeri* should have had a maximum height at withers of about 120 cm and a weight of about 150 kg, with values of about 70 % in height and about 98.4% in weight as compared with the average height and weight estimated for Italian specimens of *Elephas antiquus*.

Key words: *Elephas falconeri*, brain and body size, Middle Pleistocene, Sicily, Italy.

INTRODUCTION

Elephas falconeri, the smallest dwarfed elephant on the Mediterranean islands, was first described by Busk (1867) on Malta. Numerous, particularly significant samples were found in Sicily, in Luparello (Vaufrey, 1929; Imbesi, 1956) and Spinagallo Cave (Siracusa; Ambrosetti, 1968), as well as in the travertine cropping out at Alcamo (Trapani; Burgio & Cani, 1988). In the Spinagallo Cave deposit, oligotypic, clearly endemic mammal fauna was recovered between 1958 and 1960 (Accordi, 1962).

Based on absolute dating (isoleucine racemisation), an age of about 500 ka has been inferred for this fauna (Belluomini & Bada, 1985; Bada *et al.*, 1991). Over 3000 elephant remains were uncovered, representing at least 104 individuals belonging to all age groups, although the abundance of young and very young specimens is noteworthy.

A remarkable feature of *E. falconeri* Busk 1867 is the allometric reduction of the cranium, axial skeleton and limb bones, proportionally shorter than in mainland *E. antiquus* Falconer & Cautley 1847. *E. falconeri* seems to be characterised by precocious stunting of ontogenetic growth, as confirmed by skull features, tusk structure and cranium, axial skeleton and limb proportions (Palombo, 2001; 2003). Paedomorphic features are particularly evident in skull shape, characterised by extensive development of the brain case, linked to the need to maintain minimal functional brain volume, even when skull dimensions are greatly reduced. Actually, juvenile specimens of extant and fossil elephants, especially those belonging to the *Elephas* and *Loxodonta* genera, show very similar skull morphology to that of the adult skulls of *E. falconeri.*

Accordingly, we considered it of interest to evaluate how a reduction in size might affect the relationship between brain and body size, and whether the relatively larger brain size in *E. falconeri* depended more on precocious stunt of ontogenetic growth (paedomorphosys) or on changes in sense dependent (olfactory, optic, acoustic) and locomotion centres, induced by insular environmental conditions (e.g., Köhler & Moyà-Solà, 2004, and references therein). This paper illustrates the preliminary results of our ongoing research.

MATERIALS

To estimate brain versus body mass allometric reduction in *E. falconeri,* we used the samples found in the 20th and 50-60th years in Luparello (Vaufrey, 1929; Imbesi, 1956) and Spinagallo (Ambrosetti, 1968) Caves and in the travertine cropping out at Alcamo (Burgio & Cani, 1988; Fig. 1).

In particular, measurements of *E. falconeri* were taken from skulls and over 190 limb bones from Spinagallo Cave (Dipartimento di Scienze Geologiche, Catania University, and Museo di Paleontologia, "La Sapienza" University of Rome -MPUR), from Alcamo (Museo Geologico "G. G. Gemmellaro" – MGUP -, Dipartimento di Geologia e Geodesia, Palermo University) and from Luparello (MGUP and Institut de Paléontologie Humaine de Paris – IPH).

Moreover, measurements of *Elephas mnadriensis* Adams 1874 were taken from 7 skulls and 31 limb bones from Puntali Cave (MGUP, Museo di Paleontologia,

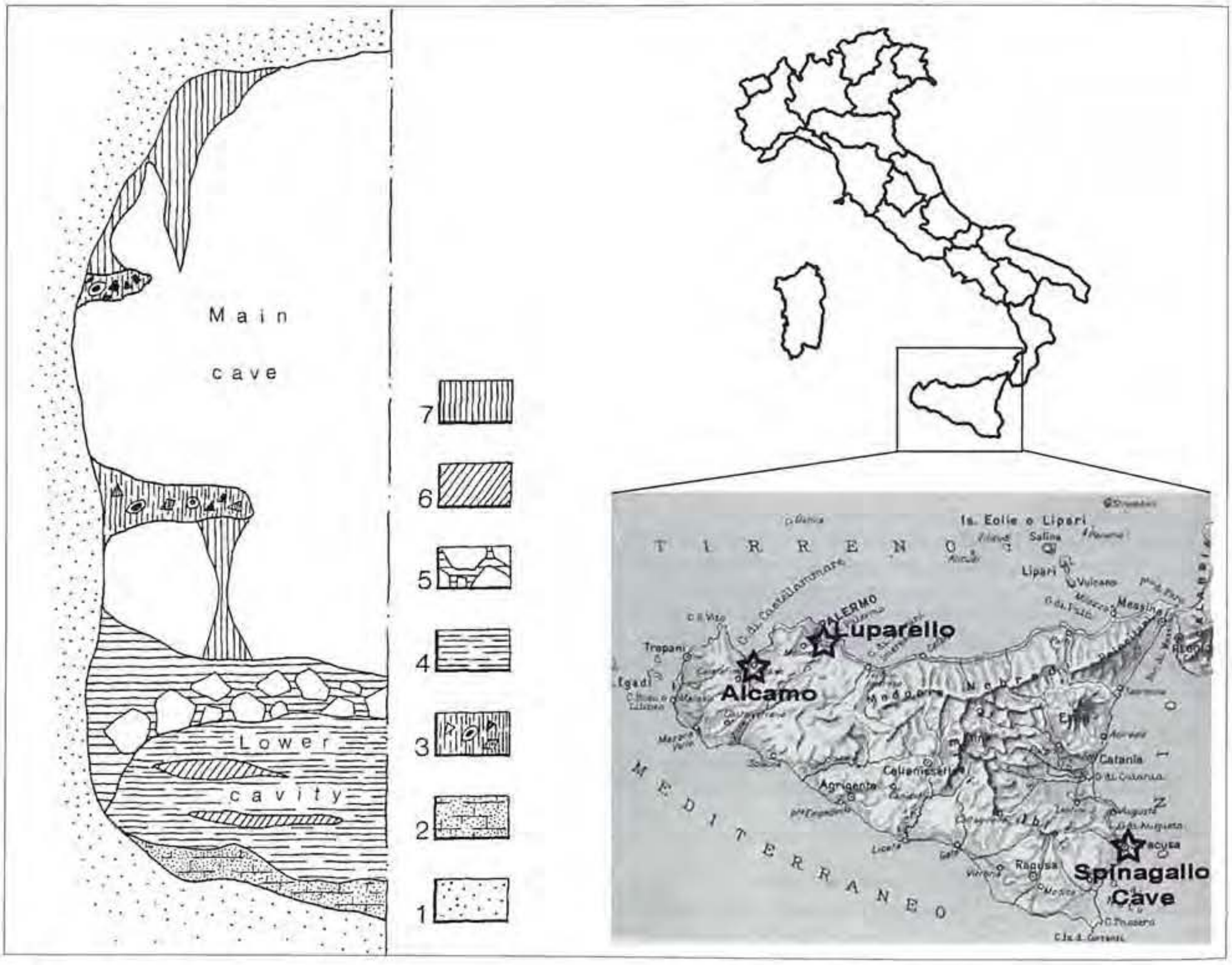
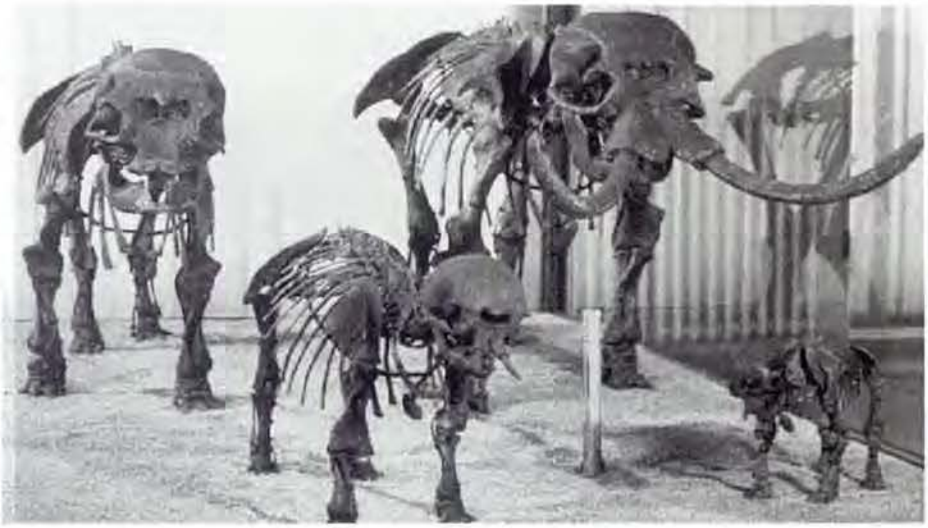


Fig. 1. Location of the most important Middle Pleistocene sites containing *E. falconeri* specimens. On the left, a schematic section of the Spinagallo Cave main cavity: 1 = Miocene limestone; 2 = "Milazzian" fossiliferous levels; 3 = bone breccia with *Elephas mnaidriensis* Adams, 1924 and *Hippopotamus pentlandi* Meyer, 1832 remains; 4 = calcareous sands with *E. falconeri* remains; 5 = floor of cemented blocks; 6 = stalagmitic levels that partly include the elephant bones; 7 = recent stalactite and stalagmite.

Fig. 1. Localització de les localitats del Pleistocè mitjà més importants amb E. falconeri. *A l'esquerra, secció esquemàtica de la part principal de la Cova de Spinagallo. 1: Calcàries del Miocè. 2: Nivells fossilifers del "Milazzià". 3: Bretxa ossifera amb restes d'*E. mnaidriensis *Adams, 1924 i* Hippopotamus pentlandi *Meyer, 1832. 4: Arenes calcàries amb restes d'*E. falconeri. *5: Pis de blocs cimentats. 6: Nivells estalagmitics que inclouen en part ossos d'elefants. 7: Estalactites i estalagmites recents.*

Fig 2. *Elephas falconeri* Busk, 1867; Spinagallo cave (Syracuse, South-Eastern Sicily), *E. falconeri* faunal complex, early Middle Pleistocene. Reconstructed skeletons of a male (on the right), a female (left) and two young males (Museo di Paleontologia, "La Sapienza" University, Rome).

Fig. 2. Elephas falconeri *Busk, 1867; Cova de Spinagallo (Syracusa, sud-est de Sicilia), complex faunístic* E. falconeri. *Pleistocè Mitjà primerenc. Esquelets reconstruïts d'un mascle (a la dreta), una femella (esquerra) i dos mascles joves (Museu de Paleontologia, Universitat de "La Sapienza", Roma).*



Padova University - MPUP) and from some limb bones from San Teodoro Cave (MGUP, IPH).

Skull and bone measurements of *E. antiquus* were taken from 2 complete skeletons from Grotte Santo Stefano (MPUR = speciment 'B' and Museo Civico "Andrea Doria", Genova = specimen "A" as in Palombo & Villa, 2003), and one nearly-complete skeleton from Riano 'Il Crocifisso'(MPUR; Maccagno, 1962); skull measurements were also taken from specimens from Pian dell'Olmo (MPUR; Maccagno, 1962), Pignataro Interamna (Museo di Paleontologia, Napoli -MPN; Osborn, 1942, D'Erasmo & Moncharmont Zei, 1955) and Val di Chiana (Museo di Paleontologia, Florence – IGF).

As far as extant species are concerned, we examined adult specimens of *Loxodonta africana* (Blumenbach, 1797) and an *Elephas maximus indicus* Cuvier, 1798 calf (Museo Civico di Zoologia, Rome); other data are courtesy of: Kruger National Park, Tulsa Zoological Park, Chester Zoo, Knoxville Zoological Garden, Indianapolis Zoo for *L. africana* and Honolulu Zoo for *E. maximus* Linnaeus, 1758.

Directly-examined brain casts come from: *E. falconeri*, two specimens from Spinagallo Cave (Accordi & Palombo, 1971) and two natural casts from Alcamo (Burgio & Cani, 1988; MGUP); *E. manaidriensis*, four more or less incomplete casts belonging to specimens kept in the MPUP (Piccoli *et al.*, 1970; Palombo, unpublished data); *E. antiquus* from Pian dell'Olmo (MPUR).

Additional data for extant and fossil taxa were obtained from Heynes (1991), Osborn (1942) and Dechaseaux (1959) respectively.

METHODS

Body mass estimation

A correct estimation of body mass of dwarfed *Elephas falconeri* constitutes the most important basis for evaluating relative brain size changes undergone by this dwarfed species after its geographic and reproductive isolation from its continental ancestor. This is not a simple task, due to the peculiar proportions of the *E. falconeri* body, thus far determined only from compiled skeletons (Fig. 2).

The characteristic dentition of the elephant makes it imperative to focus on long bone dimensions, whose size and proportions change during growth, when estimating body mass (Maglio, 1972). Moreover, as far as dwarfed mammals are concerned, due the disproportion in tooth dimension characterising insular species (see e.g. Maglio, 1972; Gould, 1975; Azzaroli, 1982; Wayne, 1986; Demetrius, 2000; Alba *et al.*, 2001), it is widely accepted that limb bone parameters and shoulder height are the most reliable body mass predictors (e.g., Damuth, 1990; Roth, 1990; Scott, 1990; Köhler, 1993).

Some authors have suggested using maximum humerus and femur length for estimating body mass in specimens smaller than 2000 kg (see Roth, 1990). As far as body size estimation of dwarfed elephants is concerned, Roth (1990) employed long bone dimensions (length and circumference of humerus and femur) as, in her opinion, they "consistently provided the best mass estimated" (Roth, 1990, p.158). The above-mentioned author applied some established formulas for testing the relationships between long bone dimensions and body mass in animals of similar size and structure to dwarfed elephants (static interspecific model). Moreover, the same author estimated body mass of dwarfed elephants also using regressions of mass over shoulder height (ontogenetic model; Roth, 1990, p. 158); the author pointed out that estimated body weights were greater than those obtained using bone length. Notably, the limbs of dwarfed elephants are more slender than those of continental ones, probably in response to a different anatomical structure required by reduced body size, changing in turn the static and dynamic equilibrium (Palombo, 1996). On the other hand, the size of the largest *E. falconeri* was nearly the same as that of an African elephant about three years old, in spite of eventual differences in overall build. Moreover, according to our data, the "height at the shoulder / body weight" ratio in a calf averages one-fourth that of an adult African elephant.

Indeed, in accordance with the paedomorphic cha-

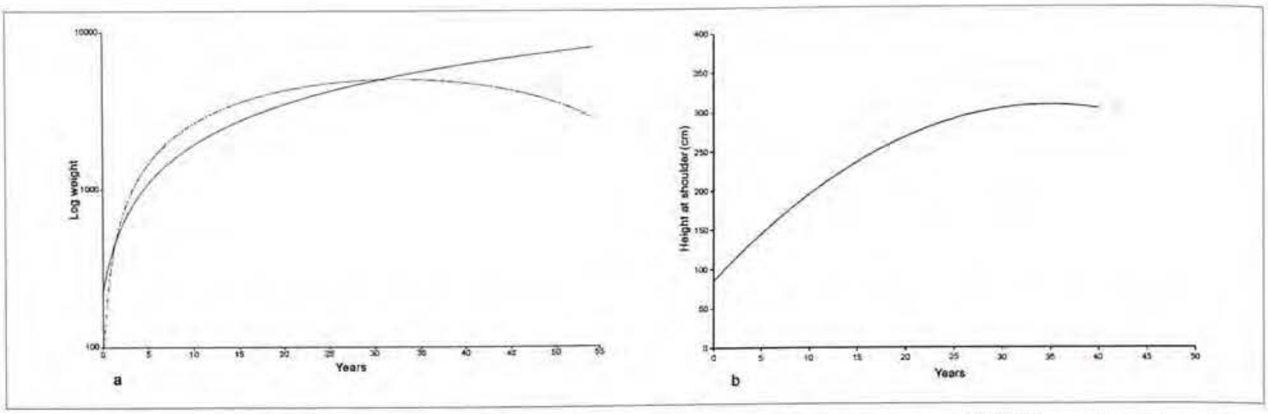


Fig. 3. Increase in body mass of African elephants during growth: polynomial line of second order (dotted) and logarithmic line (continuous), (a). Shoulder height plotted against age (b).

Fig. 3. Increment en massa corporal dels elefants africans durant el seu creixement: línia polinòmica de segon ordre (puntejat) i línia logarítmica (contínua). (a). Alçària a la creu respecte l'edat (b).

racteristics of *E. falconeri*, in order to estimate the average weight of an adult individual belonging to this species, we have to discern the allometric relationships between bone dimensions and body mass at different growth stages.

In keeping with the fact that mass can only be estimated approximately for fossil taxa, we tried to predict the body mass of *E. falconeri* by computing regressions of mass over shoulder height on the basis of a new data set obtained, along with associated body mass, from extant elephant individuals belonging to different age groups, as well as by estimating the allometric relationships between body mass and long bone dimensions during the ontogenetic growth of single individuals. This makes it possible to test the reliability of the estimated body mass using different equations.

According to our data, body mass in extant Indian and African elephants increases rapidly from birth up to 8 years, after which the increase is not so significant. Weight remains quite stable from age 40 to old age, when it slightly decreases (Fig. 3a). It is worth noting that shoulder height and body size are closely correlated (Fig. 3b).

Moreover, taking into account the columnar limb and graviportal structure of elephants (Biewener, 2000), we have estimated the body size of living individuals (whose weight was known) on the basis of hand and foot circumferences, on which body weight is nearly equally distributed. We tested the validity of methods on extant specimens using pad circumferences and shoulder height, comparing our estimated weights with the actual body weight known for each individual examined. Our data pointed to a strong correlation between both body mass and pad circumferences, and body mass and shoulder height (Fig. 4, Tab. 1).

Accordingly, we have estimated the body size of *E. falconeri* from Spinagallo Cave using our equations based on pad circumference and shoulder height, as well as the equations based on femora and humeri length, as proposed in Roth (1990).

Brain Mass Estimation

We measured cranial capacities on the basis of casts of the brain case, both in fossils and extant individuals. However, in keeping with the fact that endocranial volume is not equivalent to brain volume, due the space occupied by the *dura mater*, arachnoid and *pia mater*, as well as by cranial nerves and blood vessels (note that meninxes are particularly thick in elephants), we plotted cranial capacities directly against body mass and compared the results with those obtained converting cranial capacities to brain mass. The volume of brain case casts (cranial capacities) of specimens was transformed into brain mass, calculating brain volume from cranial capacity and then converting brain volume to brain mass. To compute brain mass, we used the following equation: brain mass (g) = brain volume (cm^3) W 1.036 (specific weight of brain substance; g/cm^3; Ebinger, 1974; Röhrs & Ebinger, 2001; Köhler & Moyà Solà, 2004).

The Encephalisation Quotient (EQ) is defined as the ratio of the actual brain mass (Mbrain) to the expected brain mass given body size. Thus: EQ = M_{brain} / E_{brain}. E_{brain} is the expected brain mass (in grams) for a mammal with body mass M_{body} (also in grams). We have calculated E_{brain} with the following formulas:

$E_{brain} = 0{,}12 M_{body}^{2/3}$ (Jerison, 1973)
$E_{brain} = 0{,}059 M_{body}^{0.76}$ (Martin, 1984)

Regression	*R^2*	*SEE*	*F*	*Sig.*
logBM =3.2039logHS - 4.096	0.93651817	0.07478	103.27	p<0.00002
logBM =3.3221logPC - 3.388	0.96625034	0.05732	143.15	p<0.00007
BM = Body mass (g); HW = height at shoulder (cm); PC = Pad circumference (cm)				

Table 1. Regression equations used in the estimating of body mass in extant and fossil elephants.

Taula 1. Equacions de regressió emprades per a estimar la massa corporal d'elefants fòssils i actuals.

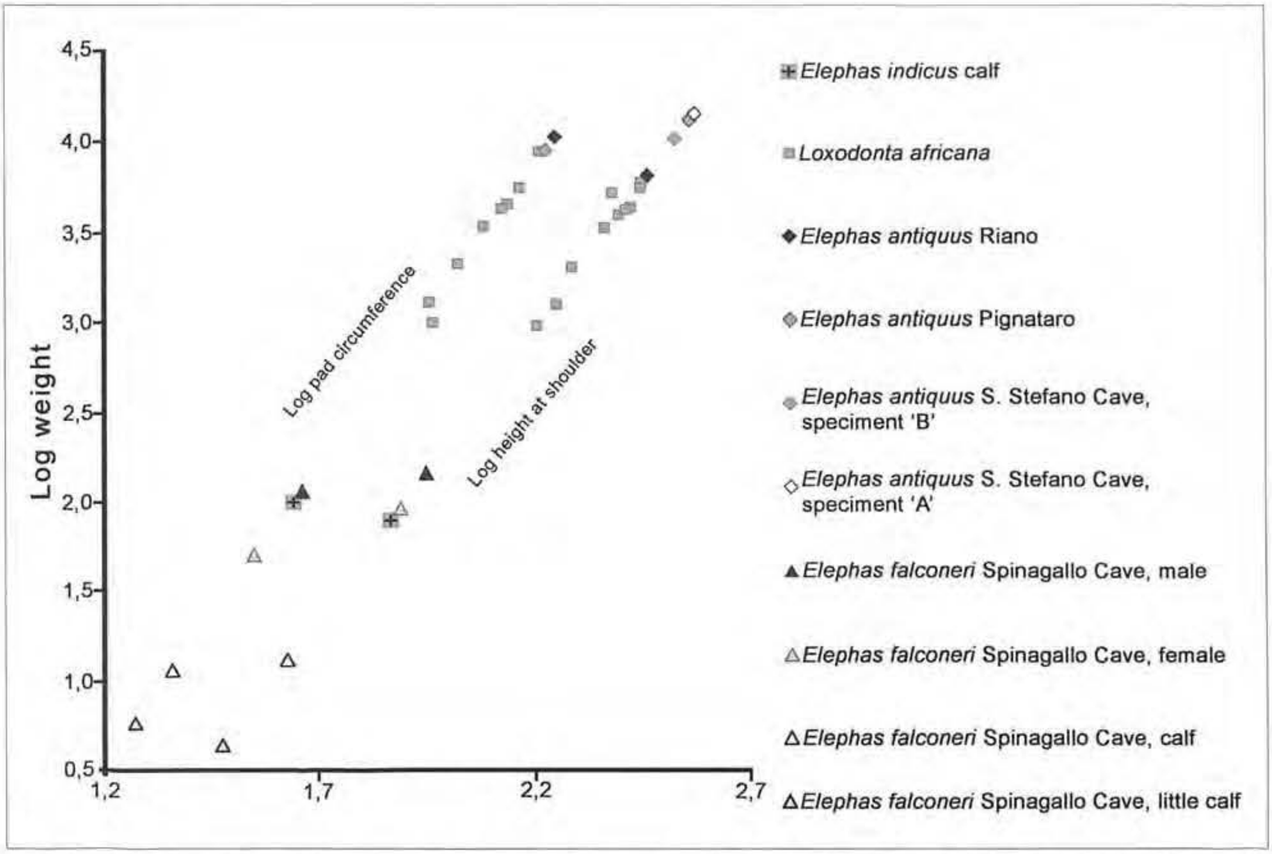


Fig. 4. Log_{10} body mass (kg) plotted against $\log_{10}$ of pad circumference (mm) and $\log_{10}$ of height at shoulder (mm) in extant elephant, *Elephas antiquus* Falconer & Cautley, 1847 and *Elephas falconeri* Busk, 1867.

Fig. 4. Log$_{10}$ *de la massa corporal (kg) respecte el log*$_{10}$ *de la circumferència de les potes (mm) i el log*$_{10}$ *de l'alçària a nivell de la creu (mm) als elefants actuals,* Elephas antiquus *Falconer & Cautley, 1847 i* Elephas falconeri *Busk, 1867.*

RESULTS

Body mass of *E. falconeri*

In Tab. 2 the body masses estimated for *E. falconeri* skeletons kept at the MPUR are reported. In particular, according to our equations, we estimated a weight of 91.1 kg for the adult female specimen (MPUR n 2), using shoulder height, and 51 kg with regression based on pad circumference; body weights calculated on the basis of humerus and femur dimensions (length -circumference) are, on the contrary, 79.8 kg - 240.2 kg and 81.3 kg -189.2 kg respectively. In addition, using the same equations, the estimated weight of E. *falconeri* (MPUR, DDG, MGUP and IPH specimens) ranges from 59.5 kg to 174.1 kg and from 183.4 kg to 520 kg on the basis of humerus length and circumference, and from 81.4 kg to 151.52 kg and from 166 kg to 517 kg on the basis of femur length and circumference. Moreover, according to the largest specimen (DDG, specimen S1) found in Spinagallo Cave, the maximal body mass obtained using femur length should be 298.27 kg.

Elephas falconeri specimens	*BM-HS*	*BM-PC*
male	141.14	114.2
female	91.12	51.07
calf	12.87	11.79
little calf	4.33	6.16
BM-HS = Body mass (kg) estimated from height at shoulder regression equation from Table 1; BM-PC = Body mass (kg) estimated from pad circumference regression equation from Table 1		

Table 2. Body mass estimation for *Elephas falconeri* Busk, 1867.

Taula 2. Estimes de la massa corporal per a Elephas falconeri *Busk, 1867.*

It is worth noting that the height value obtained using humerus and femur circumferences confirms that these regression equations are not available for elephants, as we also verified on extant adult African individuals, whose weight calculated on this basis was about 40% overestimated.

In conclusion, our preliminary analysis lead us to affirm that weights estimated on the basis of the regression of shoulder height are the most consistent with the expected values for elephants of a size similar to that of *E. falconeri*. The *E. falconeri* weights, estimated on the basis of pad circumference, are underestimated and overestimated respectively for adults and young individuals.

Indeed, an *E. maximus indicus* calf, 4 cm shorter than the *E. falconeri* female, weighs 14 kg less. On the contrary, the *E. falconeri* female had a foot circumference 7 cm smaller than the *E. maximus indicus* calf; this difference can be translated into a reduction in the estimated weight of 49 kg. In reality, the feet of adult *E. falconeri* were more digitigraded than *E. antiquus* ones, probably in keeping with the decrease in body mass, a more agile gait and the need for more secure movements on relatively uneven ground and in climbing rather steep slopes (Palombo, 1996). On the contrary, the 9% difference in weight estimated for the *E. falconeri* calf (MPUR, 3), on the basis of pad circumference and shoulder height, falls within the confidence interval, confirming allometric growth.

Morphology of the brain-case endocast

Compared to those of *E. antiquus*, *E. falconeri* endocasts are more globular in shape, with a less dorsally-flattened outline. The lateral and Sylvian fissures are narrower, the temporal lobes less protrusive, the frontal lobes more curved, the olfactory bulbs larger and in an almost ventral position and the cerebellum higher and extending less at the rear. The overall shape of the brain of Spinagallo elephants is also more compact with respect to both *E. maximus* and *L. africana* (Fig. 6); however, it does not seem related to the noticeable allometric augmentation in relative brain mass, as shown by the morphology of brains belonging to young individuals of extant *L. africana* (Fig. 7).

The sense-dependent parts of the *E. falconeri* brain show a development unlike that of E. *antiquus* and extant elephants: the olfactory bulbs are not only proportionally larger, but they also have a more extensive system of nervous terminations; the impression area of the petrosal, even if not clearly delimited, does not seem to have changed significantly; the *area striata* is wide, suggesting great functionality of the vision centre, in accordance with the large orbit size (Fig. 6a).

The shape and position of the cerebellum is quite different from that of fossil and extant adult elephants:

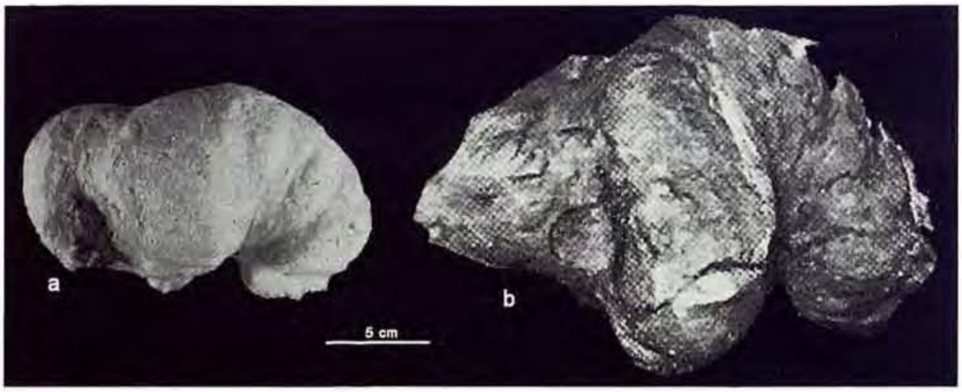


Fig . 5. Lateral view of cerebral cavity casts of *Elephas falconeri* Busk, 1867 (Spinagallo, female MPUR sn2; a) and *Elephas antiquus* Falconer & Cautley, 1847 (Pian dell'Olmo, MPUR sn1; b).

*Fig. 5. Vista lateral dels motlles de la cavitat cerebral d'*Elephas falconeri *Busk, 1867 (Spinagallo, femella MPUR sn2; a) i* Elephas antiquus *Falconer & Cautley, 1847 (Pian dell'Olmo, MPUR sn1; b).*

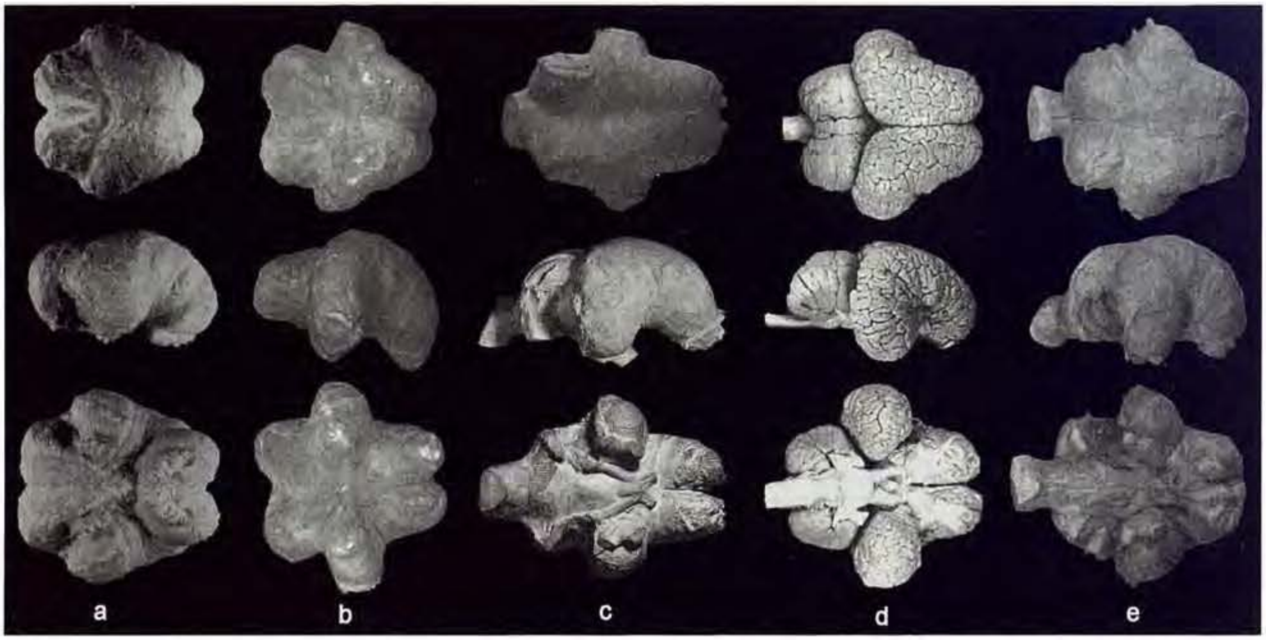


Fig. 6. Dorsal (top) lateral (middle) and ventral (bottom) views of cerebral cavity casts *Elephas falconeri* Busk, 1867 (Spinagallo, female MPUR sn2; a); *Elephas antiquus* Falconer & Cautley, 1847 (Pian dell'Olmo, MPUR sn1; b); *Mammuthus meridionalis* (Nesti, 1825; according to Dechaseaux, 1959, modified; c); *Loxodonta africana* (Blumenbach, 1797) (d); *Elephas maximus* Linnaeus, 1758 (after Osborn, 1942, modified; e). Not in scale.

Fig. 6. *Vistes dorsal (a dalt), lateral (enmig) i ventral (a sota) dels motlles de la cavitat del cervell d'*Elephas falconeri *Busk, 1867 (Spinagallo, femella MPUR sn2; a);* Elephas antiquus *Falconer & Cautley, 1847 (Pian dell'Olmo, MPUR sn1; b);* Mammuthus meridionalis *(Nesti, 1825; d'acord amb Dechaseaux, 1959, modificat; c);* Loxodonta africana *(Blumenbach, 1797) (d);* Elephas maximus *Linnaeus, 1758 (segons Osborn, 1942, modificated; e). No a escala.*

the cerebellum of *E. falconeri* is proportionally higher and shorter, whereas the middle lobe is enlarged towards the back and seems to partially cover it (Fig. 5).

In addition, it is worth noting that the elongated *M. meridionalis* brain shows quite archaic features in comparison with both *E. antiquus* and extant taxa (Fig. 6 c).

Brain versus body mass proportion

The proportion between cranial capacity/brain mass and body mass confirms, as already observed by Accordi & Palombo (1971), that brain mass in *E. falconeri* is noticeably greater than in continental adult elephants of the same age.

The encephalisation index in the adult female of *E. falconeri* is 6.62 (Jerison, 1973) and 4.30 (Martin, 1984), whereas for *E. antiquus* we have obtained an index value of 1.30 (Jerison, 1973) and 0.52 (Martin, 1984). Accordingly, the *E. falconeri* brain case is from 50% (Jerison, 1973) to 17% (Martin, 1984) larger than in its continental ancestor, surpassing the values given for primates (Sellers, 2002). Moreover, the brain to body mass proportion falls within the range of modern man and Phocenidae (Fig. 8).

The *foramen magnum*, as well as the orbit, are also proportionally larger than in *E. antiquus* (Maccagno,

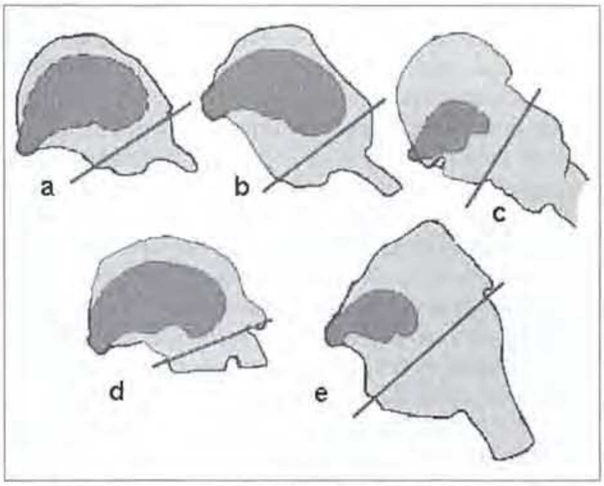


Fig. 7. Cerebral cavity and respiratory axis in: a-b = *Elephas falconeri* Busk, 1867 from Spinagallo cave, a = juvenile, b = adult female; c = *Elephas antiquus* Falconer & Cautley, 1847; d-e = *Loxodonta africana* (Blumenbach, 1797), e = foetal individual, f = adult individual. Not in scale.

Fig. 7. Cavitat del cervell i eix respiratori a: a-b = Elephas falconeri *Busk, 1867 de la cova de Spinagallo, a = juvenil, b = femella adulta; c =* Elephas antiquus *Falconer & Cautley, 1847; d-e =* Loxodonta africana *(Blumenbach, 1797), e = fetus, f = adult. No a escala.*

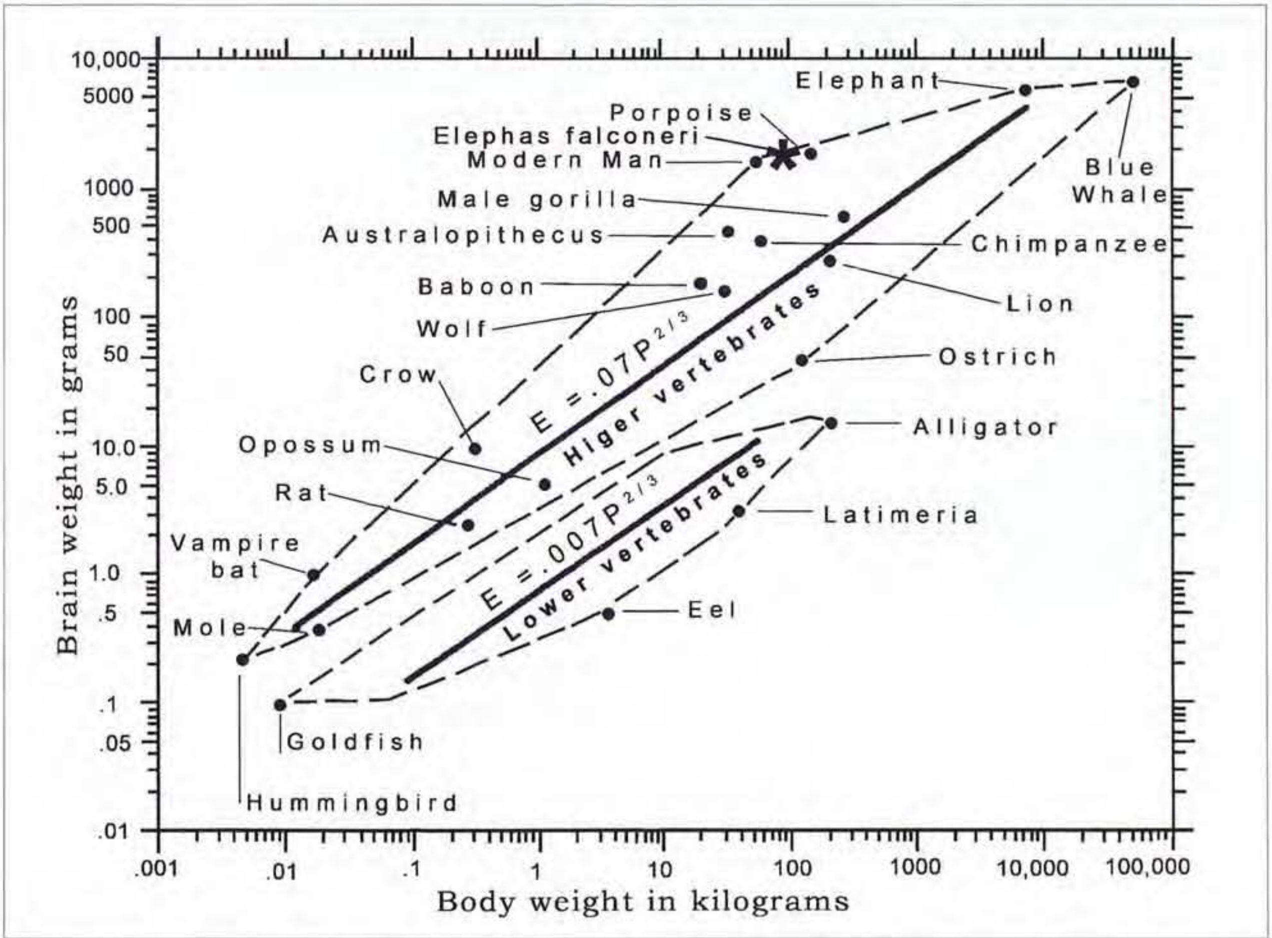


Fig. 8. Logarithm of brain weight plotted against logarithm of body weight in lower and higher vertebrates (according to Jerison, 1973, modified). It is worth noting that *Elephas falconeri* Busk, 1867 falls between modern man and Phocenidae.

Fig. 8. Logaritme del pes del cervell respecte el logaritme del pes corporal a vertebrats superior i inferiors (d'acord amb Jerison, 1973, modificat). És notable veure com Elephas falconeri *Busk, 1867 cau entre els humans moderns i els focènids.*

1962; Ambrosetti, 1968), confirming the great functionality of sense organs in the endemic dwarf elephant of Sicily. According to Köhler & Moyà-Solà (2004), body size, orbit and *foramen magnum* size are consistently correlated in extant and fossil wild bovids. In *Elephas falconeri*, the proportion of orbit size (log ∛height X width) to body mass (log ∛3 body mass) and the proportion of *foramen magnum* size (log ∛height X width) to body mass (log ∛3 body mass) are about 10% and 12% greater than in *E. antiquus*.

Moreover, Köhler & Moyà-Solà (2004) hypothesised that under altered conditions in predator free insular environments, functional demands on neural performance are reduced, allowing a reduction in brain structures and associated sense organs, as suggested, for example, by the small orbits and reduced visual brain structures of *Myotragus*. Nevertheless, our preliminary analysis performed on very young specimens of *Loxodonta africana*, similar in size to *E. falconeri*, shows that the proportion between brain mass and body mass does not vary to a great extent (Fig. 7).

DISCUSSION

The results thus far obtained from our analysis clearly demonstrate that the brain volume of *E. falconeri* was greater than that of its possible ancestor, *E. antiquus*, and, in any case, that its brain is significantly larger than that of adult individuals of extant elephants. This apparently runs counter to the fact that large insular mammals are characterised by a proportional decrease in the volume and efficiency of the central nervous system, especially as far as the functionality of the sense organs is concerned.

As clearly demonstrated by Köhler & Moyà-Solà (2004), the endemic bovid *Myotragus*, from the Plio-Pleistocene deposits of Mallorca, underwent a significant reduction in relative brain size, especially affecting the vision and locomotion centers. These changes, which parallel those shown by domesticated animals, have been interpreted as an adaptive response to insular environmental conditions, in particular to a lack of competitors and predators. As in the strongly endemic and unbalanced Balearic faunas, *E. falconeri* was also the only large Spinagallo mammal. Consequently, we would expect this species to have undergone changes in the relative size of the brain and sense organs similar to those of taxa living in anthropogenic environments or without any predation pressure, such as domesticated or endemic dwarfed mammals. However, it is worth noting that the most remarkable feature of *E. falconeri* is the peculiar shape and proportions of its skull (due to the allometric growth of the maxillary and occipital bones with respect to other cranial bones) and the steeply-inclined respiratory axis. Indeed, the skull is characterized by extensive development of the brain case, linked to the need to maintain minimal functional brain volume, even when skull dimensions are greatly reduced. Tusk structure and the proportions of the cranium, axial skeleton and limbs are consistent with such a paedomorphic feature (Palombo, 2004 and references therein). Accordingly, *E. falconeri* seems to be characterized by precocious stunting of ontogenetic growth. Actually, juvenile and subadult specimens of extant and fossil elephants, especially those belonging to *Elephas* and *Loxodonta* genera, show very similar skull morphology to that of adult skulls of *E. falconeri* (Palombo, 2001). However, as suggested by several authors (e.g. Sondaar, 1977; Roth 1990; 1992; Damuth, 1993; Grant, 1998; Köhler & Moyà-Solà, 2004.), the lack of predators in insular environmental conditions noticeably increased population density, leading to an increase in intraspecific competition for limited food resources. On the other hand, it appears that in an insular environment and in the absence of competition factors, large herbivores reached the minimum body size required depending on their trophic level and metabolic rate, in accordance with the niche available on the island (Palombo, 2004). Accordingly, the hypothesis that the paedomorphic allometric growth of *E. falconeri*, as well as an increase in the reproductive rate (Raia *et al.*, 2003), best contributed to maintaining the optimum biomass during resource allocation shifts cannot be ruled out.

Extensive development of the areas assigned to sight, which in turn affect total brain size, can be correlated with relatively large orbits, slightly shifted to a more frontal position than in the skulls of adult elephants. On the other hand, it not easy to interpret the different proportion of the cerebellum; it seems to be higher but less elongated than the cerebellum of *E. antiquus* and extant elephants. In keeping with the more agile, faster walking gait characterising the dwarfed elephant from Spinagallo with the respect to its ancestor (Palombo, 1996), the shape and extension of the cerebellum could be inferred as depending on increased energy required for locomotion.

In any case, more data are needed to clarify the meaning and importance of extension changes in each area, affecting the entire shape of the central nervous system.

CONCLUSIVE REMARKS

The relative larger size of the brain of Spinagallo specimens in respect to their ancestor is primarily due to the impossibility of proper brain function below a critical volume, as well as to the great reduction in the pneumatisation of parietal and fontal bones. Actually, the positive increased allometric size of the skull affects the posterior region of maxillary bones (which increase in height to the edge of tooth alveoli) more than the neural and facial region of the skull. Consequently, the whole architecture of the adult skull is modified and exhibits some paedomorphic features, such as an overall globose shape, similar to that of young animals. According to Gould (1977), a large brain, "by its own mechanical pressure, causes correlated features" such as a short face, a vaulted cranium and a low *foramen magnum*. The absence of the latter characteristic in the Spinagallo skull is consistent with the persistence of positive allometric heightening of the posterior maxillary region.

The brain/body proportion of *E. falconeri* is contrary to the pattern reported for insular taxa, such as

Myotragus, as well as domesticated animals. As far as *E. falconeri* is concerned, an increase in brain size seems to be related more to a precocious stunt in growth than to the special environmental conditions of the insular ecosystem. In fact, the increase in relative brain size seems to be related to the evident paedomorphic features characterising the Spinagallo elephant. Moreover, changes in shape and proportions shown with respect to the *E. antiquus* ancestor could be interpreted as an adaptive strategy for increased fitness and efficient exploitation of energy related to reduced body dimensions and, possibly, faster metabolic activity. For instance, the smallest mammals, such as rodents, which have a brief life, a high reproductive rate and an accelerated metabolism, have a proportionally large brain.

Our ongoing research, dedicated to defining the allometric growth of brain and body size in extant and fossil elephants, should highlight the actual meaning of the apparently-advanced features of the central nervous system of *E. falconeri*.

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24

SU FOSSU DE CANNAS CAVE (SADALI, CENTRAL-EASTERN SARDINIA, ITALY): THE EARLIEST DEPOSIT HOLDING PLEISTOCENE MEGACERINE REMAINS IN SARDINIA

Maria Rita PALOMBO & Rita Teresa MELIS

PALOMBO, M.R. & MELIS, R.T. 2005. Su Fossu de Cannas Cave (Sadali, central-eastern Sardinia, Italy): the earliest deposit holding Pleistocene megacerine remains in Sardinia. *In* ALCOVER, J.A. & BOVER, P. (eds.), *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 265-276.

Resum

Recentment s'han descobert diverses restes de cèrvids als sediments arenosos, vermells i fortament cimentats que omplen la cavitat superior de la Cava Su Fossu de Cannas (Sadali, Sardenya centre-oriental), tallada a les calcàries del Mesozoic de Barbagia di Seulo. Es varen trobar les restes a la part de dalt d'una cova horitzontal, estreta. L'origen d'aquest passadís es pot deure a una fase erosiva antiga (Pleistocè Mitjà?) que va afectar els sediments que primàriament omplien la cova, com s'evidencia per l'erosió del conglomerat superior i la deposició posterior de sediments vermellosos lleugerament cimentats.

Els espècimens analitzats fins ara mostren afinitats morfològiques estretes amb el megacerí endèmic de Sardenya *"Praemegaceros" cazioti* (Depéret, 1897). No obstant això, el cèrvid de Sadali es diferencia del darrer per la seva mida més gran, que supera l'espectre de variabilitat calculat per a l'espècie endèmica, i en alguns trets morfològics (tal com el *corpus mandibulae* fondo i corbat), així com per presentar unes dents proporcionalment més petites i, sobretot, per un metacarpià més gràcil. Els trets peculiars dels espècimens de Sadali suggereixen la seva pertinença a una nova espècie. No obstant això, de moment ens estimem més no batejar-la i anomenar el cèrvid de Sadali "*Praemegaceros*" n. sp., a l'espera de noves dades que permetin afinar la seva diagnosi. El cèrvid de Su Fossu de Cannas es pot considerar com el representant més primitiu del gènere "*Praemegaceros*" a Sardenya i l'ancestre de "*Praemegaceros*" *cazioti*.

Paraules clau. Cèrvid endèmic, Pleistocè, Sardenya, Geomorfologia.

Abstract

Several cervid remains have recently been discovered in the sandy, red-coloured and strongly cemented sediment filling the uppermost cavity of the Su Fossu de Cannas Cave (Sadali, central-eastern Sardinia), cut into the Mesozoic limestone in the Barbagia of Seulo. The remains were found on the ceiling of a narrow, horizontal underground cave. The origin of this passage may be due to an ancient erosional phase (Middle Pleistocene?), which affected the sediments formerly filling up the cave, as evidenced by the erosion of the uppermost conglomerate and by the further deposition of reddish, slightly cemented sediments.

The specimens analysed thus far show close morphological affinities with the endemic Sardinian megacerine *"Praemegaceros" cazioti* (Depéret, 1897). However, the Sadali cervid differs from the latter in its larger size, exceeding the range of variability calculated for the endemic species, and in some morphological features (such as the depth and curved *corpus mandibulae*), as well as in its proportionally smaller teeth and, notably, its elongated, slender metacarpal. The peculiar features of the Sadali specimens suggest its attribution to a new species. Nevertheless, for the moment, we prefer to name the Sadali cervid "*Praemegaceros*" n. sp., awaiting new data to present the diagnosis. The Su Fossu de Cannas cervid can be regarded as the most primitive representative of the genus "*Praemegaceros*" in Sardinia and the ancestor of the endemic species "*Praemegaceros*" *cazioti*.

Key Words. Endemic cervid, Pleistocene, Sardinia, Geomorphology.

INTRODUCTION

In the Pleistocene of Sardinia, cervid remains, generally ascribed to *"Megaceroides"* or *"Megaloceros"* or "*Praemegaceros*" *cazioti* (Depéret, 1897) [see Palombo (2005) for a discussion regarding nomenclature], are relatively common, mainly in eolianites or in cave deposits, attributed for the most part to the Late Pleistocene (e.g., Dehaut, 1911; Comaschi Caria, 1955; 1956; Azzaroli, 1962; Cordy & Ozer, 1973; Caloi & Malatesta, 1974; Caloi *et al.*, 1981; Klein Hofmeijer, 1997; Antonioli *et al.*, 1998; Ginesu *et al.*, 1998; Melis *et al.*, 2002; Abbazzi *et al.*, 2004; Palombo, unpublished data) (Fig. 1).

The earliest occurrence of megacerini in Sardinia thus far reported is recorded in the karst fissures "XI canide" and "XI mar2002" opening up at Monte Tuttavista

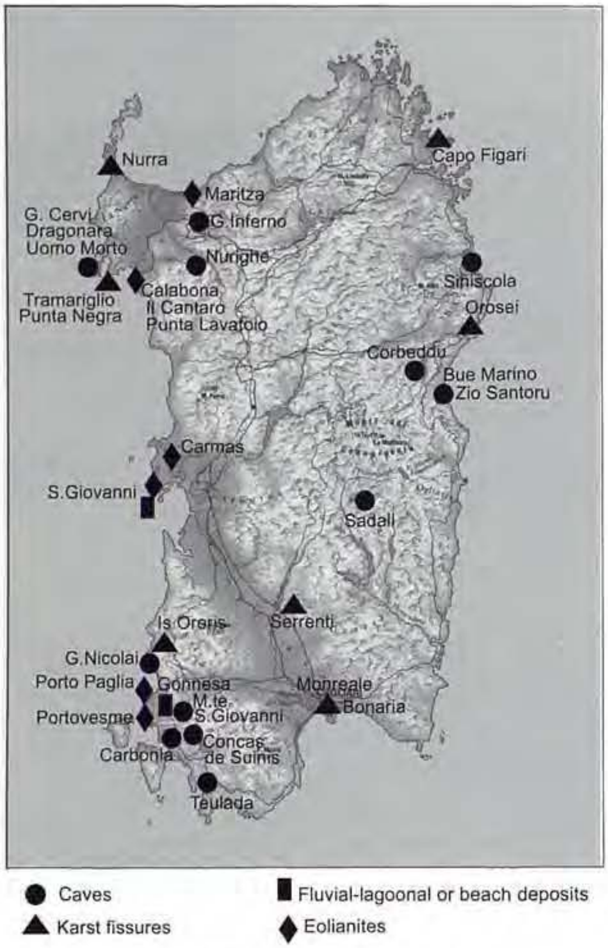

Fig. 1. Map of distribution of the most important *"Praemegaceros"* remains in Sardinia.

***Fig. 1.** Mapa de distribució de les restes més importants de* "Praemegaceros" *a Sardenya.*

(Orosei), tentatively attributed to the early Middle Pleistocene (Ginesu & Cordy, 1997; Sondaar, 2000; Abbazzi *et al.*, 2004; Palombo, in press), and from the Santa Lucia quarry (Iglesias) (proposed age 450 ± 90 ka BP, ESR date on cervid tooth enamel, Motoji Ikeya, *fide* van der Made, 1999) (van der Made & Palombo, in press)

Scanty cervid remains were recorded from Capo Figari II, in a fissure filling when an archaic arvicolid also occurred (*"Tyrrhenicola"* sp., Brandy, 1978). The proposed age is 366,959 +/- 20% years BP (ESR date on cervid tooth enamel, Motoji Ikeya, *fide* van der Made, 1999).

Since its first identification by Depéret in 1897 of the cervid remains found at Nonza, in Corsica, *"P." cazioti"* has been reported at several Sardinian and Corsican sites ranging in age from the late Middle Pleistocene to the Holocene (e.g., Caloi & Malatesta, 1974; Bonifay *et al.*, 1998; Pereira *et al.*, 2005).

Though the endemic cervid from Sardinia and Corsica is quite a well-known species, specialists still do not agree on the taxonomy and phylogenetic relationships of this taxon, which was assigned either to a new genus or regarded as phylogenetically related to *Dama, Eucladoceros* or megacerine deer (e.g., Radulesco & Sampson, 1965; Caloi & Malatesta, 1974; Klein Hofmeijer, 1997; van der Made, 1999; 2003; Sondaar & van der Geer, 2002; etc.), commonly believing that only one phyletic line was present in Sardinia, perhaps represented by more than one chrono-subspecies. The hypothesis of derivation from megacerines belonging to the *"Praemegaceros" verticornis* group is currently widely accepted, as supported by skull and mandible features (see below). In Corsica, in addition to the megacerini, a cervid closely related to red deer has been reported (*Cervus elaphus rossii* Pereira, 2001).

The discovery in the Su Fossu de Cannas Cave (Sadali, central-eastern Sardinia) (Figurel) of cervid remains larger than the Middle and Late Pleistocene endemic

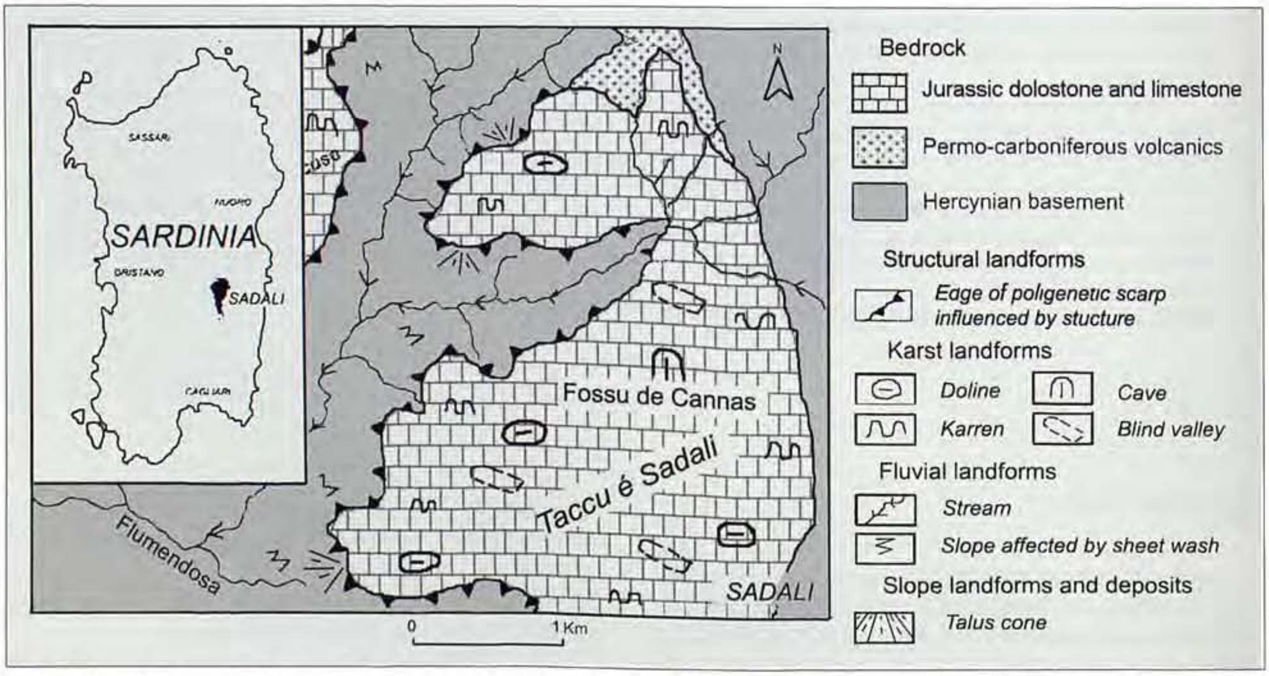

Fig. 2. Su Fossu de Cannas cave location and schematic geological map of the Sadali area.

***Fig. 2.** Localització de la cova Su Fossu de Cannas i esquema geològic de l'àrea de Sadali.*

cervid, and similar in size to those of *Cervus elaphus*, has thus been considered an extremely interesting element. In-deed, our preliminary analysis demonstrated that the cervid specimens from Sadali showed significant morphological affinity with *"Praemegaceros" cazioti* (Palombo *et al.*, 2003).

Consequently, in keeping with a graded trend to increase the size in small-bodied species and to dwarfism in large-bodied, characterising flightless non-marine mammals inhabiting islands (the "island rule" by Foster (1964) and following reformulation, as in Brown & Lomolino, 1998), we can suppose that the Sadali cervid, if actually older, was the ancestor of the Middle and Late Pleistocene Sardinian megacerini.

The aim of this paper is to evaluate, on the basis of geomorphogical data, the possible age of the fossiliferous deposits in Su Fossu de Cannas Cave and to illustrate which of the peculiar features of cervid remains recognised thus far correspond to plesiomorphic characteristics.

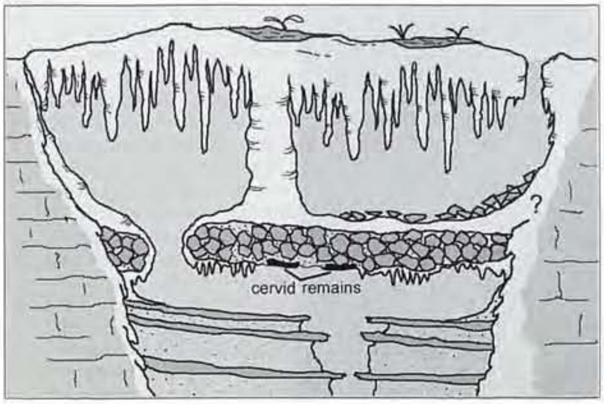

Fig. 3. Longitudinal section of Su Fossu de Cannas cave.

Fig. 3. Tall longitudinal de la cova Su Fossu de Cannas.

GEOMORPHOLOGIC FRAMEWORK

The limestone plateau of Sadali, located in central-eastern Sardinia, is one of a series of plateaus (the so-called "Tacchi") characterised by fully developed karst forms. In this area, Mesozoic dolomitic limestone sediments cover the "post-Hercynian peneplain" lying on a metamorphic Palaeozoic basement (Fig. 2).

The geomorphological evolution of the "Tacco di Sadali," in which the Su Fossu de Cannas Cave lies, has been greatly conditioned by endogenous factors. Tertiary and Plio-Pleistocene distensive tectonic movements have influenced the development of the hydrographic network and both deep and superficial karst evolution.

The most frequent among small karst forms are the karren-type microforms on the surfaces of bare rock. The most common types are the rund-karrens, flat or sometimes protruding due to the presence of well-rounded

Fig. 4. Su Fossu de Cannas Cave: the entry of the underground cave; the stalagmitic concretions cover the conglomeratic deposit.

Fig. 4. Cova Su Fossu de Cannas: entrada a la cova. Les concrecions estalagmítiques cobreixen el dipòsit de conglomerats.

Fig. 5. Su Fossu the Cannas Cave; ceiling of the horizontal underground cave: Some bones are identifiable under the flowstone.

Fig. 5. Cova Su Fossu de Cannas: reblit de la cova horitzontal. S'identifiquen alguns ossos sota les concrecions calcàries.

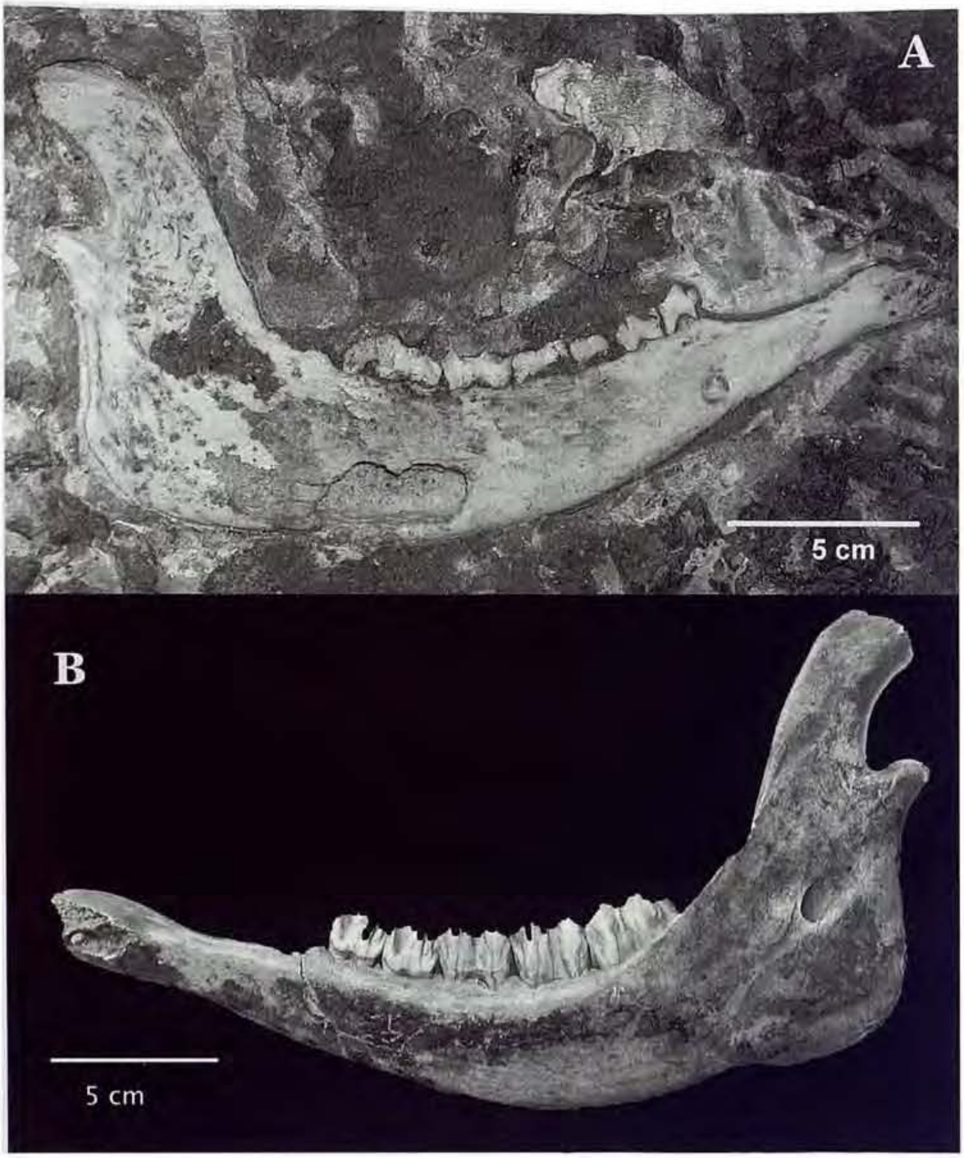

Fig. 6. a) "*Praemegaceros*" n. sp. from Su Fossu de Cannas Cave): left jaw in lingual view. b) "*Praemegaceros*" *cazioti*, Dragonara cave, S1.

Fig. 6. a) "Praemegaceros" *n. sp. de la Cova de Su Fossu de Cannas: mandíbula esquerra en norma lingual. b)* "Praemegaceros" cazioti, *Cova de Dragonara, S1.*

spikes. In the central sector of the plateau, there are several dolines caused by dissolution or collapse and small blind valleys preferentially aligned in a NE-SW direction (Fig. 2). The dolines are separated by conical, truncated-conical or in some cases "tower-shaped" rises. These rises may be interpreted as residual forms of intense, prolonged dissolution processes.

Subterranean karst phenomena are characterised by numerous, at times very extensive, cavities affected by phenomena of physical and chemical filling, with extremely variable, significant, primary and secondary morphologies.

The evolution of almost all the cavities present on the plateau has been clearly conditioned by the faulting and position of calcareous banks. Cave development is prevalently horizontal with slight inclination, and is sometimes affected by lateral complexity.

Su Fossu de Cannas Cave

Su Fossu de Cannas Cave is located in the central sector of the Sadali limestone plateau, near a small rise between two small dry valleys (Fig. 2) (Bartolo *et al.*, 1995). On the surface, near the present entrance to the cave, small dolines caused by collapse and numerous remains of flowzones and stalactites are present. The latter represent the remains of cavities brought to light by intense processes of selective erosion and alteration of Mesozoic limestone.

In the cave, only partially explored and still under study, some indefinable speleogenetic episodes can be recognised. Its basic origin is linked precisely to karst dissolution processes and clastic filling triggered by a water supply. Due to variations in climate and the water regimen, erosion and sedimentation phenomena, both chemical and caused by low-energy water flow, subsequently took place.

In spite of modifications due to the morphological evolution it has undergone, the cave has been greatly influenced by the structural geological conditions of the site. From the present entrance, a narrow opening, one enters the first, horizontally- developed room, highly concretionary and aligned along a NW-SE fault. This first cavity, with its lateral branches almost totally filled with fine sedi-

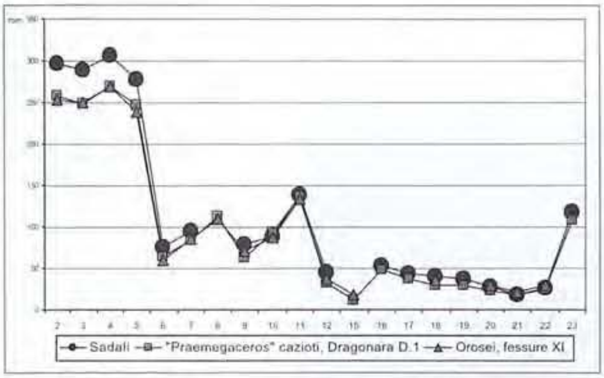

Fig. 7. Comparison of the mandibulae dimensions of *"Praemegaceros" cazioti* specimens (Depéret, 1897) from Dragonara (MPUR 1/235, Palaentological Museum, University "La Sapienza" of Rome), of the unpublished cervid from Cave XI on Monte Tuttavista (Orosei) ("Soprintendenza ai Beni Archeologici di Sassari e Nuoro") and "*Praemegaceros*" n. sp. from the Su Fossu de Cannas Cave (Sadali, Nuoro): **2** = Incisors-condylus distance; **3** = Incisors-*angulus mandibulae* distance; **4** = Incisors- coronoid apophysis distance; **5** = Distance between the incisors and the posterior edge of vertical branch; **6** = Distance between M_3 and posterior edge oh of vertical branch; **7** = M_3-condylus distance; **8** = M_3-coronoid apophysis distance; **9** = Incisors-P_2 distance; **10** = Height at condylus; **11** = Height at coronoid apophysis; **12** = Distance coronoid apophysis-condylus **16** = Height (internal) of *corpus mandibulae* behind M_3; **17** = Height (internal) of *corpus mandibulae* at M2-M1; **18** = Height (internal) of *corpus mandibulae* under P_4; **19** = Height (internal) oh *corpus mandibulae* under P_3; **20** = Height oh *corpus mandibule* at P_2 (anterior); **21** = Minimum height oh horizontal ramus; **22** = Distance incisors-condylus, Distance incisors-P2x100 ratio.

Fig. 7. Comparació de les dimensions mandibulars dels espècimens de "Praemegaceros" cazioti *(Depéret, 1897) de Dragonara (MPUR 1/235, Museu Paleontològic de la Universitat "La Sapienza" de Rome), del cèrvid no publicat de Cave XI a Monte Tuttavista (Orosei) ("Soprintendenza ai Beni Archeologici di Sassari e Nuoro") i* "Praemegaceros" *n. sp. de Su Fossu de Cannas Cave (Sadali, Nuoro):***2** *= Distància incisives-còndil;* **3** *= Distància incisives-*angulus mandibulae*;* **4** *= Distància incisives- apòfisi coronoide;* **5** *= Distància entre les incisives i la vorera posterior de la branca vertical;* **6** *= Distància entre* M_3 *i la vorera posterior de la branca vertical;* **7** *= Distància* M_3*-còndil;* **8** *= Distància* M_3*-apòfisi coronoide;* **9** *= Distància incisives-*P_2*;* **10** *= Alçària al còndil;* **11** *= Alçària a l'apòfisi coronoide;* **12** *= Distància apòfisi coronoide-còndil* **16** *= Alçària (interna) del* corpus mandibulae *rere l'*M_3*;* **17** *= Alçària (interna) del* corpus mandibulae *a nivell de* M_2*-*M_1*;* **18** *= Alcària (interna)* corpus mandibulae *sota el* P_4*;* **19** *= Alçària (interna) del* corpus mandibulae *sota el* P_3*;* **20** *= Alçària (interna) del* corpus mandibulae *sota* P_2 *(anterior);* **21** *= Alçària mínima de la branca horitzontal;* **22** *= Distància incisives-còndil / Distància incisives-*P_2 *x 100.*

ment, is characterised by a thick column located about 8 m from the entrance and by a strongly-cemented conglomerate floor, interrupted in its final stretch by a narrow shaft about 1 m deep. In the external wall of this first room, a carbonate outflow coming from a now-blocked fissure covers what is probably a residue of the floor (Fig. 3).

From the base of the shaft, a narrow, horizontal underground passage is entered; its ceiling is made of the same conglomerate as the floor of the first cavity (Fig. 4).

The floor of this passage is made up of carbonate hardpan about 30cm thick, interrupted by small collapsed areas. This hardpan lies on a thick layer of fine, sandy, red-coloured sediment, with intercalated carbonate deposits, which probably represent the filling of a vast cavity.

On the ceiling of this passage, several remains belonging to middle/large -sized cervids are encased in a fine, red, calcareous, very strongly cemented matrix, underlying the conglomerate.

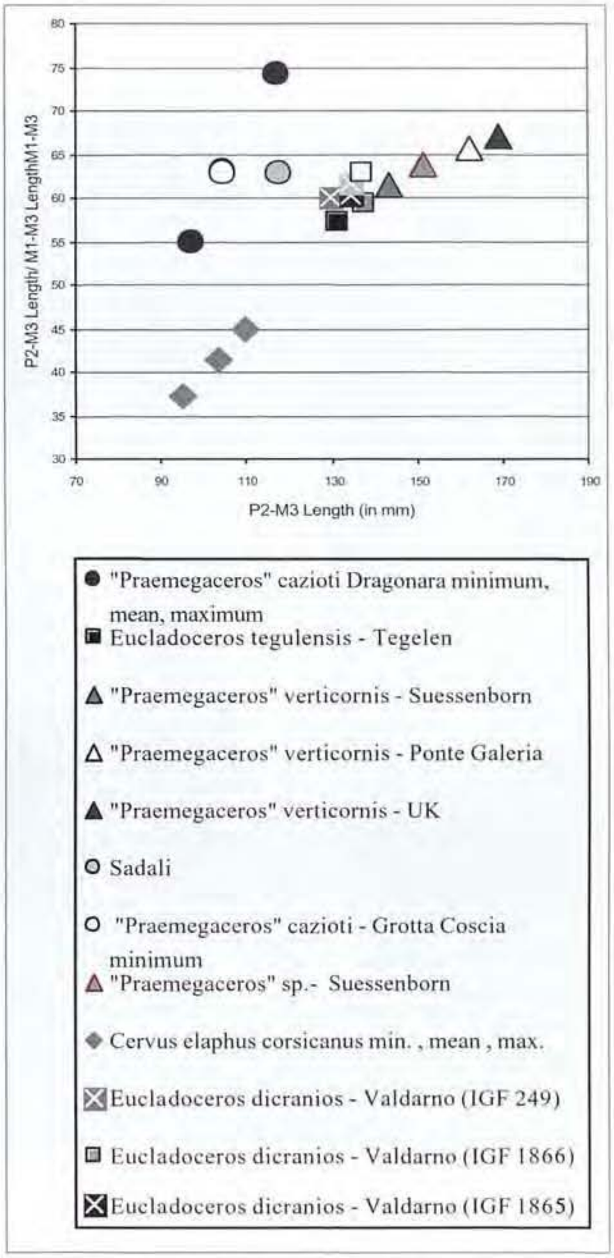

Fig. 8. Scatter diagram of the value of the index ratio "Length of premolar row" / "Length of molar row" (P_2-P_4/M_1-M_3 x 100) *versus* "Length of dental row" (P_2-M_3) in the "*Praemegaceros*" n. sp from Su Fossu de Cannas Cave (Sadali, Nuoro) cervid, in "*Praemegaceros*" *cazioti* (Depéret, 1897) from Sardinia (Dragonara, post-Tyrrhenian) and Corsica (Coscia Cave, Last Glacial, Pereira & Bonifay, 1998), in some endemic cervids, in middle-sized and large cervids from the Pliocene and Pleistocene of Europe (Azzaroli & Mazza, 1992; Kahlke, 1956-59; 1958; 1969; Kahlke, 1997; Kostopoulos, 1997; Leonardi & Petronio, 1974; 1976; Spaan, 1992; Palombo, unpublished data).

Fig. 8. Diagrama de dispersió del valor de l'index "Llargària de la sèrie premolar"/"Llargària de la sèrie molar" (P_2*-*P_4*/*M_1*-*M_3 *x 100) versus la "Llargària de la sèrie dentària" (*P_2*-*M_3*) al cèrvid* "Praemegaceros" *n. sp. de la Cova Su Fossu de Cannas (Sadali, Nuoro), a* "Praemegaceros" cazioti *(Depéret, 1897) de Sardenya (Dragonara, post-Tirrenià) i Còrsega (Cova de Coscia, Darrer Glacial, Pereira & Bonifay, 1998), a alguns cèrvids endèmics, i a cèrvids de mida mitjana i gran del Pliocè i Pleistocè d'Europa (Azzaroli & Mazza, 1992; Kahlke, 1956-59; 1958; 1969; Kahlke, 1997; Kostopoulos, 1997; Leonardi & Petronio, 1974; 1976; Spaan, 1992; Palombo, dades no publicades).*

Fig. 9. Dorsal view of metacarpal of "*Praemegaceros*" n. sp. from Su Fossu de Cannas Cave compared with the smallest and greatest, most slender and most robust metacarpals recognised in the sample of "*Praemegaceros*" *cazioti* from Dragonara cave.

Fig. 9. *Vista dorsal del metacarpià de* "Praemegaceros" *n. sp. de la Cova Su Fossu de Cannas comparat amb els metacarpians més petit i més gran, més prim i més robust, de la mostra de* "Praemegaceros" cazioti" *de la cova Dragonara.*

Discussion

Our preliminary analysis has pointed out the presence of a vast cavity affected by several sedimentation and erosion stages. The conglomerate, whose origin can be attributed to quite a high-energy water flow coming from outside, probably represents what remains of the final filling of the cavity. Subsequently, cementing processes protected the conglomerate from an erosion stage during which partial emptying out of the cave probably occurred.

The presence of scarce remains of reddish, slightly cemented sediments in the cracks of speleothemes found in the walls of the lower passage witness to erosional processes affecting the fine sediments underlying conglomerate. A preliminary micromorphological study of these deposits has shown that we are dealing with fine laminated sediments. The laminas show normal gradation with well-selected quartz granules at the base, while towards the top, the clayey matrix increases until it is dominant on the ceiling. These characteristics make one presume a fining-upward-type of sedimentation with low-energy water.

At present, no elements have been found that permit the determination of the age of the different deposits. In any case, from sediment characterisations, the degree of cementing and stratigraphic relationships, we can hypothesise that the conglomerate accumulated after deposition of the levels in which the cervid remains occur, probably during a phase of renewed high-energy water, as indicated by the dimensions and the extent of rounding of clastic limestone.

THE CERVID REMAINS

Several cervid remains, covered and masked by massive calcareous concretions, are partially visible on the ceiling of the tunnel; they apparently belong to moderately disarticulated skeletons with no evident anatomical

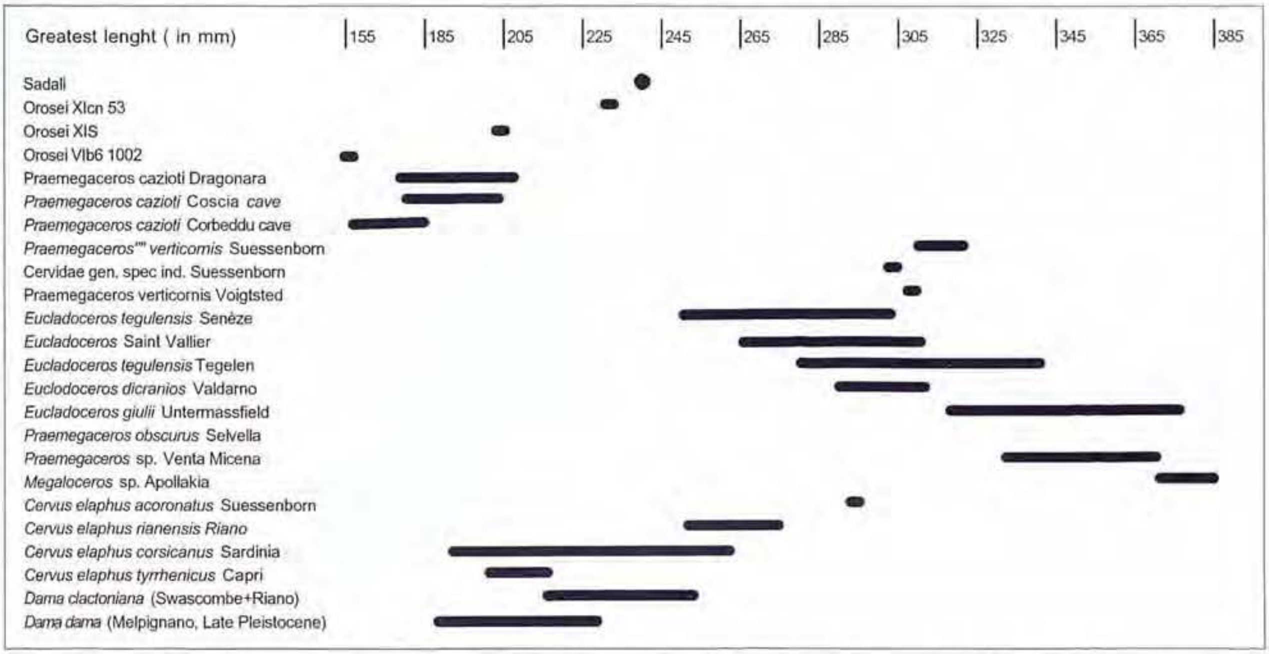

Fig. 10. Maximum length metacarpal of "*Praemegaceros*" n. sp. from Su Fossu de Cannas Cave (measured in situ) compared with metacarpal length and variability ranges of *"Praemegaceros" cazioti* (Depéret, 1897) from Sardinia (Dragonara, post-Tyrrhenian; Corbeddu Cave, Late Glacial, Hofmeijer, 1997) and Corsica (Coscia Cave, Last Glacial, Pereira & Bonifay, 1998), some endemic middle-sized and large cervids from the Pliocene and Pleistocene of Europe (Azzaroli & Mazza, 1992; Kahlke, 1956-59; 1958; 1969; Kahlke, 1997; Kostopoulos, 1997; Leonardi & Petronio 1974, 1976; Spaan, 1992; Di Stefano, 1994; Palombo unpublished data).

Fig. 10. Llargària màxima metacarpiana de "Praemegaceros" *n. sp. de la Cova Su Fossu de Cannas (mesurada in situ) en comparació amb la llargària metacarpiana i els marges de variabilitat de* "Praemegaceros" cazioti *(Depéret, 1897) de Sardinia (Dragonara, post-Tirrenià; Cova Su Corbeddu, Darrer Glacial, Hofmeijer, 1997) i Còrsega (Cova de Coscia, Darrer Glacial, Pereira & Bonifay, 1998), a alguns cèrvids endèmics de mida mitjana i gran del Pliocè i Pleistocè d'Europa (Azzaroli & Mazza, 1992; Kahlke, 1956-59; 1958; 1969; Kahlke, 1997; Kostopoulos, 1997; Leonardi & Petronio, 1974; 1976; Spaan, 1992; Palombo, dades no publicades).*

connection (Fig. 5). Such a preservation pattern is quite common in vertebrate-bearing fluvial channel deposits associated with ribbon sand sediments resulting from streams with slight bank erosion and minimum alluvial sediment reworking *(channel fill mode)*. Moreover, this taphonomic pattern can be associated with the transport or moderate reworking of carcasses by subterraneous low fluvial streams. A taphonomicaly comparable assemblage was recently identified in Nurighe cave (northwestern Sardinia) (Ginesu *et al.*, 1998; www.nurighe.it, 2003).

The most important remains thus far uncovered are the lingual side of a left jaw (Fig. 6a) and a right metacarpus. During a preliminary survey carried out in 2002 in collaboration with the "Soprintendenza per i Beni Archeologici per le province di Sassari e Nuoro", we could retrieve only the proximal epiphysis of the metacarpus (the distal part is still retained in the sediment), a proximal part of a femur and a patella. These bones, and other skeletal elements not clearly identifiable, probably belong to a single individual, a female as inferred from the lateral profile of an atlas uncovered near the condylus of the mandible.

Description

Mandible

The morphological features of the jaw are similar to those characterising the *"Praemegaceros" cazioti* specimens from Dragonara Cave (Fig. 6a), as shown by: the clearly convex lower profile; the curved alveolar limbus with the occlusal line of the tooth-row placed under the alveolar line of incisor teeth; the relatively short diastema; the massive horizontal *corpus mandibulae* with fairly weak pachyostosis; the high position of *condylus madibulae*.

The Sadali mandible, however, differs from Dragonara specimens (Fig. 6b) in its more massive *corpus mandibulae*, which extends considerably backwards, rather like a bovid. The lower profile of the *corpus mandibulae* is more regularly convex, and apparently lacks any concavity in its inferior outline in the region of the *impressio vasculosa*. Moreover, the vertical *ramus* is proportionally shorter and the diastema slightly longer (Fig. 7).

We can observe only the lingual side of teeth, less hypsodont and proportionally smaller than the specimens from Dragonara: the length of the toothrow (L_c P_2-M_3 =117.5 mm; L_c = length measured at the base of crow) is very similar to the greatest length obtained for Dragonara specimens (117.08 mm).

Moreover, the premolars are proportionally smaller, as expressed by the value of the "length of premolar row/length of molar row" index (Fig. 8).

Metacarpus

The morphology of the proximal articular surface of the metacarpus is similar to those characterising *"Praemegaceros" cazioti* specimens from Dragonara: the articular surface for the *capitatum* is large, with a slightly curved anterior profile; its posterior edge extends to con-

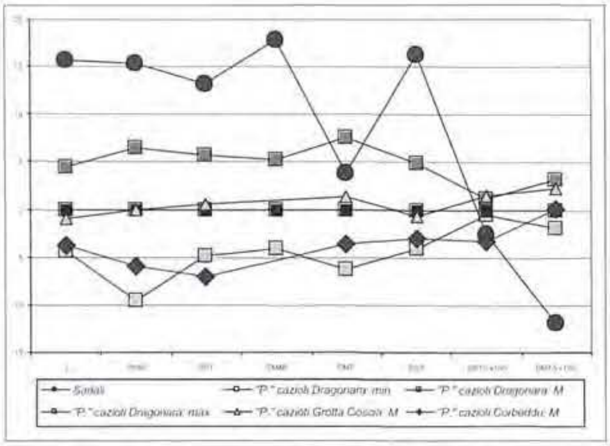

Fig. 11. Metacarpi - Logarithmic distances of the principal dimensional values of the metacarpus from of "*Praemegaceros*" n. sp. from Su Fossu de Cannas Cave and of "*Praemegaceros*" *cazioti* from Dragonara, Corbeddu Cave (Hofmeijer, 1997) and Coscia Cave (Pereira & Bonifay, 1998) (standard = average values of Dragonara sample).

***Fig. 11.** Metacarpians – Distàncies logarítmiques dels principals valors mesurats dels metacarpians de* "Praemegaceros" *n. sp. de la Cova Su Fossu de Cannas i de* "Praemegaceros" cazioti *de la Cova Dragonara, Cova de Su Corbeddu (Hofmeijer, 1997) i de la Cova de Coscia (Pereira & Bonifay, 1998) (standard = valors mitjans de la mostra de Dragonara).*

nect laterally with the postero-mesial edge of the articular surface for the *uncinatum*). However, the metacarpus of the Su Fossu de Cannas Cave cervid differs from Sardinian and Corsican megacerini in its slenderness and notably larger size (Fig. 9).

Its length, in fact, is more than 26% greater than the maximum length estimated for the metacarpus of the Dragonara sample and 29.8% greater than the standard, clearly placing it outside both the real (170-208 mm) and theoretical (162.2-213.8 mm) variability ranges calculated for this sample. The length of the metacarpus from Sadali falls within the variability range of smaller *Eucladoceros* representatives, such as the Senèze and Saint Vallier middle Villafranchian samples, as well as in the range of the large red deer reported from the late Middle Pleistocene of the Latium area (*Cervus elaphus rianensis*, Leonardi & Petronio, 1974). On the other hand, the Sadali metacarpus is smaller than those of the early Middle Pleistocene megacerini belonging to the "*Praemegaceros*" *verticornis* group, as well as of the large late Early Pleistocene cervids ascribed to the genus *Eucladoceros*, "*Praemegaceros*", *Megaloceros*, and larger than Mediterranean endemic red deer and Clacton fallow deer (Fig. 10). Moreover, the Sadali metacarpus is elongated and clearly more slender than those of "*Praemegaceros*" *cazioti* from Sardinia and Corsica; the dyaphysis and, perhaps, the proximal epiphysis (unfortunately partially damaged) show reduced transversal diameter. The slenderness of the dyaphysis is also confirmed by the robusticity index (DMT/L x 100), whose value is clearly inferior to the minimum calculated for the Dragonara sample, so that the Sadali metacarpus appears thinner than the thinnest females among the Dragonara specimens (Fig. 11). In addition, the distal epiphysis is more slender than those of megacerini ascribed to the "*Praemegaceros*" group, with the exception of the specimens from Venta Micena (Menendez, 1987), slender, and Apollonia (Kostopoulus, 1997), quite similar (Fig. 12). Principal component multivariate analysis (Fig. 13) confirms the difference in proportions between the Sadali metacarpus and "*P.*" *cazioti* specimens from the Dragonara, Corbeddu and Coscia caves.

Moreover, it is worth noticing that the Orosei specimens are also set apart from the abovementioned "*P.*" *cazioti*. These metacarpi, as well as the Sadali one, seem to have global proportions more similar to those of the small middle Villafranchian *Eucladoceros* from Senèze and Saint Vallier. The stout metacarpi of German "*Praemegaceros*" *verticornis* from Voigstedt and Süsserborn are clearly separate (Fig. 12, 13).

Femur

The most significant feature of the proximal portion of the femur is its large size (Fig. 14, 15). The Sadali specimen shares some distinctive morphological features with Dragonara femurs, such as great medial extension of the caput, lateral inclination of the greater trochanter and a reduced lesser trochanter. However, the axis of the caput forms a wider angle with the dyaphysis, and the trochanter is, consequently, higher. Taking into account the incompleteness of the specimens, we cannot understand the real meaning of this characteristic that, *per se*, would suggest a minor cursorial aptitude than the Dragonara cervid (Köhler, 1993; Kappelman *et al.*, 1997).

Discussion

The cervid remains of the Su Fossu de Cannas Cave show morphological affinity with those referring to the endemic "*Praemegaceros*" *cazioti* species, but they are larger in size than the Late Pleistocene specimens from Dragonara and similar to or slightly larger than the Middle Pleistocene "*Praemegaceros*" sp. from the fissure infillings at Monte Tuttavista.

The morphology of the jaw from Sadali on the one hand confirms both the affinities (short diastema extending upwards, curved, quite robust horizontal corpus) and the differences (reduced pachyostosis) between the endemic cervid from Sardinia and Corsica and the continental megacerini belonging to the "*Praemegaceros*" *verticornis* group; on the other, it highlights the differences between the former and continental deer belonging to the *Eucladoceros* genus.

Indeed, after the results of re-examination of skulls from Sardinian specimens from Dragonara (Caloi & Malatesta, 1974), Maritza (Cordy & Ozer, 1972) and Porto Vesme (Comaschi Caria, 1955), the basic cranial structure of the "*Praemegaceros*" *cazioti*, seems to confirm its greater affinity with representatives of the "*Praemegaceros*" genus. The Sardinia megacerine shares a typical forehead morphology with continental ones: flat, slightly convex frontal bones, the position and direction of the peduncles (though the beam is straighter and oriented more laterally and distally than that of typical antlers of cervids belonging to the "*Praemegaceros*" *verticornis* group, as shown by specimens from the Early Pleistocene Apollonia 1 site, Greece, referred to as "*Megaloceros*" sp. by Kostopoulus, 1997), the shape of the brain case, the angle between the basioccipital and palatine bones and

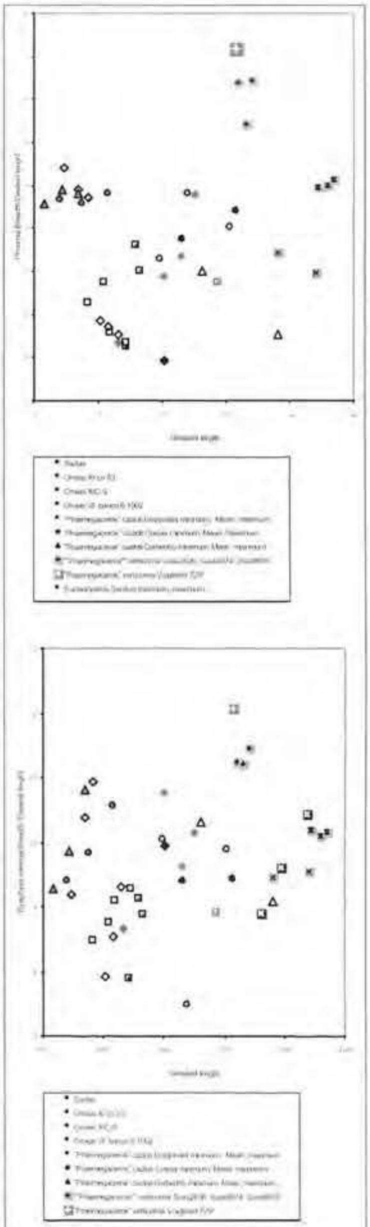

Fig. 12. Metacarpi – Scatter diagrams of : a) breath of proximal epiphysis against greatest length of metacarpus; b)minimal breath of shaft against greatest length of metacarpus antero-posterior diameter against transversal diameter of distal metacarpus c) breath of distal epiphysis against greatest length of metacarpus ; d) antero-posterior diameter against transversal diameter of distal metacarpus in "*Praemegaceros*" n. sp. from Su Fossu de Cannas Cave, "*Praemegaceros*" *cazioti* (Depéret, 1897) from Sardinia (Dragonara, post-Tyrrhenian; Corbeddu Cave, Tardiglacial, Hofmeijer, 1997) and Corsica (Coscia Cave, Last Glacial, Pereira & Bonifay, 1998), in endemic middle-sized red deer from Sardinia and Capri and in selected large cervids from the Pliocene and Pleistocene of Europe (Azzaroli & Mazza, 1992; Kahlke, 1956-59; 1958; 1969; Kahlke, 1997; Kostopoulos, 1997; Leonardi & Petronio 1974; 1976; Spaan, 1992; Palombo unpublished data).

Fig. 12. Metacarpians– Diagrames de dispersió de: a) amplària de l'epífisi proximal respecte la llargària màxima del metacarpià; b)amplària mínima de la canya (diàmetre antero-posterior) respecte el diàmetre transversal distal del metacarpià c) amplària de l'epífisi distal respecte la llargària màxima del metacarpià; d) diàmetre antero-posterior respecte el diàmetre transversal de la part distal del metacarpià a "Praemegaceros" *n. sp. De la Cova Su Fossu de Cannas,* "Praemegaceros" cazioti *(Depéret, 1897) de Sardenya (Dragonara, post-Tirrenià; Cova de Su Corbeddu Cave, Tardiglacial, Hofmeijer, 1997) i Còrsega (Cova de Coscia, Darrer Glacial, Pereira & Bonifay, 1998), a cérvols endèmics de mida mitjana de Sardenya i de Capri i a cérvols grans seleccionats del Pliocè i Pleistocè d'Europa (Azzaroli & Mazza, 1992; Kahlke, 1956-59; 1958; 1969; Kahlke, 1997; Kostopoulos, 1997; Leonardi & Petronio 1974; 1976; Spaan, 1992; Palombo dades no publicades).*

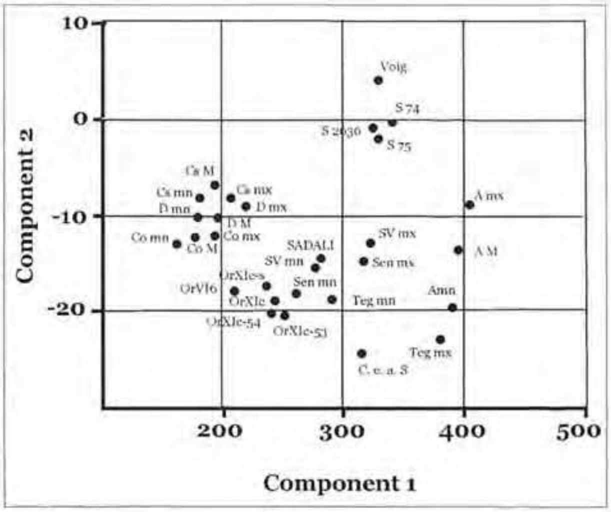

Fig. 13. Principal component diagram. Specimens as in Figure 12.

Fig. 13. Diagrama de Components Principals. Espècimens com a la Figura 12.

muzzle shape and the morphology of the mandible, curved with a short diastema extending upwards. Moreover, metacarpal proportions enable us to hypothesise a possible phylogenetic relationship with the so-called "slender-limbed megacerini" recorded in several localities in the late Early and early Middle Pleistocene in the Mediterranean area (i.e. Venta Micena, Spain, Menendez, 1987; Oubeidiyeh, Israel, Geraards, 1986; Sassa, L'Aquila, Italy, Palombo *et al.*, 2001; Redicicoli, Rome, Italy, Palombo, unpublished data).

The endemic cervids from Sardinian and Corsican Pleistocene deposits were also attributed to the genus *Dama* principally on the basis of their limb proportions (van der Made, 2003; Sondaar 2000, personal communication to M.R.Palombo). Indeed, the author hypothesised that the zeugopodium of this cervid was not shortened, as usually observed in insular artiodactyls. However, it is worth noting that the Su Fossu de Cannas Cave cervid is characterised, with respect to the maximum observed in *"Praemegaceros" cazioti*, by slightly larger mandibular size, proportionally smaller teeth and a shorter premolar row, whereas the metacarpus is of clearly larger dimensions. For the endemic megacerini of Sardinia and Corsica, this fact would suggest a process of allometric reduction in body size, with retarded shortening of the metapodials; accordingly, "*Praemegaceros*" *cazioti* would have, in any case, proportionally shorter metapodials than its ancestor species, contrary to what has already been hypothesised.

CONCLUSIONS

The geomorphological context of the area and the morphological and speleogenetic characteristics of the Fossu de Cannas cave lead one to believe that karst phenomena probably began immediately after the emergence of calcareous rocks (Eocene?). Sedimentation inside the cave occurred during successive flooding by tractive

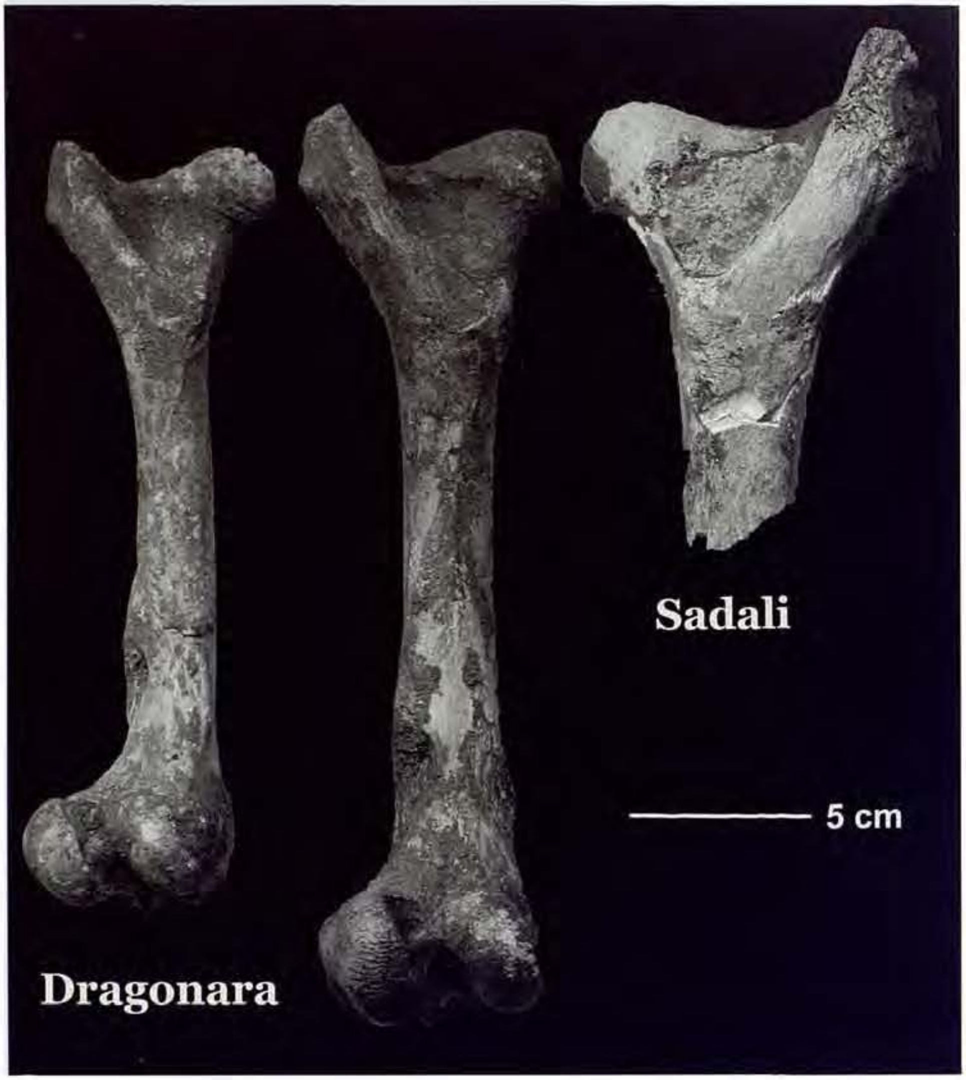

Fig. 14. Plantar view of femur of *"Praemegaceros"* n. sp. from Su Fossu de Cannas Cave compared with the smallest and greatest femora recognised in the sample of *"Praemegaceros" cazioti* from Dragonara cave.

Fig. 14. Vista plantar del fèmur de "Praemegaceros" *n. sp. de la Cova Su Fossu de Cannas comparada amb la dels fèmurs més petit i més gran de la mostra de* "Praemegaceros" cazioti *de la Cova Dragonara.*

currents and decantation water, episodes of redeposition of clay masses and concretioning phases. The conglomerate covering the fine sediments and the cervid remains deposited on the surface of the latter indicate that an important erosive phase occurred, probably as a consequence of climatic-environmental change and tectonic movements of considerable importance (late Early Pleistocene?). The presence of this conglomerate would also indicate the external existence of a morphological rise, no longer present, in the area surrounding the cave.

All this points to a hypothesis of very complex speleogenetic evolution, even in view of the long space of time in which karst processes themselves were able to take place. This led to the development of several speleogenetic cycles involving the formation of caves, their filling and subsequent partial demolition, as evidenced by the remains of calcareous flows and stalagmites in the area around the Fossu de Cannas Cave. At present, one can only hypothesise that general filling took place concomitant with cold, damp periods attributable to the late Early/Middle Pleistocene, and demolition of the morphologic rises around the cave during successive alternating hot and cold periods (late Middle Pleistocene-early Late Pleistocene?).

The specimens analysed thus far, whose dimensions exceed the range of variability calculated for the endemic *"Praemegaceros" cazioti* species (Depéret, 1897), show close morphological affinities with the endemic Sardinian megalocerine. However, the Sadali cervid differs from the latter in its larger size and in some morphological features (such as the depth and concave horizontal corpus of the mandible and the longer diastema), as well as in its proportionally smaller teeth and, notably, its elongated, slender metacarpal.

The peculiar features of the Sadali specimens suggest its attribution to a new species. Nevertheless, taking into account the richness of the deposit and the fact that numerous remains have not yet been uncovered we prefer, for the moment, to refer the Sadali cervid as *"Praemegaceros"* n. sp, awaiting further data to perfect the diagnosis of this new taxon.

The Su Fossu de Cannas cervid can be regarded as the most primitive representative of the genus *"Praemegaceros"* in Sardinia and as the ancestor of the endemic species *"Praemegaceros" cazioti.* Moreover, it is worth noting that the general rule thus far hypothesised for endemic artiodactyls, e.g shortening of *zeugopodium* bones, also seems to be confirmed for the evolu-

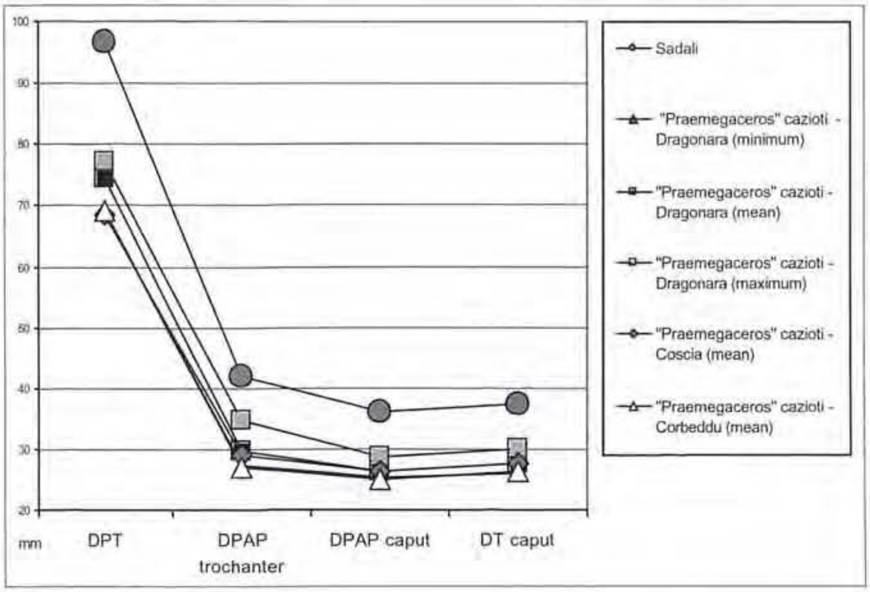

Fig. 15. Femur - Logarithmic distances of the principal dimensional values of the femora of "*Praemegaceros*" n. sp. from Su Fossu de Cannas Cave and of "*Praemegaceros*" *cazioti* from Dragonara, Corbeddu Cave (Hofmeijer, 1997) and Coscia Cave (Pereira & Bonifay, 1998) (standard = average values of Dragonara sample).

Fig. 15. *Fèmur - Distàncies logarítmiques dels principals valors mesurats dels fèmurs de* "Praemegaceros" *n. sp. de la Cova Su Fossu de Cannas i de* "Praemegaceros" cazioti *de la Cova Dragonara, Cova de Su Corbeddu (Hofmeijer, 1997) i de la Cova de Coscia (Pereira & Bonifay, 1998) (standard = valors mitjans de la mostra de Dragonara).*

tionary process of Sardinia and Corsica giant deer. Accordingly, metapodial and lower teeth proportions can be regarded as plesiomorphic characteristics, whereas the morphology of the *corpus mandibulae* seems to be apomorphic.

Typical "*Praemegaceros-Tyrrhenicola* fauna" as described in literature (Sondaar, 2000; Sondaar & van der Geer, 2002; Melis & Palombo, this volume), has clearly been documented in Sardinia and Corsica since the Middle Pleistocene. A small-sized species (*Microtus* (*Tyrrhenicola*) sp.), more archaic than Late Pleistocene ones, seems to have been present since the early Middle Pleistocene (van der Made, 1999; Abbazzi *et al.*, 2004; Marcolini *et al.*, 2003; Pereira *et al.*, 2003), whereas no certain date for the first appearance of megacerini in Sardinia is available thus far. Moreover, at Monte Tuttavista, the archaic vole was found in a faunal complex where *Rhagapodemus minor* is still present, whereas "*Praemegaceros*" first occurs together with *Ragamys orthodon*. Accordingly, the entry of the vole might predate that of the cervid. However, in keeping with the size and the proportions of the scanty specimens from the Su Fossu de Cannas Cave, the hypothesis that this cervid might be older than Monte Tuttavista ones cannot be ruled out.

The lack of any micromammal remains, both in the fossiliferous conglomerate and in the other deposits in the Su Fossu de Cannas Cave, makes it difficult to hypothesise which faunal complex the cervid belongs to (but see Palombi, in press).

We hope that ongoing research will clarify the evolution of the cave and the age of fossiliferous deposits, enabling us to better define the biochronological setting and the differentiation process of Sardinian endemic cervid.

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25

NEW DATA ON THE EXTINCT ENDEMIC RODENTS *TYRRHENICOLA* AND *RHAGAMYS* (RODENTIA, MURIDAE) OF CORSICA (FRANCE) WITH SPECIAL EMPHASIS ON THEIR DENTAL MORPHOLOGY AND ADAPTATION

Elisabeth PEREIRA , Jacques MICHAUX & Sophie MONTUIRE

PEREIRA , E., MICHAUX, J. & MONTUIRE, S. 2005. New data on the extinct endemic rodents *Tyrrhenicola* and *Rhagamys* (Rodentia, Muridae) of Corsica (France) with special emphasis on their dental morphology and adaptation. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 277-286.

Resum

S'estudien nous fòssils corsos de les localitats de Castiglione 1 i 3 (Oletta) i La Coscia (Rogliano) dels rosegadors recentment extingits *Rhagamys* i *Microtus (Tyrrhenicola)*, un ratolí de camp i un talpó respectivament. Són comparats amb conjunts que ja s'havien estudiat prèviament, alguns revisats i completats gràcies a noves excavacions [Punta di Calcina (o Conca, Corse du Sud) i Corte (Haute-Corse)]. Una evolució morfològica suau d'ençà del Pleistocè Mitjà caracteritza *M. (Tyrrhenicola)*, la qual es documenta per canvis en les proporcions de morfotipus dels primers molars, igual que per un increment en la mida, sent els exemplars més petits els que provenen de Punta di Calcina. Els índexs morfomètrics relatius a la primera meitat del primer molar inferior, així com els anàlisis multivariats, recolzen els resultats previs i permeten una distinció més precisa entre les poblacions successives. Per això, *Microtus (Tyrrhenicola)* es pot emprar per proposar cronologies relatives. D'altra banda, a les dues localitats més antigues es troben dues espècies de *Rhagamys*: *R. minor* i *R. orthodon*. El primer va viure durant un període curt, Punta di Calcina i Corte, al contrari que el darrer, que va viure fins l'Holocè. Tot i que les dues espècies difereixen considerablement en mida, l'evolució morfològica és suau en les dues espècies. La comparació de les morfologies oclusives dels molars a *Rhagamys* i les formes relacionades *Rhagapodemus* i *Apodemus* recolza la hipòtesi que *Rhagamys*, així com *Rhagapodemus*, es trobaven adaptats a una dieta abrasiva i que aquesta tendència evolutiva ja es trobava present al continent, abans de l'aïllament. Es discuteixen les grans similituds entre els patrons dentaris de *Rhagamys* i *Tokudaia* sota la perspectiva del seu origen comú amb les espècies d'*Apodemus*. Es proposa el murí japonès recent de l'arxipèlag de les Ryukyu com a model per a reconstruir *Rhagamys*, i per això s'hipotetitza que *Rhagamys* pot haver tingut un aspecte de talpó, una hipòtesi que es pot contrastar en base a l'estudi del material esquelètic. L'anàlisi de les dades de Còrsega du a la conclusió que l'evolució de *Rhagamys* i *Microtus (Tyrrhenicola)* va estar forçada per la competència en correlació amb esdeveniments d'immigració. Quan *M. (Tyrrhenicola)* va arribar, la línia evolutiva de *Rhagamys* es va dividir. Però *M. (Tyrrhenicola)* també va evolucionar, la mida es va incrementar i el patró dentari es va fer més complex. L'esdeveniment evolutiu immediatament anterior a la línia de *Rhagamys* fou la insularitat, que va comportar un gran canvi morfològic i de mida. Entre aquests esdeveniments i la seva extinció, l'evolució a aquestes espècies fou més aviat suau. Aquestes conclusions recolzen la interpretació de Sondaar (2000) sobre el paper de la competència a l'evolució insular.

Abstract

New Corsican fossils of the recently extinct endemic rodents *Rhagamys* and *Microtus (Tyrrhenicola)*, respectively a field mouse and a vole, from the localities of Castiglione 1 and 3 (Oletta) and La Coscia (Rogliano) are examined. They are also compared to previously studied assemblages, some of which recently revised or completed by new excavations [Punta di Calcina (or Conca, Corse du Sud) and Corte (Haute-Corse)]. A slight morphological evolution since Middle Pleistocene characterises *M. (Tyrrhenicola)* which is supported by changes in proportions of morphotypes for first lower molars, as well as by a size increase, the smaller specimens being found at Punta di Calcina. Morphometric indexes relative to the anterior half of the first lower molar as well as multivariate analyses support previous results and allow a more precise distinction between the successive populations. *Microtus* (*Tyrrhenicola*) can thus be used to propose a relative chronology. Two species of *Rhagamys* are present aside in the two older localities, Punta di Calcina and Corte: *R. minor* and *R. orthodon*. The former had a short duration contrary to the latter that lived until Holocene times. If the two species differ considerably in size, morphological evolution is slight in both species. The comparison of the molar occlusal morphologies in *Rhagamys* and allied forms as *Rhagapodemus* and *Apodemus* supports the hypothesis that *Rhagamys* as well as *Rhagapodemus* where adapted to an abrasive diet and that this evolutionary trend was already present on the continent before isolation. Strong similarities between *Rhagamys* and *Tokudaia* dental patterns are discussed under the light of the common ancestry they share with *Apodemus* species. The extant Japanese murine rodent from Okinawa archipelago is proposed as a model to reconstruct the extinct *Rhagamys* and consequently it is hypothesised that *Rhagamys* may have a vole-like morphology, such a hypothesis may be falsified by the study of skeletal material. The analysis of data from Corsica drives to the conclusion that evolution of both *Rhagamys* and *Microtus* (*Tyrrhenicola*) was forced by competition in correlation with immigration events. When *M. (Tyrrhenicola)* settled, the *Rhagamys* lineage split. But *M. (Tyrrhenicola)* also evolved, size increased and the dental pattern became more complex. The immediate anterior evolutionary event in the *Rhagamys* lineage was insularity that induces a strong morphological and size change. Between these different events up to their extinction, evolution in these rodents was rather weak. Such conclusions support Sondaar's (2000) interpretation of the role of competition in insular evolution.

Key words: Corsica, *Rhagamys*, *Microtus* (*Tyrrhenicola*), Insularity, Pleistocene, Paleobiology.

INTRODUCTION

The last ten years have seen a fruitful fieldwork in Corsica as well as in Sardinia. Important and numerous data on the Pleistocene fauna have been published and a much more complete view of the past mammalian diversity is now available as well as for birds, reptiles and amphibians. Among extinct endemic mammals, the rodents belong to two families, Gliridae and Muridae. The former is known only in Sardinia (localities of Capo Figari and Monte Tuttavista area (Zammit-Maepel & de Bruijn, 1982; Ginesu & Cordy, 1997; Turmes, 2002). The latter include Murinae and Arvicolinae. Several species of extinct field mice (*Murinae*) have been described in Sardinia: *Apodemus mannu* Thaler 1974 (in Pecorini *et al.* 1974), *Rhagapodemus azzarolii* Angelone & Kotsakis 2001 from Mandriola (initially recognised as *Rhagapodemus hautimagnensis*), *Rhagamys minor* Brandy, 1978 and *Rhagamys orthodon* (Hensel, 1856). Voles belong to the subgenus *Microtus* (*Tyrrhenicola*). *Microtus (Tyrrhenicola) henseli* Forsyth Major, 1905 is known from Middle Pleistocene to Holocene in Corsica and Sardinia. This species was preceded by a more primitive species recently recognised in some faunas of the Monte Tuttavista area in Sardinia (Ginesu & Cordy, 1997; Turmes, 2002) which are early Middle Pleistocene, and probably also present in Corsica (Pereira, 2001; Pereira *et al.*, 2001; Pereira & Salotti, 2002). As summarised here, such a situation is much more complex than it was believed twenty years ago. The present paper will focus on some aspects of the dental morphology of these rodents. It is necessary to recall that it is widely accepted that dental morphology in mammals is related to the diet and that change in dental morphology in a lineage is also interpreted as adaptive. Endemic species are important to evolutionary studies because their lineages may illustrate under isolation trends that can be compared to those already known for other lineages – extinct or extant - under similar conditions, or compared to relate lineages which evolved under continental conditions. A better knowledge of the endemic lineages will also provide interesting results for biochronology because the dating of the Corsican Pleistocene mammal bearing localities is still difficult. The Corsican fossil mammal bearing localities which are referred to in the present paper are Punta di Calcina, Corte, Castiglione 3CG, Castiglione 1-niv3/4, La Coscia " abri nord-ouest, secteur nord-ouest", Castiglione.3 Fracture PL, and Fontaneddu. References will be found in Pereira *et al.* (2001) and Pereira & Salotti (2002). Fig. 1 gives the location of the sites.

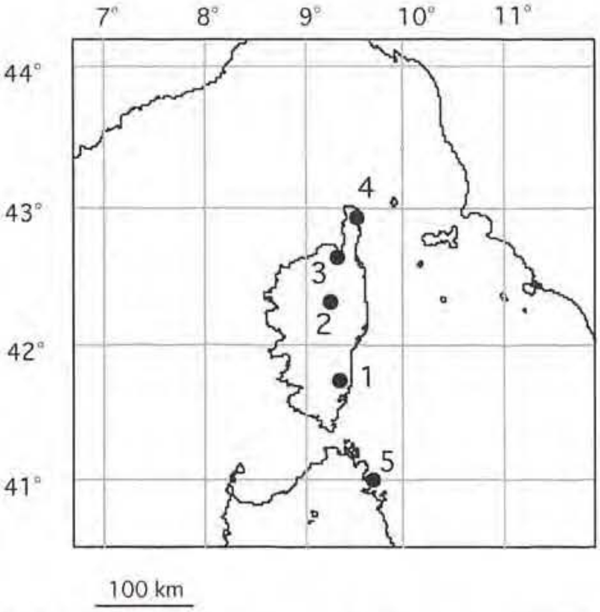

Fig. 1. Location map of the Pleistocene (Holocene excluded) fossil mammal bearing localities considered in the present paper. Corsica: 1, Punta di Calcina, 2, Corte, 3, Castiglione (several sites), 4, La Coscia. Sardinia, 5, Capo Figari.

Fig. 1. *Mapa de les localitats del Pleistocè (excloses les de l'Holocè) que han subministrat els materials considerats a aquest treball. Còrsega: 1, Punta di Calcina, 2, Corte, 3, Castiglione (several sites), 4, La Coscia. Sardenya, 5, Capo Figari.*

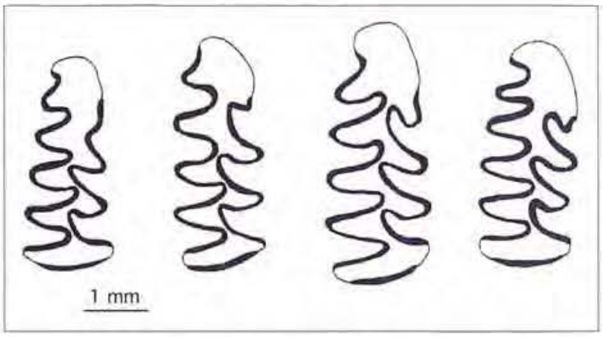

Fig. 2. *Microtus (Tyrrhenicola)*: primitive (1) and derived (2, 3, 4) morphotypes of first lower molar.

Fig. 2. Microtus (Tyrrhenicola)*: morfotipus primitiu (1) i derivats (2, 3, 4) del primer molar inferior.*

MICROTUS (*TYRRHENICOLA*) LINEAGE

Microtus (*Tyrrhenicola*) is an example of an insular evolution in a short span of time contrary to the murine *Rhagamys*: *Tyrrhenicola* cannot be older than the Biharian mammal age, clearly younger than 1.6 Ma that is late Early Pleistocene (Kretzoi, 1969; van der Meulen, 1973). *M.* (*Tyrrhenicola*) *henseli* Forsyth Major, 1905 is characterised by its large size and its peculiar dental pattern already described since a rather long time (among others, see Chaline, 1972). It has been considered related to *Microtus* (*Allophaiomys*) by van der Meulen (1973). More primitive populations of *M.* (*Tyrrhenicola*) have been recognised and they are distinct by their smaller size and less derived morphology from the younger populations that are referred to *M. (Tyrrhenicola) henseli*. These primitive populations have been recognised in Sardinia (Ginesu & Cordy, 1997; Turmes, 2002) and one Corsican population is clearly primitive, the one of Punta di Calcina (Pereira *et al.*, 2001). Molar size in these populations is much more similar to the size observed in most species of extinct and extant voles of the genus *Microtus*. These primitive populations of *M. (Tyrrhenicola)* are also different in shape, their first lower molar recall what is known among species of *M. (Allophaiomys)*.

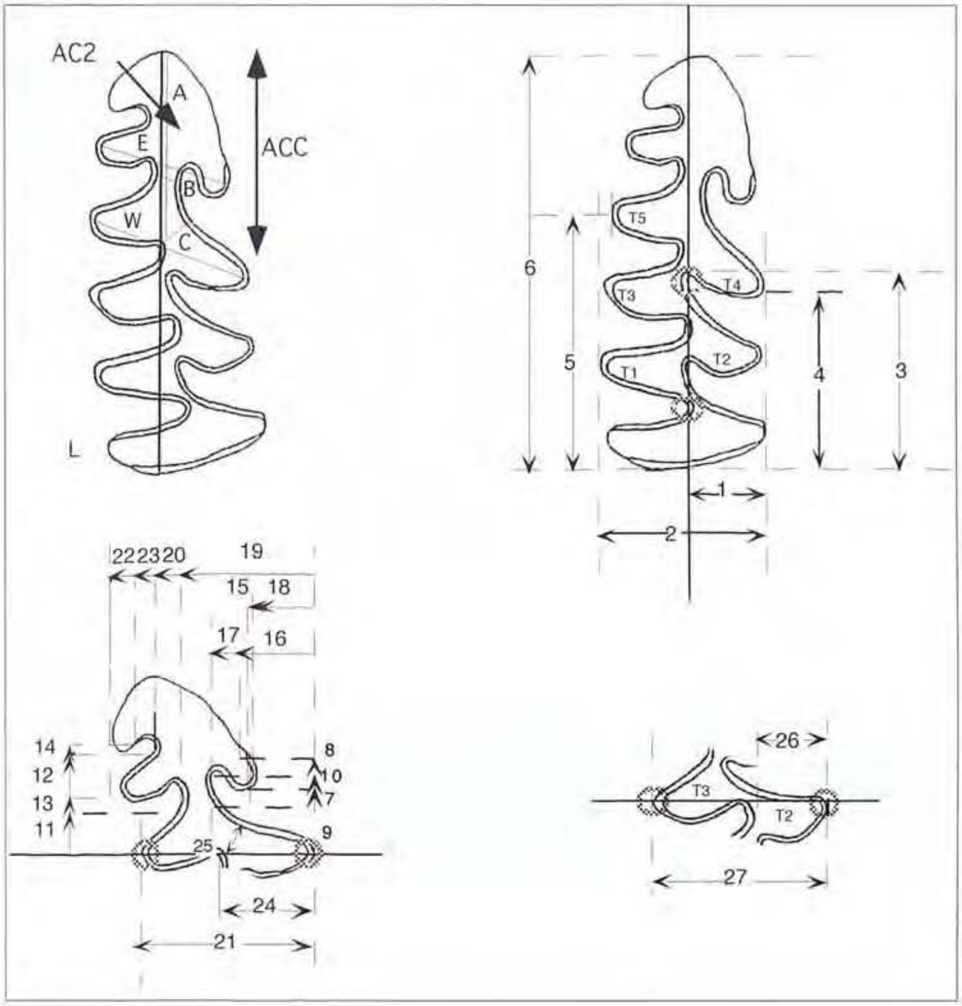

Fig. 3. *Microtus* (*Tyrrhenicola*). **A:** measurements according van der Meulen (1973) and Pereira (2001). L, total length, A, length of the anteroconid complex, W, length of the pitymyan rhombus, E, width of AC2, B, closure of AC2, C, width of the pitymyan rhombus (T4-T5). **B:** Brunet-Lecomte (B). See Brunet-Lecompte (1988) and Laplana *et al.* (2000). Two indexes are calculated LRPA [(V6-V3/V6)*100)], and the tilting of the pitymyan rhombus (T4-T5) or RP [V4-V3/V6*100)].

Fig. 3. Microtus (Tyrrhenicola). *A: mesures segons van der Meulen (1973) i Pereira (2001). L, Llargària total, A, Llargària del complex anteroconid, W, Llargària del romb pitimià, E, Amplària de AC2, B, Tancament de AC2, C, Amplària del romb pitimià (T4-T5). B: Brunet-Lecomte (B). See Brunet-Lecompte (1988) i Laplana* et al. *(2000). S'han calculat dos indexs: LRPA [(V6-V3/V6)*100)], i la inclinació del romb pitimià (T4-T5) o RP [V4-V3/V6*100)].*

Contrary to *Rhagamys* (see below) there is little doubts that only one linear specific lineage of *M. (Tyrrhenicola)* ever lived. In such a case, the directional morphological change can support a chronological succession of the involved populations. After definition of morphotypes (Fig. 2) following the work of Mezzabotta *et al.* (1996), a comparison between Corsican populations has been conducted by Pereira (Pereira, 2001; Pereira *et al.*, 2001). A morphometric analysis (Fig. 3) has been performed on the basis of some morphological characters worth of interest: shape, position and confluence of triangles on first lower molar following Van der Meulen's approach (fig. 22, p. 56, 1973). Indexes (Tab. 1) relative to the closure between triangles T4 and T5 and the anteroconid complex or ACC (index B/W), the width of the confluence of triangles T4 and T5 (C/W) and the relative length of the anterior complex (A/L) have been compared (Pereira, 2001; Pereira *et al.*, 2001). Based on parameters defined by Brunet-Lecomte (1988), and modified after Laplana *et al.* (2000) another analysis (Tab. 2) has been done which supports these results. The relative length of the anteroconid complex (LRPA = [(V6-V3/V6)*100)]) and the tilting of the pitymyan rhombus made of triangles T4 and T5 (RP = [V4-V3/V6*100)]) have been calculated. Values are significantly different between the populations of Punta di Calcina (N M/1: 32) on one side, and those of Corte (N M/1: 20) and Castiglione 3 CG (N M/1: 73) on the other side, and that Corte is near Castiglione 3 CG. Castiglione 1 (N M/1: 33), La Coscia (N M/1: 39) and Funtaneddu (N M/1: 14) are younger. The tilting (RP) is the strongest in Punta di Calcina that supports the primitive characteristic of this population. The relative differentiation of the enamel (Pereira, 2001; Pereira *et al.*, 2001) also supports another trend already known among voles as the differentiation becomes stronger in younger populations. The ancestral continental species of *Microtus (Allophaiomys)* of *M. (Tyrrhenicola)* is still unknown. Since the *M. (Tyrrhenicola)* present in the Punta di Calcina population, size increased and if all the younger populations have a very similar size, morphology continues to evolved toward a dental pattern with more enamel folds. Such a change in shape of the lower molars in *M. (Tyrrhenicola)* is related to an increase in length of the functional enamel crest. This may be an answer to competition with other species yet present on the island in relation to overlap of food spectra. In that case, at least *Rhagamys* may have been a competitor, possibly together with *Prolagus*, as both were already present when *Tyrrhenicola* immigrated.

A biochronological scale for the Corsican localities can be proposed on the basis of the morphological analyses of the *M. (Tyrrhenicola)* populations. For example, the indexes (Fig. 4) calculated for first lower molars (Pereira, 2001; Pereira *et al.*, 2001) give the following succession of localities: from the oldest to the youngest: 1) Calcina, 2) Cast.3CG and Corte, 3) Cast.3Fr PL, 4) Cast.1, La Coscia and Funtaneddu. The distinction between the chronological level 1 and 2 is clearer than the distinction of level 3 from both the older and the later ones. A comparison between evolutionary stages of populations between Corsica and Sardinia may be also interesting in order to go deeper in the analysis of this insular lineage. Unpublished data from Turmes (2002) clearly indicate that some population from the faunas of the Monte Tuttavista area are effectively primitive. A comparison with data of Mezzabotta *et al.* (1996) also indicates that there is some difference between Sardinia and Corsica for *M. (Tyrrhenicola) henseli*, a fact that may indicate a more complex evolution of the lineage when considering the two islands.

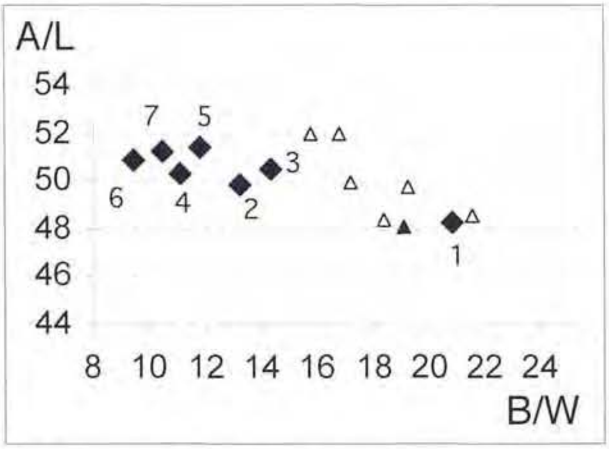

Fig. 4. *Microtus (Tyrrhenicola).* Distribution pattern of Corsican populations (squares) and Sardinian ones (triangles) according relative for lower first molar, length of the anteroconid complex (A/L) and closure of the anterior cap (B/W). For Corsica, data *in* Pereira et al. (2001), for Sardinia, in Mezzabotta et al. (1994). Corsican localities: 1, Punta di Calcina, 2, Castiglione -3CG, 3, Corte, 4, Castiglione-3Fr-PL 5, Fontaneddu 6, Castiglione-1, La Coscia, 7. For Sardinian Pleistocene localities, see Mezzabotta et al. (1994).

Fig. 4. Microtus (Tyrrhenicola). *Patró de distribució de les poblacions corses (quadrats) i sardes (triangles) d'acord a la relació al primer molar inferior, de la llargària del complex anteroconid (A/L) i el tancament de la cobertra anterior (B/W). Per a Còrsega, dades a Pereira* et al. *(2001), per a Sardenya, a Mezzabotta* et al. *(1994). Localitats corses: 1, Punta di Calcina, 2, Castiglione -3CG, 3, Corte, 4, Castiglione-3Fr-PL 5, Fontaneddu 6, Castiglione-1, La Coscia, 7. Per a les localitats pleistocèniques sardes, veure Mezzabotta* et al. *(1994).*

THE *RHAGAMYS* LINEAGE

Rhagamys orthodon (Hensel, 1856) is an extinct murine from Corsica and Sardinia larger than the present day broad-toothed field mouse *Apodemus mystacinus. Rhagamys minor* Brandy 1978 was later recognised. Smaller than the former, it has some primitive characters and it has been considered as its ancestor (Brandy, 1978). *Rhagamys minor* was described from Capo Figari (Sardinia), a locality referred to early Middle Pleistocene. Recently, it has been found in some of the newly studied

Localities	L	A	W	E	B	C	A/L	B/W	B/E	C/W
Funtaneddu	3,70	1,91	1,34	1,19	0,16	0,26	51,49	11,77	13,25	19,31
Fracture PL Moy	3,50	1,76	1,27	1,08	0,14	0,26	50,32	11,05	12,98	20,59
La Coscia	3,55	1,82	1,25	1,10	0,13	0,26	51,22	10,46	11,69	21,06
Corte	3,57	1,80	1,24	1,08	0,17	0,25	50,45	14,34	16,49	20,39
Cast.1niveaux3/4	3,68	1,88	1,25	1,12	0,12	0,27	50,89	9,47	10,39	21,51
Cast.3CG	3,61	1,80	1,28	1,09	0,17	0,26	49,84	13,20	15,43	20,34
Punta di Calcina	3,34	1,61	1,13	0,91	0,23	0,26	48,25	20,82	26,01	23,02

Table 1. First lower molar measurements of *Microtus (Tyrrhenicola)* from Corsica. Only mean values of variables L, A, W, E, B, C, and indexes A/L, B/L, B/E C/W are given. See Pereira (2001) for complete data set.

Taula 1. *Mesures del primer molar inferior de* Microtus (Tyrrhenicola) *de Còrsega. Només es donen les valors mitjanes de les variables L, A, W, E, B, C, i dels índexs A/L, B/L, B/E C/W. Veure Pereira (2001) per al conjunt de dades al complet.*

ANOVA	p level LRPA	Scheffe	p level RP	Scheffe
Castiglione-Corte	0.0152	S	0.8233	
Castiglione-Punta di Calcina	0.7395		< 0.0001	S
Corte-Punta di Calcina	0.0120	S	< 0.0001	S
t-test	p level V3	p level V4	p level RP	p level V6
Castiglione-Corte	< 0.0001	< 0.0001	0.5288	0.0002
Castiglione-Punta di Calcina	0.005	0.326	< 0.0001	0.0003
Corte-Punta di Calcina	0.0775	< 0.0001	< 0.0001	0.8936

Table 2. *Microtus (Tyrrhenicola):* Comparison of first lower molar of the Castiglione, Corte and Punta di Calcina populations: ANOVA and t-test for LRPA, and V3, V4, and index RP (see text for explanations).

Taula 2. Microtus (Tyrrhenicola): *Comparació del primer molar inferior de les poblacions de Castiglione, Corte i Punta di Calcina: ANOVA i test per LRPA, i V3, V4 i índex RP (veure el text per explicacions).*

Sardinian localities of the Monte Tuttavista area (Ginesu & Cordy, 1997; Turmes, 2002). It has also been recognised in two early Middle Pleistocene Corsican localities, Punta di Calcina and in the slightly geologically younger one of Corte (Pereira, 2001; Pereira & Michaux, 2001; Pereira *et al.*, 2001) (Fig. 5,6). But *Rhagamys minor* is also associated with *Rhagamys orthodon* in the sample of Capo Figari collected in the seventies by Louis Thaler (Brandy, 1978) as well as in the two Corsican localities. Such a situation calls for alternative interpretations: (1) two contemporaneous species are present in the fauna documented in these three sites, (2) two species are present because the latter assemblages are chronologically heterogeneous (fossils of different ages have been mixed during the filling of the cavities). The fact that the faunas from the Monte Tuttavista area (Sardinia) do not show such an association of two species (Ginesu & Cordy, 1997; Turmes, 2002) is not a definitive argument in favour of the heterogeneity hypothesis. The faunas found at Monte Tuttavista may simply not document the peculiar time span during which two *Rhagamys* species have lived together in Corsica as well as in Sardigna. We conclude here to the co-occurrence of two species of *Rhagamys* during a possibly short time. The two *Rhagamys* species diverged in size but both did not evolve significantly in dental morphology (Pereira & Michaux, 2001). Second upper molars are important clues (Pl. 1). *Rhagamys minor* in Punta di Calcina and Corte (Pl. 1, G-I) still exhibit primitive characters but at a lesser stage than in Capo Figari (Pl. 1, J-K). Accessory cusps on the anterior external side of upper second molar are still present, however *Rhagamys orthodon* is more evolved (Pl. 1, A-F). *Rhagamys minor* had short life duration, contrary to *Rhagamys orthodon*, which lasted until Holocene. In conclusion, a cladogenesis is hypothesised in the *Rhagamys* lineage. The fact that the co-occurrence of two *Rhagamys* species is documented when *Tyrrhenicola* is present under a primitive morphological stage, favours the hypothesis of an interaction between species resulting in a cladogenesis in the *Rhagamys* lineage in response to the immigration of *Tyrrhenicola*. Size divergence goes with the cladogenetic event.

Martin-Suarez & Mein (1998) and Angelone & Kotsakis (2001) have recently discussed the origin of the insular lineage. The two latter authors completed and revised the Sardinian Mandriola fauna originally described by

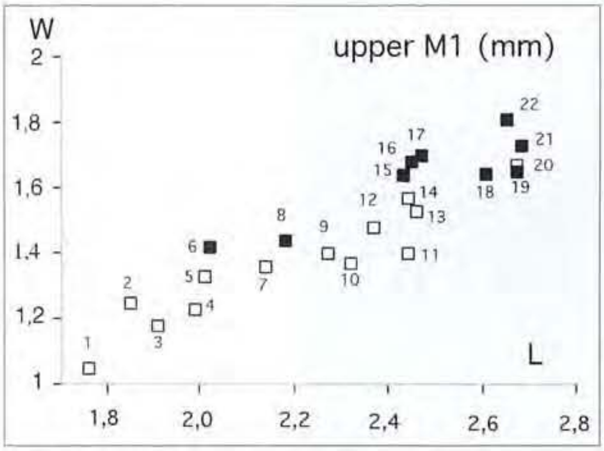

Fig. 5. Variation of first upper M1 mean size in the *Rhagamys* lineage. *Rhagapodemus primaevus*: 4, Lissieu (Hugueney & Mein, 1965), 5, Maramenna (Kotlia *et al.*, 1998); *Rhagapodemus ballesioi*: 1, Hautimagne (Mein & Michaux, 1970), 3, Gundersheim (Fejfar & Storch, 1990); *Rhagapodemus hautimagnensis*:, 7, Ptolemais (van de Weerd,1979), 10, Hautimagne (Mein & Michaux, 1970); *Rhagapodemus frequens*: 11, Gundersheim (Fejfar & Storch, 1990), 13, Seynes (Bachelet, 1990), 14, Turquey (Ünay & de Bruijn, 1998); *Rhagapodemus debruijni*: 9, India (Kotlia et al., 1998); *Rhagapodemus athensis*: 19, Toukobounia (de Brujn & van de Weerd, 1975); *Rhagapodemus azzarolii*: 2, Mandriola (Angelone & Kotsakis, 1998); *Rhagamys minor*: 6, Punta di Calcina (Pereira *et al.*, 2001), 8, Capo Figari (Pereira *et al.*, 2001.); *Rhagapodemus vandeweerdi*: 12, Maritza (de Bruijn & van de Weerd, 1975); *Rhagamys orthodon*: 15, Punta di Calcina, 21, Castiglione- 3Fr-Pl, La Coscia, 16, Corte, 17, Capo Figari, 18, Castiglione-1, 20, Castiglione -3CG (all sites, Pereira *et al.*, 2001).

Fig. 5. *Variació de la mida mitjana del* M^1 *a la línia evolutiva de* Rhagamys, Rhagapodemus primaevus*: 4, Lissieu (Hugueney & Mein, 1965), 5, Maramenna (Kotlia* et al.*, 1998),* Rhagapodemus ballesioi*: 1, Hautimagne (Mein & Michaux, 1970), 3, Gundersheim (Fejfar & Storch, 1990);* Rhagapodemus hautimagnensis:*, 7, Ptolemais (van de Weerd,1979), 10, Hautimagne (Mein & Michaux, 1970);* Rhagapodemus frequens*: 11, Gundersheim (Fejfar & Storch, 1990), 13, Seynes (Bachelet, 1990), 14, Turquey (Ünay & de Bruijn, 1998);* Rhagapodemus debruijni*: 9, India (Kotlia* et al.*, 1998);* Rhagapodemus athensis*: 19, Toukobounia (de Brujn & van de Weerd, 1975);* Rhagapodemus azzarolii*: 2, Mandriola (Angelone & Kotsakis, 1998);* Rhagamys minor*: 6, Punta di Calcina (Pereira* et al.*, 2001), 8, Capo Figari (Pereira* et al.*, 2001.);* Rhagapodemus vandeweerdi*: 12, Maritza (de Bruijn & van de Weerd, 1975);* Rhagamys orthodon*: 15, Punta di Calcina, 21, Castiglione- 3Fr-Pl, La Coscia, 16, Corte, 17, Capo Figari, 18, Castiglione-1, 20, Castiglione -3CG (totes les localitats, Pereira* et al.*, 2001).*

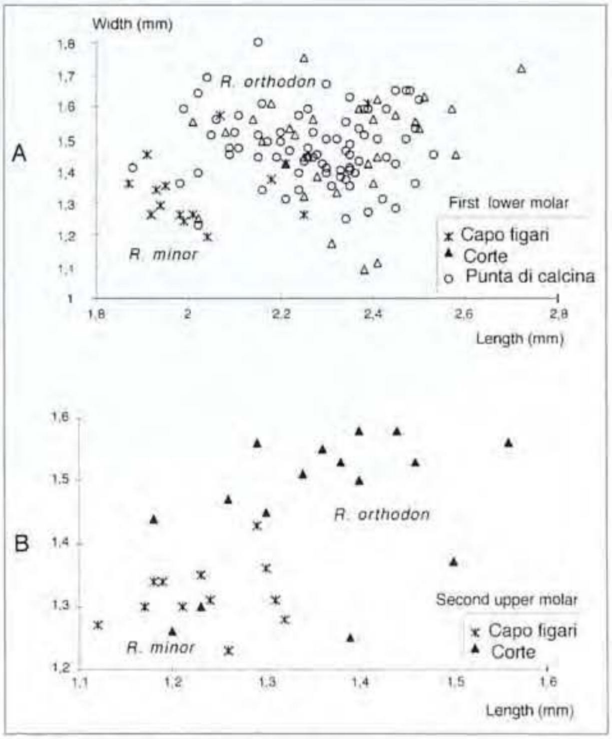

Fig. 6. Scatter diagram for first lower molar (a) and upper second molar (b) of *Rhagamys* samples from Capo Figari (Sardinia), Punta di Calcina and Corte (Corsica); data from Pereira (2001) and Pereira et al. (2001).

Fig. 6. Diagrama de dispersió per al primer molar inferior (a) i segon molar superior (b) de mostres de Rhagamys *de Capo Figari (Sardenya), Punta di Calcina i Corte (Còrsega); dades de Pereira (2001) i Pereira* et al. *(2001).*

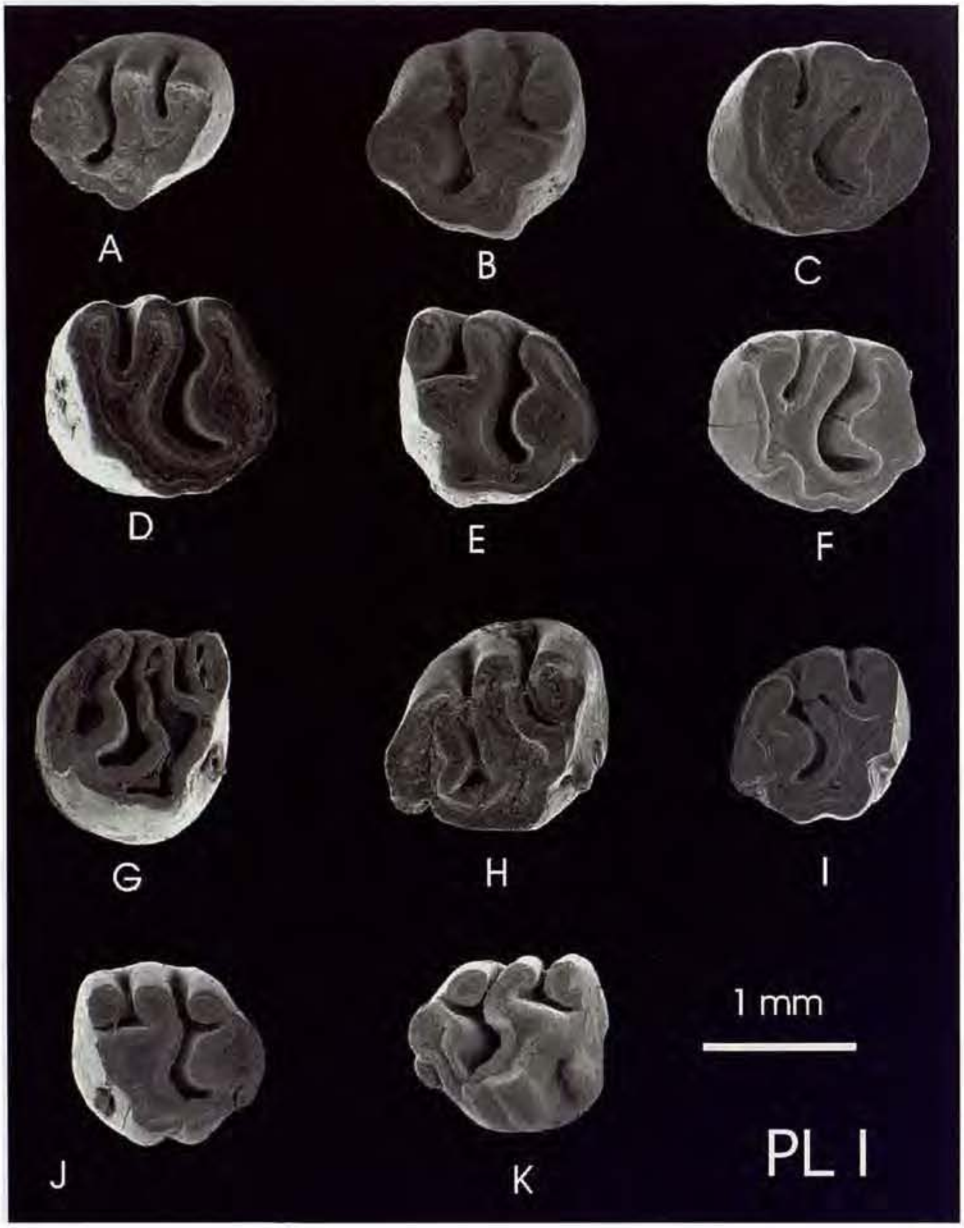

Plate I. *Rhagamys orthodon* M^2: A, B, sin., C, dex., Punta di Calcina (Corsica); D, E, dex., Corte (Corsica); F, dex., Capo Figari (Sardinia); G, H: locality of Corte (Corsica). *Rhagamys minor* M^2: G, sin, Corte (Corsica); J, dex., K, sin., Capo Figari (Sardinia). A-E, collections of the University of Corsica, Corte, and F-H, University of Montpellier II.

Lamina I. M^2 de Rhagamys orthodon: *A, B, esq., C, dret., Punta di Calcina (Còrsega); D, E, dex., Corte (Còrsega); F, dret., Capo Figari (Sardenya); G, H: localitat de Corte (Còrsega). M^2 de* Rhagamys *minor: G, esq., Corte (Corsica); J, dret., K, esq., Capo Figari (Sardenya). A-E, col·leccions de la Universitat de Còrsega, Corte, i F-H, Universitat de Montpellier II.*

Pecorini *et al.* (1974). They concluded that the *Rhagapodemus* of Mandriola must be assigned to a new species they named *Rhagapodemus azzarolii. Rhagapodemus azzarolii* is smaller and less evolved than *Rhagamys minor*. Its ancestor would be the continental *Rhagapodemus ballesioi*, and *Rhagapodemus azzarolii* would be the ancestor of the younger *Rhagamys* species. The age of the Mandriola fauna in Sardinia is also disputed: either an early Pliocene age ca. 5.3 ma, or a middle Pliocene age ca. 3.5 Ma according respectively to Pecorini *et al.* (1974) and Angelone & Kotsakis (2001). However another problem was raised because Martin-Suarez & Mein (1998) consider *Rhagamys minor* as a member of the genus *Rhagapodemus*. They propose to use of the genus *Rhagamys* only for the most derived species *Rhagamys orthodon* a conclusion not shared by Angelone & Kotsakis (2002) who underline the arbitrary boundary in what they consider a single phyletic lineage and because they consider *Rhagapodemus azzarolii* already an insular species.

Molar size, hypsodonty and morphology

There is a general trend toward a greater size in the *Rhagamys* lineage as already documented among others by Michaux (1971) and more recently by Martin-Suarez & Mein (1998). Figure 5 illustrates such a trend documented by measurements taken from the literature. A similar trend is illustrated by the insular forms *Rhagapodemus azzarolii, Rhagamys minor* and *Rhagamys orthodon* independently of the lineage splitting. Height of molars is another important parameter to recognise the grade of evolution of a species. Combined with length or width it is used to calculate hyspsodonty indexes (Tab. 3). As *Rhagamys* and *Rhagapodemus* teeth are not ever growing, only maximum values given by teeth from juvenile individuals can be used to calculate such indexes. For *Rhagapodemus azzarolii*, crown height has been estimated from the hypsodonty ratio given in the original publication. Molars do not show a rise in hypsodonty from *R. azzarolii* either to *R. orthodon* or *R. minor*.

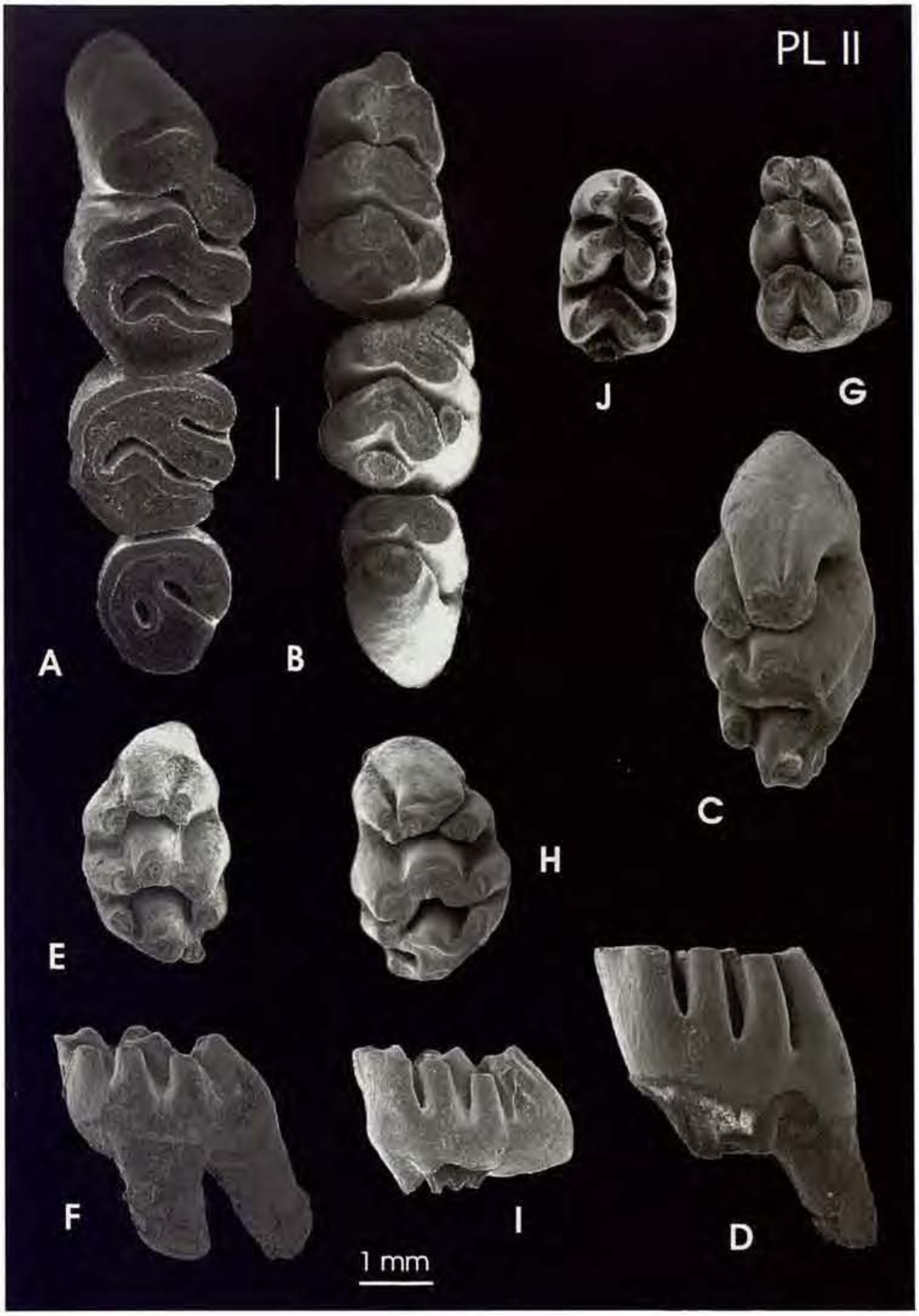

Plate II. *Rhagamys, Rhagapodemus* and *Apodemus* tooth morphology. *Rhagamys orthodon*: A,B, C, D; *Apodemus* cf. *jeanteti*: E, F, G; *Rhagapodemus hautimagnensi*: H, I; *Rhagapodemus primaevus*: J. Fossil bearing localities: A, B, Castiglione (reworked material); C, D, Corte; E, F, G, H, I, Mont-Hélène; J, Castelnou-3. A, upper row; C, D, E, F, upper M1, B, lower row; G, J, m_1. D, I, F: labial views. All photographs organised in order to indicate right teeth.

Lamina II. Morfologia dentària de Rhagamys, Rhagapodemus *i* Apodemus. Rhagamys orthodon*: A,B, C, D;* Apodemus *cf.* jeanteti*: E, F, G;* Rhagapodemus hautimagnensi*: H, I;* Rhagapodemus primaevus*: J. Localitats fossilíferes: A, B, Castiglione (material retreballat); C, D, Corte; E, F, G, H, I, Mont-Hélène; J, Castelnou-3. A, sèrie superior; C, D, E, F, M1, B, sèrie inferior; G, J, m_1. D, I, F: vistes labials. Totes les fotografies preparades per mostrar les dents dretes.*

It is not in the scope of the present paper to give or reconsider the detailed comparison between molar morphologies in *Rhagapodemus* and *Rhagamys* species as several authors have recently published on these subjects (Martin Suarez & Mein, 1998; Pereira & Michaux, 2001). However, we will consider the adaptive interpretation of the molar morphology in *Rhagapodemus* and *Rhagamys* (Pl. II). Murine rodents have basically low-crowned molars with numerous well-individualised major cusps as for example in *Apodemus* (Plate II, E, F, G). The major cusps, which are organised in longitudinal rows (three at upper molars, two at lower molars), are linked transversally together to form chevrons of characteristic shape. These rows of cusps determine two valleys. The two rows of cusps of the lower molars glide forwards during the chewing stroke in the two valleys of the upper teeth. Hypsodonty introduces changes to this occlusal pattern: cusps become more cylindrical in lateral view and more parallel (Plate II, F, I, D). The dentine area of the cusps tilts much less in *Rhagamys* than in *Apodemus* and an intermediate situation can be seen in *Rhagapodemus*. In *Rhagamys orthodon* (Plate II, A, B, C, D), the occlusal surface is no more characterised by the longitudinal valleys and is nearly flat. In the intermediate stage represented by *Rhagapodemus* the longitudinal valleys rapidly disappear with wear. There are also secondary cusps and crests in teeth of murine rodents. These structures are rather low and are reached by wear only in old indivi-

Locality	Genus and species	LM1	WM1	HM1°	H/L	Lm1	Wm1	Hm1	H/L
Punta di Calcina	*Rhagamys minor*	2,02	1,42	1,74	0,86	1,97	1,4	1,86	0,94
Corte	-	-	-	-	-	2,02	1,25	1,79	0,89
Cast. 3 Fr Pl	*Rhagamys orthodon*	2,65	1,81	-	-	2,38	1,53	2,1	0,88
Corte	-	2,45	1,68	2,17	0,88	2,34	1,46	2,18	0,93
Cast. 1	-	2,62	1,65	2,37	0,90	2,36	1,53	2,34	0,99
Cast-3CG	-	2,68	1,73	2,47	0,92	2,48	1,49	2,39	0,96
P. Calcina	-	2,43	1,64	2,26	0,93	2,29	1,48	2,25	0,98
Capo Figari	-	2,47	1,70	1,21	0,48	2,22	1,45	1,86	0,84
Mandriola	*Rhagapodemus azzarolii*	1,85	1,23	1,01	0,55	1,88	1,17	1,05	0,56

Table 3. Hypsodonty in insular populations of *Rhagapodemus* and *Rhagamys*. See Pereira (2001) and Pereira & Michaux (2002) for complete data set.

Taula 3. *Hipsodòntia a les poblacions insulars de* Rhagapodemus *i* Rhagamys. *Veure Pereira (2001) i Pereira i Michaux (2002) per al conjunt de dades al complet.*

duals. Secondary cusps and crests have been involved in the evolution towards *Rhagamys*. Some of them as accessory outer lingual cusps on M^2 (Plate 1) progressively disappear whereas others, as the posterior one on M^1 and M^2, or the accessory labial cusps on lower molars, become higher and as high as major cusps. Some remain distinct; others fuse with the neighbouring major cusp as recalled by Martin-Suarez & Mein (1998) for lower accessory cusps on the labial side of first lower molar (Plate II, B, J). Such modifications are observed in many cases of simplification of the crown in murine rodents, as for example in the *Otomys* lineage (Sénégas & Avery, 1998). In consequence, some secondary structures are progressively involved in the chewing process; the length of the working enamel crests being increased. A last striking characteristic of hypsodonty in the *Rhagamys* lineage is that cusps become higher in comparison with the lower part of the crown (Plate II, F, I, D); such a hypsodonty is qualified as tubercular hypsodonty (Herskovitch, 1967). Enamel thickness is also another interesting character: in *Apodemus* as well as in old *Rhagapodemus* species (Plate II, E, H, J, D) the enamel is differentiated when comparing mesial and distal faces of major cusps contrary to *Rhagamys* (Plate II, A, B). These changes go with hypsodonty, as more weakly differentiated enamel is present in later members of the *Rhagamys* lineage.

Jugal teeth evolution and adaptation in *Rhagamys*

Difference in crown height in mammalian molars is interpreted as correlated to the diet, which also goes with higher or lesser differentiation of the enamel thickness. Such changes that occurred in a lineage through time are similarly interpreted as adaptive. Rodents give many examples, among others, the European Theridomyines rodents during the Oligocene (Vianey-Liaud, 1976). The evolution of the *Rhagapodemus-Rhagamys* group can be consequently interpreted as correlative of an adaptation to a more abrasive diet. Such an evolution can be correlated to the vegetation and climatic modifications toward more wet-dry seasonal and overall warm and arid climate that happened in Europe during the Upper Miocene (Van Dam, 1997). According to the calibration of the biochronological scale and the present day data on European murine rodents (de Bruijn *et al.*, 1996; Steininger *et al.*, 1996), during the Late Miocene, a diversification occurred. Aside some lineages with conservative molar morphology that did not change very much, two main ones differentiated derived dental characters: the *Occitanomys - Stephanomys* lineage ca. 9.0 Ma, and the *Rhagapodemus- Rhagamys* one ca. 7.0 Ma. If the dental morphology of *Stephanomys* and *Rhagamys* are very different, they have many characteristics interpreted as an adaptation to a more abrasive diet (for *Stephanomys*, see Renaud *et al.*, 1996; Van Dam, 1997; Renaud & Van Dam, 2002). *Rhagamys* is consequently the insular branch of a continental lineage already adapted to an abrasive diet, insularity having allowed evolution to be accelerated and morphological change to go further on.

Another clue to the interpretation of *Rhagamys* is to be found in a comparison with extant murine rodents. The latter form a group of about 500 species which includes several forms with molars equally well adapted to an abrasive diet but morphologically different of both *Stephanomys* and *Rhagamys* (for example, *Bandicota* and *Crateromys*, see figures in Misonne, 1969). However among extant murine rodents, there is a species very much alike to *Rhagamys orthodon*: *Tokudaia osimensis*. This species lives on some islands of the Okinawa archipelago (Japan) where it is rare and threatened (Wang *et al.*, 1989). Its dental morphology is very similar to the one of *Rhagamys orthodon:* flat occlusal surface, hypsodonty, and undifferentiated enamel. The Japanese species is linked to field mice group because of its dental pattern very similar to the one of *Rhagamys* (Kowalski & Hasegawa, 1976; Kawamura, 1988). Studies in molecular phylogeny recently strongly support this hypothesis (Michaux *et al.*, 2002; Jansa & Weksler, 2003). Paleontological data from eastern Asia obtained in the last ten years document the presence of Pliocene *Rhagapodemus*-like species in China and India from Late Miocene to Early Pleistocene faunas (Storch, 1987; Kotlia *et al.*, 1998). *Tokudaia* and *Rhagamys* thus illustrate a case of parallel evolution under insularity because they share a common ancestry in the Palaearctic genus *Apodemus*. Owing to *Tokudaia*, some characteristics that cannot be fossilised can be hypothesised for the extinct species. *Tokudaia* has a vole-like aspect and a spiny fur. There are enough bones in the Corsican fossil material to answer the first part of the question. *Tokudaia* lives in a shrubby forest with undergrowth of coarse grass and ferns (Nowak, 1999). The interpretation of Late Miocene climatic evolution is not in contradiction with the hypothesis that zones with such a vegetation were spreading, that induced the adaptation of some rodents to the newly developed environments. More, the Mediterranean vegetation was already established in the Pliocene (Fauquette *et al.*, 1999).

CONCLUSION

New data and consideration of both tooth morphology and function in *Microtus* (*Tyrrhenicola*) and *Rhagamys* molars bring new light on the evolution of these remarkable extinct rodents from Corsica and Sardinia. Independently of any consideration about the appropriate naming of the species, *Rhagapodemus azzarolii*, *Rhagamys minor* (*Rhagapodemus minor* by Martin Suarez & Mein, 1998) and *Rhagamys orthodon* represent an original insular branch of the continental murine genus *Rhagapodemus*. *Rhagamys* is thus the term of an evolution that begun on the European continent. Insularity first accelerated evolution no later than the upper Pliocene, and later, evolution accelerated in response to the immigration of *M. (Tyrrhenicola)* in the early Middle Pleistocene. Competition also had an effect on *M. (Tyrrhenicola)*. Turmes (2002) observed similar facts on the two rodents in the succession of the fossil bearing sites of the Monte Tuttavista area. Hypsodonty that was already acquired in the *Rhagamys* stage did not change significantly but as the two species were similarly adapted, they diverged by their size because they had to compete for resources. Such an interpretation was proposed to understand the pattern of size and shape differentiation during the evolutionary radiation of the European Miocene murine rodents (Renaud *et al.*, 1999). Insularity remains a major topic in evolutionary biology. Regarding mammals, Thaler (1973) clearly stressed the main aspects of evolution on islands, and he described the insularity syndrome in the case of rodents and of large herbivores. However, rhythm and conditions of the evolution of species was still difficult to reconstruct. Sondaar (2000) at the light of examples taken in different geographical area, Mediterranean and South-east Asia, of the fate of endemic island faunas, recalled that once an endemic fauna has been established, the fauna remains quite stable in composition and morphology, independently of the global climatic evolution. However, if immigration events happened, competition becomes the driving force of change. Pleistocene Corsican faunas bring arguments in favour of such an interpretation.

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A synthesis of knowledge on the large Pleistocene mammalian fauna from Corsica

Elisabeth Pereira, Michelle Salotti & Marie Françoise Bonifay

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Resum

Durant els darrers deu anys, el coneixement sobre la fauna de grans mamífers del Pleistocè de Còrsega s'ha incrementat significativament gràcies a l'estudi de vuit conjunts fossilífers provinents de 6 jaciments fossilífers : Castiglione 1 et 3 (Oletta/Haute-Corse), La Coscia abri sud, abri nord-oeust (Rogliano, Cap Corse, Corte (Haute-Corse), Punta di Calcina (Corse du Sud). Divuit espècies extingides (6 micromamífers i 12 macromamífers) es troben distribuïdes en un interval de temps que abasta des del Pleistocè Mitjà fins a la fi del Pleistocè Superior. Aquests taxa, o bé són endèmics de Còrsega i Sardenya, o bé només de Còrsega i fins a la data no es coneixen de nivells sards d'edat similar o més primerenca. Els estudis revelen una fauna disharmònica, i no il·lustren cap cas de nanisme o gegantisme insular durant aquest interval temporal. Durant el Pleistocè Mitjà, els membres d'aquesta fauna ja havien adquirit les característiques de les espècies evolucionades sota condicions d'insularitat. D'ençà del Pleistocè Mitjà, la fauna no va sofrir cap renovació d'espècies, si bé va perdre alguns dels seus elements durant el Pleistocè Mitjà o a la fi d'aquest període, o al límit Tardiglacial/Holocè. En comparació i contrastant amb el que esdevé a altres illes mediterrànies, la diversitat de la macrofauna de mamífers de Còrsega és notable i cal emfatitzar que els carnívors es troben relativament ben representats al Pleistocè Mitjà, amb dues famílies (Canidae, Mustelidae) i cinc taxa reconeguts (*Canis* sp., Cuoninae indeterminat, *Cyrnolutra castiglionis*, dos Mustelidae indeterminats). Respecte els artiodàctils, hi ha dues famílies (Cervidae, Suidae) i tres gèneres (*Megaloceros, Cervus, Sus*). Aquesta contribució tracta de representar algunes dades sobre la morfologia i la distribució estratigràfica dels macromamífers de Còrsega i tracta d'indicar els problemes relacionats amb les migracions i extincions d'espècies al Pleistocè.

Paraules clau: Còrsega, Pleistocè, Mamífers, Insularitat, Endemisme, Biodiversitat.

Abstract

During the past ten years, the knowledge about the Corsican Pleistocene large mammalian fauna has significantly increased owing the study of eight assemblages extracted from six fossiliferous deposits : Castiglione 1 et 3 (Oletta/Haute-Corse), La Coscia abri sud, abri nord-oeust (Rogliano, Cap Corse, Corte (Haute-Corse), Punta di Calcina (Corse du Sud). Eighteen extinct species (6 small mammals and 12 large ones) are distributed in a time interval extending from the Middle Pleistocene up to the end of Upper Pleistocene. These taxa are either endemic to Corsica and Sardinia or only known in Corsica and up to now unknown from Sardinia levels of similar age or earlier. Studies indicate an unbalanced fauna, without any illustration of island dwarfism or gigantism during the involved time interval. At the time of the Middle Pleistocene, the members of this fauna already acquired characteristics of species having evolved under conditions of isolation. Since the Middle Pleistocene, the fauna underwent no species renewal but lost some of its members during the Middle Pleistocene or at the end of this period, or at the Tardiglacial/Holocene boundary. In comparison with and by contrast to some other Mediterranean islands, the diversity of the Corsican large mammal fauna is worth to be emphasised even if carnivores are rather well represented in the Middle Pleistocene with two families (Canidae, Mustelidae) and five recognised taxa (*Canis* sp., Cuoninae indet., *Cyrnolutra castiglionis*, two Mustelidae indet.). With respect to artiodactyls, there are two families (Cervidae, Suidae) and three genera (*Megaloceros, Cervus, Sus*). This contribution intends to present some data on the morphology and the stratigraphical distribution of the members of the Corsican large mammal fauna and to point out the problems connected with Pleistocene migration and extinction of species.

Keywords: Corsica, Pleistocene, Mammals, Insularity, Endemism, Biodiversity.

Introduction

For a long time islands have held a particular interest to naturalists, biologists and paleontologists. Island environments have an original, impoverished fauna which is often endemic and unbalanced, with particularities due to ancient or recent geographic or genetic isolation, and also to the island's own peculiarities. Each island thus has its own particular fauna, and each fauna has its own history. A study of these environments provides data as to establish the adaptive capacities of the faunas and human groups present in these restrictive environments and always allows us to expect a better understanding of the evolutionary processes linked to the effects of insularity (migration routes and data, variations in size and/or morphofunctional variations, interactions between animals, interactions between humans and animals, data about and causes of extinctions). Corsica is part of the large Mediterranean islands which have yielded an original fauna of Quaternary vertebrates, the representatives of which are well known nowadays. The geological nature of Corsica partly explains the scarcity of bone remains from the Plio-Pleistocene or earlier, and, consequently, the scarcity of previous works. Actually, contrary to what happens in Sardinia (de Bruijn & Rümke, 1974; Pecorini *et al.*, 1974; Esu & Kotsakis, 1983; Cordy & Ginesu, 1994), there is no known site in Corsica with terrestrial vertebrates from the Tertiary (Miocene) or from the beginning of the Quaternary (Pliocene and Lower Pleistocene). Cenozoic fossil vertebrate fauna is practically unknown on the island and it was necessary to wait until the year 2000 to discover, in Tertiary terrains from the end of the Oligocene (Ferrandini *et al.*, 2000), the traces of a small mammal, the oldest known one in Corsica, of the order of the Artiodactyls, *Pomelomeryx boulangeri*, Pomel, 1853.

The most ancient paleontological discoveries date back to the XVIII century, the XIX century, and the beginning of the XX century, and consist of scarce "Pleistocene" Quaternary sites or breaches situated essentially in Haute-Corse ex. Grotta al Margine (Forsyth-Major, 1880); Brietta, Funtaneddu, Teppa di u Lupino (Tobien, 1935); La Coscia sud (Depéret, 1897; Sigogneau, 1960; Bonifay, 1976). Until the beginning of the 90s, due to the scarcity of the Corsican sites and their imprecise datings, works on the Pleistocene paleofauna of Corsica were clearly behind in comparison with the numerous works existing for other Mediterranean islands (e.g., Balearic Islands and Sardinia: Kotaskis, 1980; Alcover *et al.*, 1981; Caloi & Palombo, 1990; Sondaar *et al.*, 1995; van der Made, 1999; Sondaar, 2000). The works were essentially carried out on the study of Holocenic archaeological locations, which are very abundant on the island, often dated in the Neolithic, the faunas of which were widely studied by JD Vigne (Vigne, 1992; Vigne *et al.*, 1997). Nowadays this lag has been partially overcome, thanks to the results of research carried out in the last ten years. The discovery of new fossil sites -such as La Coscia nord-ouest (Rogliano, Cap Corse ; Bonifay *et al.*, 1998; Bonifay, 2001), Castiglione (Oletta, Haute-Corse; Salotti *et al.*, 2000, 2001), Gritulu (Luri, Haute-Corse; Vigne *et al.*, 2000)- but also the re-excavations of old sites –such as Corte (Haute-Corse) and Punta di Calcina (Conca, Corse-du Sud), see Pereira *et al.* (2001)- have produced an important advance in the knowledge of the Corsican Pleistocene paleofauna, which was only known in part. Moreover, thanks to the obtention of absolute and/or relative datings, these sites are well dated and cover a period of time comprising between the Middle Pleistocene and the beginning of the Holocene. A collective research programme coordinated by M.F. Bonifay was carried out entitled *«Les gisements pléistocènes corses dans le contexte des îles méditerranéennes»*, which has made it possible to study the Castiglione, La Coscia, Corte and Punta di Calcina sites. Within the framework of an international research project coordinated by JD Vigne entitled "*Paysages, Renouvellements de Faune et Anthropisation de la Corse au Tardiglaciaire et au début de l'Holocène*", Gritulu was studied.

This research all together has enriched the collections of Pleistocene fossil vertebrates (Table 1), has renewed the knowledge on these paleofaunas and has considerably recorded their history and evolution on the island with time. Numerous paleontological syntheses currently give credit to the originality of this paleofauna with an elevated ratio of endemism and with several new species or subspecies (Hervet & Salotti, 2000; Pereira & Salotti, 2000; Bailon, 2001; Bonifay, 2001; Hervet, 2001; Louchart, 2001; Mourer *et al.*, 2001; Pereira & Michaux, 2001; Louchart, 2002). According to Bonifay (2001), this paleofauna is an endemic fauna typical of a temperate climate, with weak biodiversity, which unquestionably differs quantitatively and qualitatively from that found at the same time on the continent, thus reflecting an evident disharmony. Within the framework of this work we aim only to present a balance of the knowledge available on the fauna of the large Pleistocene mammals in Corsica. Two sites, Castiglione and La Coscia, which stand out for the quality and also the quantity of their faunistic assemblage, have profoundly modified our knowledge on this megafauna, yielding dental or bone remains from six new species, amongst which there are several carnivores.

Reptiles
Lacerta nov. sp.
Mammals
Episoriculus corsicanus Bate, 1945
Talpa tyrrhenica Bate, 1945
Microtus (Tyrrhenicola) henseli Forsyth-Major, 1882
Rhagamys orthodon Hensel, 1856
Rhagamys minor Brandy, 1978
Prolagus sardus Wagner, 1829
Cynotherium sardous Studiati, 1857
Canis sp.
Cuoniné indét.
Mustelidé indét.
Mustelidé indét.
Lutra sp. ?
Algarolutra majori Malatesta, 1978
Cyrnolutra castiglionis Pereira & Salotti, 2001
Megaloceros (Nesoleipoceros) cazioti Depéret, 1897
Cervus elaphus rossii Pereira, 2002
Sus sp. ?
Oiseaux
Gyps melitensis Lydekker, 1890
Buteo rufinus jansoni Mourer-Chauviré, 1975
Aquila chrysaetos
Aquila nov. sp.
Falco peregrinus cyrneus
Tyto balearica cyrneichnusae
Bubo insularis Mourer-Chauviré & Weesie, 1986
Athene angelis Mourer-Chauviré *et al.*, 1997
Turdus nov. sp.
Pyrrhocorax graculus castiglionis
Pyrrhocorax pyrrhocorax macrorhynchos

Table 1. Extinct Pleistocene vertebrate of Corsica.

Taula 1. Vertebrats pleistocènics extingits de Còrsega.

CONTRIBUTION OF THE CASTIGLIONE AND LA COSCIA SITES TO THE KNOWLEDGE OF THE FAUNA OF LARGE MAMMALS

Castiglione

The Castiglione site (Oletta, Haute-Corse, Fig. 1) is situated to the south of the city of Saint-Florent, to the west of the river Alisu, on the east side of a hill, la Cima di Buttogio (206 m snm). Discovered in 1991 by speleologists from two Corsican associations, it is quite well known nowadays (Pereira *et al.*, 1999; Salotti *et al.*, 2001). With a surface of around 3 km^2, the hill is made up of cipolins from the Late Jurassic and the Lower Cretaceous which rest on calcareous schist and shiny schist. The hill is affected by numerous vertical fractures, of tectonic origin, running north-south and west-east, which can form large subterranean networks. These networks, with a development which can reach over 1000 metres, contain numerous fossil-bearing places rich in bones belonging to terrestrial and flying vertebrates. Actually, sixteen open caverns have been catalogued, but only four provide access to a subterranean network of variable length. To date, only cavities 1 and 3 have been the object of systematic excavations and paleontological studies. The contribution of this site to the knowledge of the fauna of large mammals has been evidenced from the paleontological study of the bones taken from one of the deposits in cavity 3, situated between -33 and -39 m in depth, the so-called Cast.3CG deposit. It is a deposit of natural origin which is presented under the form of a landslide. Dated in the Middle Pleistocene, it has yielded a homogeneous assemblage which has been interpreted as the result of an accumulation of owl pellets, and also of bone remains left in nests of birds of prey, nests which would probably have been located on a cliff that has now disappeared; a cliff made up of cipolins, which nowadays, on the surface, no more than a few pieces can be found (Salotti *et al.*, 2003). Nine land mammals have been extracted from this deposit; there are four new endemic forms, *Canis* sp., *Cuoninae* indet., *Cynolutra castiglionis* Pereira & Salotti, 2000 and *Cervus elaphus rossii* Pereira, 2001.

The first carnivore, *Canis* sp., can be distinguished from the Corsican-Sardinian endemic species *Cynotherium sardous* by the shape and dimensions of its molars. Its M^1 are much longer and above all wider. Even though the shape of the molars is reminiscent of *Canis* type molars, their taxonomic position within the European *Canis* of the Middle Pleistocene is as yet uncertain. Due to some morphological characteristics this fossil is near to *Canis etruscus* and *Canis arvensis*, whereas its very small dental dimensions place it near fossil and present day jackals (Pereira, 2001). The second carnivore is only known by its lower dentition. Its carnassial tooth (M_1) has three characteristics of the continental *Cuon* group, but the presence of a third molar places it far from these. With our current state of knowledge it is difficult to establish its genus and species denomination since it has morphological similarities to the *Cynotherium* (to the *sardous* species, the only species of the genus) and *Xenocyon* (to the *dubius* species, a Villafranchian form from China) genera.

As far as the otter *Cyrnolutra castiglionis* is concerned, it is only actually known in Corsica. It is distinguished by it morphological characteristics and by its dimensions of the otters of the Pleistocene known in the Mediterranean basin (in Sardinia, Sicily and Malta) and of the common otter (*Lutra lutra*). It is a small otter, with robust bones, with strong muscular insertions. Its shortened limbs (especially the feet) and the morphology of its sacrum (flattened, with a very large sacral canal) suggest a tail with great mobility, and these seem to be characteristic of a form that was very adapted to aquatic life.

The remains of these three carnivores are associated with *Cynotherium sardous*, and also with a new subspecies of endemic deer, *Cervus elaphus rossii*. This is an original form which can be differentiated from present day and fossil continental deer by a reduction in bone length of its limbs (but not of its teeth), and also by the acquisition of the particular adaptive bone anatomic features, which affect the proximal and/or distal region of the limb bones and which concern the areas of muscular insertion, with the consequence of the acquisition of greater stability. This form bears no parentage with the Corsican-

Fig. 1. The Cima di Buttogio massif (Oletta, Haute-Corse).

Fig. 1. Vista de la Cima di Buttogio (Oletta, Haute-Corse).

Fig. 2. La Coscia nord-west deposit (Rogliano, Cap-Corse).

Fig. 2. Localitat de La Coscia nord-oest (Rogliano, Cap-Corse).

Sardinian variety present in Corsica nowadays, *Cervus elaphus corsicanus*, which it is clearly differentiated from because of its large dental and bone dimensions.

These four forms seem to be characteristic of the Middle Pleistocene in Corsica and, so far, no Sardinian sites have been documented for the same time (e.g., Capo Figari, Van der Made, 1999, or different karstic fissures from Monte Tuttavista, Cordy, 1997; Turmes, 2002). They are forms which had acquired their differential characteristics in the Middle Pleistocene – which allows us to suppose the great antiquity of their presence on the island – and which seem to have disappeared between the Middle Pleistocene and Late Pleistocene. The competition, on the one hand between the three canids (*Canis* sp., Cuoninae indet. and *Cynotherium sardous*) present from the Middle Pleistocene and on the other hand between the two cervids (*C. e. rossii* and *Megaloceros (N.) cazioti*), may have influenced their disappearance.

Cavity 3 of the Castiglione site is not the only one to have provided new forms. In the Middle Pleistocene deposits of cavity 1 in Castiglione quite a large maxillary fragment of a yet to be determined Mustelidae has been found and also the molar of a Suidae (*Sus* sp.). Finally, the PL fracture of cavity 3, dated in the Late Pleistocene, also provides information as to the extinction date of *Cynotherium sardous* and of *Megaloceros cazioti*, the two only large mammal survivors at the end of the Late Pleistocene. At the same time a great number of island birds also disappear (Louchart, 2002).

La Coscia

The location of La Coscia is by the sea, at the tip of Cap Corse. It is made up of two caves which were discovered in 1954 (Coscia south) and in 1992 (Coscia north) respectively; caves which are excavated in the metamorphosed calcareous and dolimitic rocks of the Triassic-Liassic (Bonifay *et al.*, 1998, Bonifay, 2001). It is in the "Coscia north-west" cave, a large cavern 25 metres in diameter and 8 metres high, that the excavations carried out since 1992 in one of the sectors, the north-west sector, have yielded an original faunistic assemblage from the Wurmian Period. It is made up essentially of remains (fallen antlers; cranium and postcranium remains) of *Megaloceros (Nesoleipoceros) cazioti* Depéret, 1897, one of the endemic forms characteristic of the Corsican-Sardinian Middle and Late Pleistocene. Actually, the deer represents around 80% of the remains extracted from the stratigraphic sequence of this sector (20179 remains had been catalogued in 2003, and there were 17633 determinable ones). The taphonomic study of this assemblage is in the press. The first results (Pereira & Brugal, 2003; Fig. 2) indicate that the assemblage records a frequentation of the place by cervids (above all by males and to a lesser extent by females) during all the seasons of the year, although the summer is the time of lowest frequentation. The origin of the accumulation of *M. cazioti* remains in the cave in the La Coscia north-west cave is a fact which is probably related to the unknown eco-ethology of the species. Other spectacular accumulations of ungulates are equally known in different insular Mediterranean Quaternary sites: megacerine deer (in Sardinia, Klein-Hofmeijer, 1996; Sicily, Gliozzi & Malatesta, 1982), hippopotamuses (e.g., Cyprus, Simmons, 1999), bovids (e.g., Balearic Islands, Encinas & Alcover, 1997; Seguí *et al.*, 1998). Carrying out comparisons between locations should enable us to find out the causes of these important concentrations, perhaps due to environmental restrictions.

The La Coscia north-west cave can thus be presented, like cavities 1 and 3 in Castiglione, as a main location to find out about the Corsican Pleistocene. It has mainly allowed us, as far as the fauna of mammals is concerned, to better characterise morphologically the Caziot deer and to discover the remains of another, so far undetermined, carnivore belonging to the Mustelidae family. This is a carnivore with a rectilinear shaped tibia which, without doubt, is reminiscent of present day species with terrestrial habits, like the wolverine, marten or badger, or the fossil Mustelidae *Enhydrictis galictoides* (Forsyth-Major, 1901) from the Middle Pleistocene of the Sardinian site of San Giovanni, near Grisons. Coscia north-west will equally contribute to enriching the knowledge of the endemic avifauna of the island.

We must not, however, forget the contribution of the La Coscia south cave, with a Wurmian stratigraphic sequence which has provided a suid tooth of a status yet to be clarified and the remains of a small-sized fox, near the size of present day foxes *Vulpes vulpes ichnusae* (Salotti, 1990; Bonifay, 1994). This discovery entails the problem of the arrival date for this carnivore, which is absent from the oldest Pleistocene deposits, on the island.

CONCLUSION

Thanks to the discoveries made in the Corsican Pleistocene sites, the fauna of mammals is now better documented. Eighteen species (6 micro- and 12 macro-mammals) are thus distributed between the Middle and Late Pleistocene; there are eight new ones (Table 1). Thus, in the Middle Pleistocene the mammalian fauna is relatively homogeneous with 8 taxons (*Cynotherium sardous, Canis* sp., *Cuoninae* indet., *Cyrnolutra castiglionis,* Mustelidae indet., *Megaloceros (N.) cazioti, Cervus elaphus rossii, Sus* sp.), among which there are 5 carnivores. This changes the image we normally have of insular faunas which are poor in predators and which have a temporary disharmony in the food chains. Nevertheless, at the end of the Late Pleistocene, the mammalian fauna present in Corsica is an impoverished fauna with 6 taxons (a shrew *Episoriculus corsicanus* Bate, 1944, a mouse *Rhagamys orthodon* Hensel, 1856, a vole *Microtus (Tyrrhenicola) henseli* Forsyth-Major, 1882, a pika *Prolagus sardus* Wagner, 1829, a cuon *Cynotherium sardous* Studiati, 1857 and the Caziot's deer *Megaloceros (N.) cazioti* Depéret, 1897. Of these taxons only the micromammals will survive beyond the Pleistocene/Holocene boundary, and have a long period of cohabitation with Mesolithic and Neolithic humans. As far as the two large mammals are concerned, current datings document their presence in Corsica to 10000 AC (Salotti *et al.*, 2000; Vigne *et al.*, 2000). Their disappearance could be linked, like that of different insular birds, to the short, very cold, glacial episode at the end of the Late Glacial (Younger Dryas Episode, 10.500 years ago, Vigne, 2000). Actually, these two taxons are absent in the levels dated in the VIII millennium AC of the main Mesolithic Holocenic stratigraphies.

In Corsica, studies of the mammalian fauna of the Pleistocene have made it possible to highlight the absence of dwarfism and gigantism phenomena found on other islands, such as the Greek ones (Tsoukala, 2001), even taking into account that *Microtus* and *Rhagamys* seem to be large in comparison with their ancestors. They also show, for the mammals which run through the whole Late Middle Pleistocene and Late Pleistocene without becoming extinct, great morphological and biometrical stability (Pereira & Salotti, 2002). What is more, with these taxons having already acquired their specific or subspecific insular characteristics in the Middle Pleistocene, they show their great antiquity on the island.

Is the history of this fauna in agreement with what is now known about the history of the population of the entirety of vertebrates in Corsica?

Eight main sea level oscillations are known from the Late Miocene to nowadays. The greatest took place 5.8 Ma ago, at the end of the Miocene, in the Messinian, due to the partial drying up of the Mediterranean. During this salinity crisis, Corsica and Sardinia stopped being islands and connections between Sardinia, Corsica and Tuscany were established, even between Africa and Corsica via Sicily. This period played a role in the colonisation of Corsica, with the penetration and passage on foot over dry land of new European and/or African fauna. At the end of the Messinian (beginning of the Pliocene), the Mediterranean was refilled and the Corsican-Sardinian mass once again became an island. The species that had penetrated during that crisis continued their local evolution, in a closed environment, until the beginning of the Quaternary (Lower Pleistocene). This ancient fauna is generally known under the name of *Nesogoral* fauna (Ginesu & Cordy, 1997; van der Made, 1999; Sondaar, 2000; Turmes, 2002). The Sardinian site of Mandriola, for instance, from the Lower and Middle Pliocene, gives an idea of the taxons that entered during this crisis and of their evolution. Among mammals, a hedgehog (*Erinaceidae* indet.), a mole (*Talpa* sp.), a shrew (*Episoriculus cf. gibberodon*) a large pika (*Prolagus* cf. *figaro*), two large sized mice (*Rhagapodemus hautimagniensis*; *Apodemus mannu*), a dormouse (*Eliomys (Tyrrhenoglis) figarensis)* and a boar (*Sus* aff. *sondaari).*

The end of the Pliocene and the beginning of the Quaternary are characterised by a series of very large climatic variations. It is thanks to one of the great consecutive marine regressions of the most ancient glaciations of the Pleistocene (Gunz or Mindel) when an important migratory wave is placed, giving rise to the Corsican-Sardinian mammalian faunas of the Middle and Late Pleistocene. This step would have taken place around 800,000 years ago. Then we see the appearance of new taxons which come from well known Villafranchian species from Italy: this is the *Microtus (T.) henseli* fauna; among the newcomers, the megacerine deer (*Megaloceros (N.) cazioti*), the Sardinian cuon (*Cynotherium sardous*) and another pika (*Prolagus sardus*). Actually, it is at the beginning of the Middle Pleistocene when in Sardinia the replacement of *Nesogoral* fauna by *Microtus (Tyrrhenicola)* fauna is recorded (Ginesu & Cordy, 1997; Sondaar, 2000).

In the Middle Pleistocene, practically all the present day fauna of amphibians and reptiles can already be found in Corsica, and no new herpetological species appears during the Middle and Late Pleistocene (Vigne *et al.*, 1997; Bailon, 2001), thus suggesting the absence of migratory movements. In fact, the practical absence of new mammals in the Late Pleistocene also suggests the non-renovation of the mammalian fauna during this period.

Although the history and evolution of the Pleistocene population of vertebrates in Corsica is currently known in part, the issues related to the determinations of the continental ancestors of this paleofauna and the causes of the Pleistocene extinctions are yet to be answered. A better knowledge of the evolution of the marine beds between Corsica and its neighbouring continents coordinated with the discovery of new Corsican-Sardinian sites will enable us to finely hone the data and migratory routes, which as yet are hypothetical and essentially based on works about Sardinia. Thus, we will obtain answers to the queries we still have.

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27

PRESENCE OF *LATONIA* (ANURA, DISCOGLOSSIDAE) IN THE INSULAR PLIOCENE OF MENORCA (BALEARIC ISLANDS)

Josep QUINTANA, Josep Antoni ALCOVER, Salvador MOYÀ-SOLÀ & Borja SANCHIZ

QUINTANA, J., ALCOVER, J.A., MOYÀ-SOLÀ, S. & SANCHIZ, B. 2005. Presence of *Latonia* (Anura, Discoglossidae) in the Insular Pliocene of Menorca (Balearic Islands). *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 293-296.

Resum

S'ha trobat per primera volta al Pliocè de Menorca (Illes Balears) el gènere extingit de discoglòssid *Latonia*. Ha estat detectat a Punta Nati 6 i Punta Nati 12, dues localitats d'origen càrstic que es poden datar al Pliocè, però en canvi no s'ha trobat al Pleistocè de Menorca ni de cap altra de les Balears. La *Latonia* insular menorquina probablement representa una espècie no baptiada, però els seus elements cranians més diagnòstics encara no s'han trobat. Al Pleistocè de Mallorca i Menorca s'han trobat representants de gran mida del gènere *Discoglossus*. No obstant això, les dades moleculars i paleontològiques indiquen que la línia evolutiva de *Discoglossus* no prové directament de cap *Latonia* del Neògen. Menorca va mantenir durant el Pliocè una condició insular, i la *Latonia* de Menorca podria ser o bé un antic nadiu pre-messinià o bé un immigrant messinià. A llavors, les presències successives de *Latonia* i *Discoglossus* a les Illes Balears probablement representen esdeveniments diferents d'immigració i extinció.

Abstract

The extinct discoglossid genus *Latonia* has been recovered for the first time in the Pliocene of Menorca (Balearic Islands). *Latonia* has been detected in Punta Nati 6 and Punta Nati 12, two localities of karstic origin that can be dated in the Pliocene, but it has not been found in the Menorcan Pleistocene, nor in the Pleistocene of any other Balearic island. The Menorcan insular *Latonia* probably represents an unnamed species, but their taxonomically most diagnostic cranial elements have not been found yet. Representatives of the living genus *Discoglossus*, of large size, have been identified in the Pleistocene of Mallorca and Menorca. However, molecular and palaeontological data indicate that Pleistocene *Discoglossus* lineages are not direct descendants of any Neogene *Latonia*. Menorca has maintained during the Pliocene an insular status, and Menorcan *Latonia* could be an old pre-Messinian native relict or a Messinian immigrant. Therefore, the successive presences of both *Latonia* and *Discoglossus* in the Balearic Islands probably represent separated immigration and extinction events.

Resumen

Se constata por primera vez la presencia de *Latonia*, un género extinto de discoglósidos, en el Plioceno de Menorca (Islas Baleares). *Latonia* se ha encontrado por el momento en Punta Nati 6 y Punta Nati 12, dos yacimientos de origen cárstico datados como pliocenos, pero no se ha encontrado en el Pleistoceno de Menorca ni tampoco en el Pleistoceno de ninguna otra isla balear. Este representante insular de *Latonia* posiblemente pertenezca a una especie todavía innominada, pero no se han encontrado aún los elementos craneales taxonómicamente más informativos en este grupo. Se han identificado representantes del género actual *Discoglossus*, de talla grande, en el Pleistoceno de Mallorca y Menorca. Sin embargo, los datos moleculares y paleontológicos indican que los linajes pleistocenos de *Discoglossus* no son descendientes directos de ninguna *Latonia* del Neógeno. Menorca ha mantenido su condición insular durante todo el Plioceno, y *Latonia* en la isla puede ser un antiguo relicto pre-mesiniense o un inmigrante mesiniense. En consecuencia, las presencias sucesivas de *Latonia* y *Discoglossus* en las Islas Baleares probablemente representen diferentes eventos de inmigración y extinción.

INTRODUCTION

The batrachian insular faunas are in general poorly known from a palaeontological point of view. In the case of the Balearic Islands, with the exception of few fragments from the Upper Oligocene, the available fossil record has been recovered in Tardiglacial, Pleistocene and Holocene sites (Alcover *et al.*, 1984; Sanchiz, 1998), and therefore there is no direct information on its Neogene faunal history.

A recent palaeontological survey made by some of the authors in karstic filling deposits from the NW of the island of Menorca has resulted in the discovery of several sites that have yielded anuran samples of presumably Pliocene age. In this note we provide a preliminary description and identification of these first Neogene Balearic amphibians, in the hope that future research will allow a more complete view of their evolutionary history.

FOSSIL LOCALITIES AND TAPHONOMY

Quintana (1998) gives a general geological and geographical setting of the fossil sites Punta Nati 6 and Punta Nati 12, near the town of Ciutadella de Menorca. Pending future analyses, an accurate geological dating by direct criteria is not yet possible, but nevertheless the karstic sediments containing the fossil anurans fill in Uppermost Miocene (Messinian) calcarenites, and are covered by Pleistocene red slimes, thus providing an indeterminate Pliocene age (Quintana, 1998, 2001). A giant rabbit (Quintana, this volume) and the large tortoise *Cheirogaster gymnesica* (Quintana, 1998, 1999) predominate among the vertebrates present in these assemblages. Other herpetological remains previously studied include viperid and colubrid snakes (Bailon *et al.*, 2002, and this volume), amphisbaenids (García-Porta *et al.*, 2002) and geckos (Bailon *et al.*, this volume).

Concerning taphonomy, in Punta Nati 6 the anurans are mixed with all the other vertebrates and some evidence of transport can be observed. However, in Punta Nati 12 there is no apparent transportation of sediments, and the amphibians are mostly concentrated in centimetric accumulation layers (Fig. 1). However, in both localities the fossil anurans probably derive from the predation of nocturnal birds of prey, most likely from the extinct large owl *Tyto balearica*.

Comparative material

Dry disarticulated skeletons belonging to the collection of the Museo Nacional de Ciencias Naturales (CSIC, Madrid) have been used. They include all the living *Alytes* and *Discoglossus* species, with the exception of *D. montalentii* which was loaned by M. Delfino (Florence). Terminology follows Sanchiz (1998).

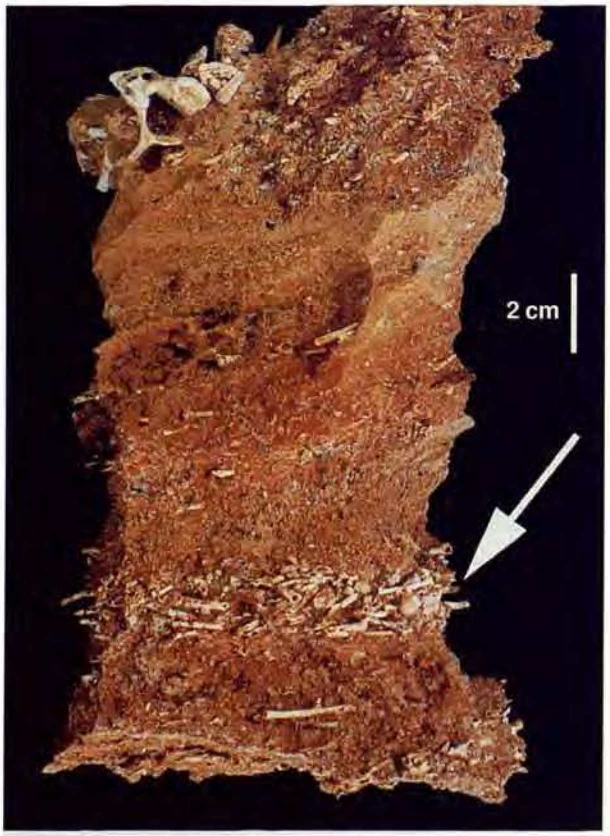

Fig. 1. Sample of the deposit Punta Nati 12. An arrow indicates the thin layer in which most of the amphibians are found.

Fig. 1. Mostra del depòsit Punta Nati 12. Una fletxa indica la capa prima on s'han trobat la major part dels amfibis.

SYSTEMATIC PALAEONTOLOGY

Family Discoglossidae Günther, 1859 "1858"
Genus *Latonia* Meyer, 1843
Latonia sp.

Material: Most of the elements recovered are incomplete fragments, extracted from the sediment by acetic acid techniques. The material from Punta Nati 6 and 12 is currently deposited in the Institut de Paleontología M. Crusafont (Sabadell) (IPS), with the exception of a small sample from Punta Nati 6 which is stored in the private collection of Josep Quintana (Ciutadella de Menorca) (CJQ).

Punta Nati 6: Premaxillar fragment (IPS 1); sphenethmoid (IPS 1); frontoparietal fragment? (IPS 1); prootic-exoccipital (IPS 1); angulosplenial (IPS 1); atlas (IPS 1); V2-V4 (CJQ 1; IPS 2); V5-V8 (CJQ 2; IPS 3); vertebral centra (CJQ 1; IPS 1); sacral vertebrae (CJQ 3; IPS 2); urostyles (CJQ 3; IPS 1); scapulae (IPS 5); cleitra (IPS 1); humeri (CJQ 2; IPS 3); radioulnae (CJQ 3; IPS 5); ilia (CJQ 3; IPS 12); femora (CJQ 1; IPS 1); tibiofibulae (CJQ 2; IPS 12). In this site several bones (humeri, femora and tibiofibulae) have been found with signs of pathological processes and traumatisms, similar to those described by Sanchiz & Pérez (1974), which will be published elsewhere.

Punta Nati 12: Prootic-exoccipitals (IPS 8); cleithra (IPS 2); scapulae (IPS 2); humeri (IPS 2); ilia (IPS 3); ischium (IPS 1); femora (IPS 8); tibiofibulae (IPS 14); tibiale-fibulare (IPS 1).

DESCRIPTION

Most of the material is fragmented and badly preserved, but all the recovered elements show the typical discoglossine features, at the subfamily level, basically in full agreement with the described *Discoglossus* and *Latonia* morphologies. These general discoglossine features will not be commented here, being available in many earlier works (e.g. Púgener & Maglia, 1997; Rage & Hossini, 2000; Roček, 1994). Moreover, there is no evidence that could suggest the presence of more than one taxon in the samples.

Skull

A minute fragment showing not very dense tubercular ornamentation (Punta Nati 6) might perhaps come from the most anterior frontoparietal region, but the attribution of this fossil must remain open to question. If the assignment of this fragment to the anuran sample is confirmed, it would indicate the presence of *Latonia*, but would be taxonomically uninformative within the genus. The available fragments of sphenethmoid and prootic-exoccipital are damaged, and being its variation not very well known within *Latonia* species, they cannot provide any specific identification. The only angulosplenial in the sample is broken and the paracoronoid tubercle cannot be observed.

Vertebral column

Vertebrae from all the different regions of the column have been recovered. They all agree with the morphology

Fig. 2. *Latonia* sp. (CJQ uncataloged). Punta Nati 6. Sacral vertebra in dorsal view.

Fig. 2. ***Latonia*** *sp. (CJQ no catalogat). Punta Nati 6. Vertebra sacra en norma dorsal.*

Fig. 3. *Latonia* sp. (CJQ 1339). Punta Nati 6. Right radioulna in lateral view.

Fig. 3. Latonia *sp. (CJQ 1339). Punta Nati 6. Radioulna dreta en norma lateral.*

present in *Latonia*, which is not very different among species, and also similar to the *Discoglossus* one. Nevertheless, a complete sacrum (Fig. 2) shows a shape of the transverse processes that allows the distinction between *Discoglossus* and *Latonia*. The sacral wings are more posteriorly oriented that in typical *Discoglossus*, and the width of its distal part is in proportion smaller, particularly in relation with the proximal part (narrower in *Discoglossus*). These sacral features have never been properly quantified, and we cannot exclude that extreme variants of *Discoglossus* could approach the fossil morphology, but at least qualitatively the distinction seems clear. The urostyle shows a small lateral crest, less developed than in specimens of *Latonia gigantea* of roughly similar sizes. In *Discoglossus* this urostylar crest is almost absent or merely a longitudinal ridge.

Pectoral girdle

The scapular fragments agree with the morphology of both *Latonia* and *Discoglossus*. Distinction between these genera might become possible from a biometrial point of view, but no data of this sort has been published yet. The cleithral fragments are not taxonomically informative.

Forelimb

Humeral and radioulnar (Fig. 3) remains, in the absence of a statistical sample, provide no reliable features to distinguish between *Discoglossus* and *Latonia*.

Pelvic girdle

Several almost complete proximal parts of the ilium have been recovered (Fig. 4). Besides other discoglossine features, these ilia present a rather flat *tuber superior* continued by a dorsal crest, a long *pars ascendens* and a highly reduced *pars descendens*. This type of *tuber superior* and particularly the *pars descendens* are similarly found in *Latonia*, but they differ from corresponding morphologies present in all *Discoglossus* species, in which a rather dorsally swollen *tuber* and a small but clearly developed *pars descendens* can be observed. The ilial morphology, as described above, is a strong indication in favour of the taxonomic attribution of this sample to the genus *Latonia*. The distinction seems qualitatively clear, and many biometric approaches can quantify it (e.g., Sanchiz & Alcover, 1984).

Hindlimb

The main locomotor's segments of the leg show similar morphologies in all discoglossine groups, and the available fossil samples (in Menorca and elsewhere) do not allow any statistical taxonomic discrimination.

Size

The genus *Latonia* is one of the largest anurans known (Roček, 1994). No statistical analyses are possible at this point, but the Menorcan *Latonia* seems to attain similar sizes than the giant continental Miocene and Pliocene *L. gigantea* (Rage & Hossini, 2000; Roček, 1994).

Fig. 4. *Latonia* sp. (CJQ 1344). Punta Nati 6. Right ilium in external (A) and inner (B) lateral views, the later reversed for an easier comparison.

Fig. 4. Latonia *sp. (CJQ 1344). Punta Nati 6. Ilium dret en norma lateral externa (A) i interna (B); la darrera foto, invertida per permetre una comparació més fàcil.*

DISCUSSION

The genus *Latonia* is one of the most frequently found anurans in the European Tertiary, with a Neogene distribution from Iberia to Russia and Anatolia (Roček & Rage, 2000; Rage & Roček, 2003). During the Pliocene a possible gradual withdrawal of *Latonia* from Central Europe to the Mediterranean has been suggested (Rage & Roček, 2003). Similar forms are known as early as the European Maastrichtian (Venczel & Csiki, 2003), and also from the Miocene of Morocco (Sanchiz & Alcover, 1984; Hossini, 2000). *Latonia* seems to have become extinct in the Lower Pleistocene, being Pietrafitta (Italy) the youngest locality where it has been recorded (Rage & Roček, 2003). The Menorcan insular *Latonia* probably represents an unnamed species, but their taxonomically most diagnostic cranial elements have not been found yet.

If we accept that transmarine migrations are unlikely ways for anuran dispersion (but see Vences *et al.*, 2003), the Western Mediterranean palaeogeographical history (e.g. Fromhage, *et al.*, 2004; Martínez-Solano *et al.*, 2004) provides two possible scenarios to explain the presence of *Latonia* in the insular Pliocene of Menorca: either a) *Latonia* is a native pre-Messinian relict on the island, present at least after the Langhian-Serravalian transition (or even pre-Miocene), or b) *Latonia* is a Messinian immigrant, its insular status attained after the end of the Mediterranean Salinity Crisis, dated 5.33 Ma ago (Krigsman *et al.*, 1999). Unfortunately, the only identifiable pre-Pliocene anuran recorded in the Balearic Islands is a maxillary fragment from the Upper Oligocene of Peguera (Mallorca), assigned to *Eopelobates* because of its cell-like polygonal ornamentation (Sanchiz, 1977). A misidentification for *Latonia* is unlikely, because *Latonia* maxillae vary within species from having smooth surfaces to a tubercular sculpture (sometimes aligned) covering only a triangular area in the posterior part of the bone (Roček, 1994). *Latonia* has been recorded only in Menorca, but we cannot exclude its Pliocene presence in Mallorca because localities of this age, including amphibians, have not been found in this island.

In both Mallorca and Menorca an extinct fossil *Discoglossus*, larger in size than any other species, has been found in the Pleistocene. Against the opinion of Roček & Rage (2000), the living *Discoglossus* lineages, including the Balearic form, cannot be considered as direct descendants of Neogene *Latonia*. Both the fossil record (e.g. Sanchiz, 1998; Venczel, 2004) and the molecular time studies on *Discoglossus* (*sensu stricto*) diversification (Fromhage, 2004; Martínez-Solano, 2004) give earlier time estimations for its origin. Therefore, the successive presences of both *Latonia* and *Discoglossus* in the Balearic Islands probably represent separated immigration and extinction events.

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EL CONEJO GIGANTE DE LOS DEPÓSITOS CÁRSTICOS DE PUNTA NATI-CALA'S POUS (MENORCA, ILLES BALEARS)

Josep QUINTANA, Salvador MOYÀ y Meike KÖHLER

QUINTANA, J., MOYÀ, S. & KÖHLER, M. 2005. El conejo gigante de los depósitos cársticos de Punta Nati-Cala's Pous (Menorca, Illes Balears). *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 297-308.

Resum

Sense cap dubte, el conill gegant és el vertebrat fòssil més espectacular obtingut als depòsits càrstics pliocènics de Punta Nati – Cala's Pous. El tractament de les bretxes mitjançant àcid acètic ha permès recuperar una mostra molt important d'ossos del conill gegant, cosa que ha permès l'estudi detallat de la morfologia i dels canvis al·lomètrics soferts per aquest taxon. La morfologia del P_3 relaciona aquest lepòrid amb el gènere *Alilepus*, un lepòrid present al Miocè superior – Pleistocè inferior d'Europa, Àsia i Nord-Amèrica. No obstant, els canvis esquelètics presents permeten situar el conill gegant en un nou gènere. A més d'un pes molt elevat (el seu pes medi s'ha estimat en 14 kg), el conill gegant de Menorca es diferencia dels lepòrids continentals corredors per presentar un crani, bulles timpàniques i òrbites oculars petits, i un diastema més curt. Per contra, la cresta nucal i l'escama occipital són àmplies i estan ben desenvolupades, caràcters aquests que semblen relacionar-se amb canvis a la musculatura del coll. A nivell postcranial, ambdues extremitats són un 25% més curtes, en comparació amb les dels lepòrids continentals. A més, els peus i les mans del lepòrid gegant són curts, molt amplis i completament plantígrads. La reducció del peu afecta els metatarses i falanges, però no els calcanis. Aquests canvis semblen relacionar-se amb una marcada flexió a l'extremitat posterior, amb la qual s'hauria contrarestat l'excés de tensió al tendó comú del calcani. A més, l'estudi de la línia d'acció del tríceps i l'avantatge mecànic semblen indicar una major flexió de l'extremitat anterior. La columna vertebral (especialment les vèrtebres toràciques i lumbars) és molt curta i corbada. Les modificacions als processos espinosos, costals i mamillars indiquen importants canvis musculars a l'extremitat posterior i a la zona pèlvica i lumbar. Molts d'aquests caràcters i alguns canvis a les superfícies d'articulació, origen i inserció musculars estan també presents a *Pentalagus furnessi* (Stone, 1900), un lepòrid que viu actualment a algunes de les illes de l'arxipèlag Ryukyu (Japó). Aquests canvis revelen modificacions importants a nivell esquelètic i de locomoció, desenvolupades a un context lliure de depredadors, on una locomoció lenta basada en moviments medio-laterals es veu especialment afavorida, davant una locomoció ràpida, en la qual predominen els moviments sagitals, típica dels lepòrids continentals.

Paraules clau: Conill gegant, Miocè superior, Pliocè, Menorca, plantigradia.

Resumen

Sin duda, el conejo gigante es el vertebrado fósil más espectacular recuperado en los depósitos cársticos pliocénicos de Punta Nati-Cala's Pous. El tratamiento mediante ácido acético ha permitido recuperar una muy importante muestra de huesos del conejo gigante, lo que ha permitido el estudio detallado de la morfología y de los cambios alométricos sufridos por este taxón. La morfología del P_3 relaciona este lepórido con el género *Alilepus*, un lepórido presente en el Mioceno superior-Pleistoceno inferior de Europa, Asia y Norte América. Sin embargo, los cambios esqueléticos permiten situar el conejo gigante de Menorca en un nuevo género. Además de un peso muy elevado (su peso medio ha sido estimado en 14 kg), el conejo gigante de Menorca se diferencia de los lepóridos continentales corredores por un cráneo, bullas timpánicas y órbitas oculares pequeñas y un diastema más corto. Por el contrario, la cresta nucal y la escama occipital son amplias y están bien desarrolladas, caracteres que parecen relacionarse con cambios en la musculatura del cuello. A nivel poscraneal, ambas extremidades son un 25% más cortas comparadas con las de los lepóridos continentales. Además, los pies y las manos del conejo gigante son cortas, muy anchas y completamente plantígradas. La reducción del pie afecta a metatarsos y falanges, pero no al calcáneo. Tales cambios parecen relacionarse con una marcada flexión en la extremidad posterior con la que se habría contrarestado el exceso de tensión en el tendón común del calcáneo. Además, el estudio de la línea de acción del triceps y la ventaja mecánica parecen indicar una mayor flexión de la extremidad anterior. La columna vertebral (especialmente las vértebras torácicas y lumbares) es muy corta y curvada. Las modificaciones en los procesos espinosos, costales y mamillares indican importantes cambios musculares en la extremidad posterior y en la zona pélvica y lumbar. Muchos de estos caracteres y algunos cambios en las superficies de articulación, origen e inserción musculares están también presentes en *Pentalagus furnessi* (Stone, 1900), un lepórido presente actualmente en algunas islas del archipiélago Ryukyu (Japón). Tales cambios revelan importantes modificaciones a nivel esquelético y de locomoción, desarrolladas en un contexto libre de depredadores, donde una locomoción lenta basada en movimientos medio-laterales se ve especialmente favorecida frente a una locomoción rápida en la que predominan los movimientos sagitales, típica de los lepóridos continentales.

Palabras clave: Conejo gigante, Mioceno superior-Plioceno, Menorca, plantigradía.

Summary

Doubtless, the giant fossil rabbit of Menorca is the more spectacular mammal from the Pliocene karstic deposits of Punta Nati-Cala's Pous (Ciutadella de Menorca). More than thousand bones of this rabbit (usually fragments) were recovered with the acetic acid method. This permits the accurate study of morphology and the allometric changes in this taxon. The P_3 morphology related this rabbit with *Alilepus* genus, an upper Miocene-low Pleistocene leporid from Europe, Asia and North America. However, the skeletal changes permit to place the giant rabbit in a new genus. In addition to the big weight (the medium weight was 14 kg), the giant rabbit differs from the "typical" rabbits for a small skull, tympanic bulla, eye-socked and diastema. These characters are related with vision and hearing changes and brain reduction. In exchange, the nuchal crest and the occipital squama are wider and well developed and seem to be related with changes in neck musculature. In a post-craneal level, the hind and forelimbs are 25% reduced in comparison with continental leporids. The giant rabbit was completely plantigrad, with hands and feet short and wide. The feet length reduction is related with metatarsal and phalanxes, but not with calcaneus. Both features involve a marked flexion in the hind limb that counter the excess stress in the common calcanean tendon. On the other hand, the study of the triceps action line and the mechanic advantage indicates a high flexion in the forelimb than "typical" leporids. The spine (specially thoracic and lumbar vertebras) is very short and curved. The modifications in the spinous, costal and mamillary processes indicates important changes in lumbar, pelvic and hind limb musculature. Some of these characters, and changes in the joint surfaces and muscles origin-insertions are present in *Pentalagus furnessi* (Stone, 1900), an island rabbit fron the Ryukyu Archipelago (Japan), and reveal main skeletal and locomotion modifications, developed in a free predators context, were low locomotion and medium-lateral motions are specially favoured in front of the sagital ones, well developed in continental leporids.

Keywords: Giant rabbit, Upper Miocene-Pliocene, Menorca, plantigrady.

INTRODUCCIÓN

La aparición de un nuevo macromamífero dentro de las faunas mio-holocénicas de las Baleares resulta sorprendente, teniendo en cuenta que estas son conocidas ya desde principios del siglo pasado.

El estudio del conejo gigante de Menorca ha permitido, además, abrir una puerta totalmente nueva al conocimiento de las antiguas faunas insulares, tanto de Menorca como del resto de las Baleares, y replantear, a la luz de los nuevos descubrimientos (tanto geológicos como paleontológicos), algunas de las cuestiones relacionadas con los modelos paleobiogeográficos preestablecidos, referidos a las antiguas faunas vertebradas de las islas Baleares.

Si bien solo se trata de una primera aproximación, el estudio morfológico y funcional del conejo gigante de Menorca ya deja entrever las especiales características de este taxón, y pone de manifiesto, una vez más, el enorme interés que estas faunas representan en relación al fenómeno de la evolución.

ANTECEDENTES HISTÒRICOS

La primera referencia sobre la presencia de un lepórido en los yacimientos de Punta Nati-Cala's Pous corresponde a Pons-Moyà *et al.* (1981) al citar cf. *Alilepus* en el yacimiento de Cala's Pous (también conocido como de "Torre Vella" o yacimiento 11 de Punta Nati-Cala's Pous) (Bate, 1914; Quintana, 1998).

El primer resto postcraneal del conejo gigante de Menorca (una epífisis proximal de un fémur izquierdo) (Fig. 1) fue encontrado el 25 de marzo de 1988 en el yacimiento 1 de Punta Nati-Cala's Pous (Quintana, 1998). Posteriormente, en junio de 1992 se localizó el yacimiento 6 de Punta Nati-Cala's Pous, el más rico de la zona y del que se han recuperado la mayor parte de restos óseos con el que se ha realizado el estudio del conejo gigante.

SITUACIÓN GEOGRÁFICA Y GEOLÓGICA

Los yacimientos de Punta Nati-Cala's Pous se localizan en el noroeste del término municipal de Ciutadella, en la isla de Menorca (Fig. 2). Constituyen un grupo numeroso de depósitos de pequeña extensión, formados por unos limos muy duros de color rojo, que fosilizan tanto las dolomías jurásicas como las calcarenitas mesinienses de la zona (Quintana, 1998).

La zona de Punta Nati-Cala's Pous es, desde el punto de vista paleontológico, especialmente interesante, al estar representados tres episodios faunísticos diferentes (Quintana, 1998). El conejo gigante y la fauna que lo acompaña representarían el segundo de estos episodios faunísticos, situado temporalmente entre el Mioceno superior (Mesiniense) y el Pleistoceno en sentido amplio, es decir, en el Plioceno s.l.

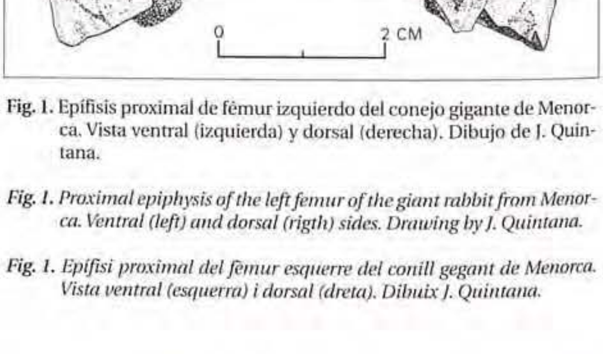

Fig. 1. Epífisis proximal de fémur izquierdo del conejo gigante de Menorca. Vista ventral (izquierda) y dorsal (derecha). Dibujo de J. Quintana.

Fig. 1. *Proximal epiphysis of the left femur of the giant rabbit from Menorca. Ventral (left) and dorsal (rigth) sides. Drawing by J. Quintana.*

Fig. 1. *Epífisi proximal del fémur esquerre del conill gegant de Menorca. Vista ventral (esquerra) i dorsal (dreta). Dibuix J. Quintana.*

FAUNA ASOCIADA AL CONEJO GIGANTE

Junto al conejo gigante aparece una interesante fauna herpetológica: la tortuga gigante de Menorca (*Cheirogaster gymnesica* Bate, 1914), un anfisbénido (*Blanus* sp) (Garcia-Porta *et al.*, 2002), varios vipéridos (*Vipera natiensis* y *Vipera* sp) (Bailón *et al.*, 2002), uno o varios lacértidos, posiblemente pertenecientes al género *Podarcis* y un único anfibio (*Latonia* sp) (Quintana *et al.*, 2005).

La fauna ornítica es igualmente interesante, al aparecer nuevos géneros y especies de aves: un procellariforme (*Pterodromoides minoricensis* Seguí *et al.*, 2001), una grulla (*Camusia quintanai* Seguí, 2002), una becada (*Scolopax carmesinae* Seguí, 1999), una lechuza (*Tyto balearica* Mourer-Chauviré *et al.*, 1980), un mochuelo (*Athene* sp.) y un cuervo (*Corvus* sp.) (Seguí, 1998).

Los únicos mamíferos que aparecen junto al conejo gigante corresponden a un glírido (*Muscardinus cyclopeus* Agustí *et al.*, 1982) y un quiróptero (*Rhinolophus* cf. *grivensis*) (Pons-Moyà *et al.*, 1981).

En cuanto a los moluscos terrestres, el elemento más característico de estos depósitos es *Oestophora* sp. Aparecen también *Tudorella ferruginea* Lamarck, 1822, *Rumina* cf *decollata* (Linnaeus, 1758), *Vitrea* sp y varios helícidos e higrómidos (Quintana, 1995).

Junto con la fauna aparecen, en ocasiones, algunas semillas muy bien conservadas de *Cneorum triccocon* y, más raramente, de *Crataegus monogyna*, así como otras semillas no identificadas (Traveset *et al.*, en preparación).

MATERIAL Y MÉTODOS

Tratamiento ácido

Dada la dureza de la roca matriz, los huesos del conejo gigante fueron recuperados mediante el tratamiento químico de la misma, utilizando ácido acético en una disolución acuosa al 10 %. Durante todo el proceso, los huesos fueron consolidados con Paraloid (o acriloid) B-67 en una concentración del 10%.

Todo este proceso se llevó a cabo en el Institut de Paleontologia "M. Crusafont" de Sabadell (Barcelona) por un periodo aproximado de cuatro años; todas las piezas recuperadas del conejo gigante mediante el tratamiento ácido (unas 1170, la mayoría fragmentos) se encuentran actualmente depositadas, de forma temporal, en esta institución.

Material de comparación

La morfología del conejo gigante de Menorca ha sido comparada con la de 10 géneros diferentes de lepóridos actuales (*Oryctolagus* Lilljeborg, 1871, *Pronolagus* Lyon, 1904, *Sylvilagus* Gray, 1867, *Romerolagus* Merriam, 1896, *Pentalagus* Lyon, 1904, *Nesolagus* Major, 1899, *Caprolagus* Blyth, 1845, *Bunolagus* Thomas, 1929, *Poelagus* St. Leger, 1932 y *Lepus* Linnaeus, 1758), representados por 20 especies (1 de*Oryctolagus*, 3 de *Pronolagus, 1 de Poelagus, 4 de Sylvilagus*, 1 de *Romerolagus, 1 de Pentalagus*, 1 de *Nesolagus, 1 de Caprolagus*, 1 de *Bunolagus* y 6 de *Lepus*) correspondientes a 94 ejemplares diferentes. En la mayoría de los casos, cada ejemplar se corresponde con un esqueleto más o menos completo.

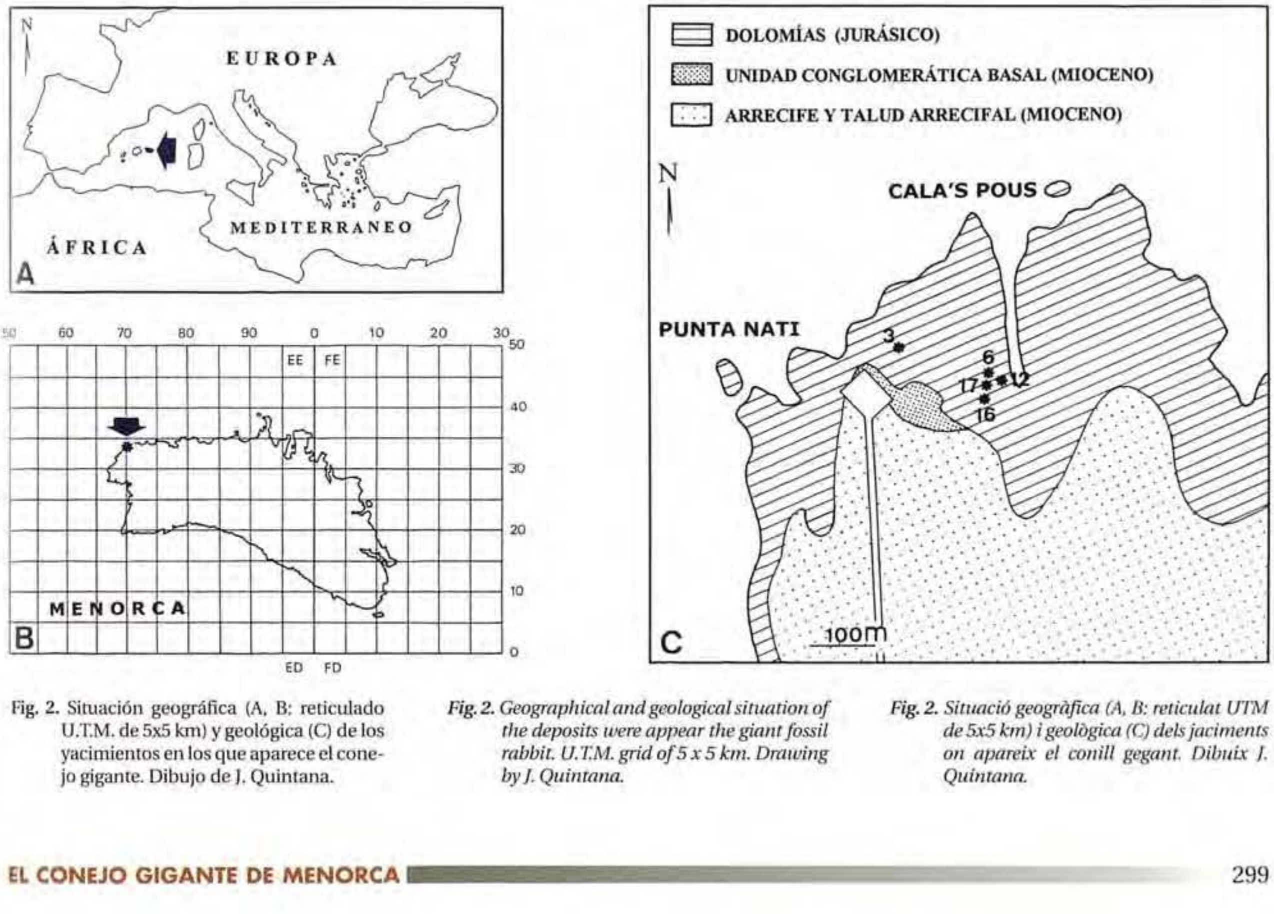

Fig. 2. Situación geográfica (A, B: reticulado U.T.M. de 5x5 km) y geológica (C) de los yacimientos en los que aparece el conejo gigante. Dibujo de J. Quintana.

Fig. 2. Geographical and geological situation of the deposits were appear the giant fossil rabbit. U.T.M. grid of 5 x 5 km. Drawing by J. Quintana.

Fig. 2. Situació geogràfica (A, B: reticulat UTM de 5x5 km) i geològica (C) dels jaciments on apareix el conill gegant. Dibuix J. Quintana.

Estimación de la masa corporal

La obtención del peso medio del lepórido gigante se ha realizado mediante las rectas alométricas obtenidas a partir del volumen y la superficie de la cabeza del fémur, obtenidas mediante medición directa (superficie) o utilizando la metodología de Ruff (1990) para el cálculo de peso en primates antropoides (en el caso del volumen de la cabeza del fémur), el diámetro transversal de la epífisis proximal (D.T.P) y distal (D.T.D), también en el caso del fémur, la longitud de la serie dental en la mandíbula, la superficie del cóndilo medial y lateral (y la suma de ambos), el diámetro transversal y antero-posterior de la epífisis proximal (D.T.P y D.A.P.P) y antero-posterior de la epífisis distal en el caso de la tibia, el D.T.P, D.A.P.P., D.T.D. y el D.A.P.D en el caso del radio, y el D.T.D. y el D.A.P.D. en el caso del húmero.

El peso medio (14.092,21 g) se ha obtenido a partir de la media de todos los pesos calculados (n=236), entre los que no se han incluido los valores máximos y mínimos (n=34).

CRÁNEO

A diferencia de los lepóridos típicamente corredores, el cráneo del conejo gigante de Menorca se caracteriza por una bulla timpánica y una órbita ocular más pequeña; la zona posterior del cráneo es dorso-ventralmente más baja y muestra una cresta nucal muy ancha. Además, el margen dorsal del foramen magnum se sitúa a la misma altura que el margen superior de los cóndilos occipitales (Fig.3). Los huesos frontales son más anchos y el paladar más estrecho. El mal estado de conservación de la zona nasal en los cráneos recuperados no permite apreciar ni la longitud ni la anchura de la zona facial.

El cráneo del conejo gigante de Menorca es muy semejante al de *Pentalagus furnessi* Stone, 1900, del que se distingue por el mayor desarrollo de la cresta nucal y por la orientación del meato acústico externo, que en el conejo gigante se sitúa más lateralmente.

Los principales cambios observados en el cráneo del conejo gigante se relacionan, por tanto, con la reducción de algunos órganos de los sentidos, concretamente, la vista y el oído. La ausencia de depredadores condicionó, muy posiblemente, tales cambios. La vista, el oído y la rapidez son las únicas defensas que posee un lepórido continental frente a posibles depredadores. Al haber evolucionado en ausencia de depredadores, la vista y el oído del conejo gigante de Menorca se habrían modificado en función de las nuevas condiciones ecológicas.

Si bien la capacidad craneana no ha podido ser medida, la reducción en la zona posterior del cráneo (Fig. 3) podría ser indicativa de una reducción en el tamaño del cerebro, al haberse modificado el sistema nervioso ante la falta de ciertos estímulos relacionados con la depredación.

El paladar más estrecho posiblemente sea indicativo de una reducción del tamaño craneal, que no afectaría ni a la longitud de las series dentales ni a la anchura de la cresta nucal o de los huesos frontales.

La mayor anchura de la cresta nucal posiblemente está relacionada con un mayor desarrollo de la musculatura insertada en la zona posterior del cráneo, cuyas funciones principales están relacionadas con la extensión e inclinación lateral del cuello y la cabeza (músculo splenius y romboide), la sujeción y el movimiento de la escápula y la extremidad anterior (músculo romboide), y la extensión de las primeras articulaciones de la cabeza y el cuello (músculos rectos dorsales mayor y menor) (Schwarze, 1984).

MANDÍBULA

La mandíbula del conejo gigante (Fig. 4) muestra un diastema muy corto. La fosa masetérica y pterigoidea presentan una gran superficie relativa. En cambio el proceso coronoideo y la serie dentaria inferior muestran un desarrollo similar al de otros lepóridos. Asimismo, la rama mandibular está menos inclinada hacia la parte posterior de la mandíbula.

Todas estas características parecen relacionarse con el acortamiento de la zona facial del cráneo; la mayor superficie de la fosa masetérica y pterigoidea estaría relacionada con un mayor desarrollo del músculo masetérico que compensaría, muy posiblemente, la reducción del brazo de palanca debida a la menor inclinación de la rama mandibular, al aproximar la línea de acción del masetero a la cabeza mandibular (Walker & Liem, 1994).

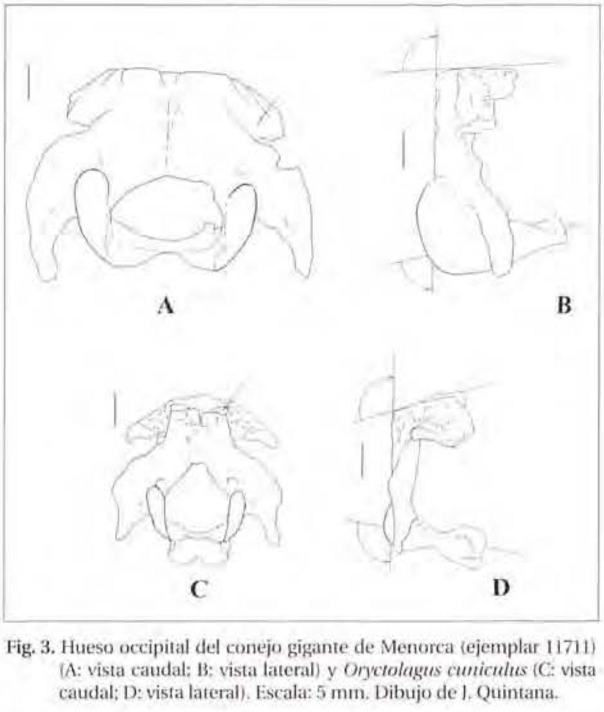

Fig. 3. Hueso occipital del conejo gigante de Menorca (ejemplar 11711) (A: vista caudal; B: vista lateral) y *Oryctolagus cuniculus* (C: vista caudal; D: vista lateral). Escala: 5 mm. Dibujo de J. Quintana.

Fig. 3. Occipital bone of the giant rabbit from Menorca (11711 specimen) (A: caudal view; B: lateral view) and Oryctolagus cuniculus *(C: caudal view; D: lateral view). Scale: 5 mm. Drawing by J. Quintana.*

Fig. 3. Os occipital del conill gegant de Menorca (exemplar 11711) (A: vista caudal; B: vista lateral) i Oryctolagus cuniculus *(C: vista caudal; D: vista lateral). Escala: 5 mm. Dibuix J. Quintana.*

Fig. 4. Mandíbula izquierda del conejo gigante de Menorca (ejemplar 1401), vista lateral. Escala gráfica en mm. Fotografía de J. Quintana.

Fig. 4. Left mandible of the giant rabbit from Menorca (1401 specimen), lateral view. Scale in mm. Photography by J. Quintana.

Fig. 4. Mandíbula esquerra del conill gegant de Menorca (exemplar 1401), vista lateral. Escala gràfica en mm. Fotografia J. Quintana.

P3

Presenta una morfología muy sencilla y variable, con un hipofléxido y un mesofléxido enfrentados. El mesofléxido puede presentar un desarrollo semejante al hipofléxido (con un istmo muy estrecho), estar menos desarrollado (con un istmo muy amplio) o faltar. La morfología del hipofléxido y del mesofléxido es también variable. El hipofléxido puede ser liso, ligeramente ondulado y más raramente, muy ondulado, siendo muy estrecho en su parte media, debido al mayor desarrollo de la parte anterior del hipocónido. En ocasiones aparecen uno o dos islotes. Pueden aparecer también unas escotaduras poco marcadas en la parte anterior y lingual del trigónido. El protofléxido muestra también una morfología variable: más o menos abierto, liso o con una ondulación. El talónido es amplio, al igual que el hipocónido, que muestra una flexión en su parte media que lo divide en dos partes. Su parte posterior está labialmente más desarrollada (Fig. 5).

El polimorfismo en el P3 del conejo gigante puede compararse al polimorfismo que presentan los lepóridos continentales. En ningún caso puede considerarse, por lo tanto, como una consecuencia de la evolución en condiciones de insularidad. La presencia en una misma población de morfologías con mesofléxido y otras con islotes, parece desmentir la idea según la cual las morfologías con mesofléxido serían las formas más antiguas, y las morfologías con islotes (o sin islotes) corresponderían a las formas más modernas.

El estudio de la morfología del P3 del conejo gigante de Menorca relaciona este lepórido con el género continental *Alilepus* Dice, 1931, de distribución geográfica muy amplia, estando presente en el Mioceno superior-Plioceno inferior de Eurasia y en el Plioceno de Norteamérica (López-Martínez, 1989; White, 1991).

EXTREMIDAD ANTERIOR

El conejo gigante de Menorca muestra una extremidad anterior un 26 % más corta comparada con la de otros lepóridos (Fig. 6) (la longitud de todos los huesos largos se reduce, excepto en la 2ª y 3ª falange). El radio y la ulna son, junto con los metacarpos, los huesos que muestran un mayor acortamiento (Tabla 1). El conejo gigante muestra también una mano plantígrada, tal como indica la posición lateral del dedo pulgar y la situación dorsal de la foseta para la ulna (Fig. 7). La

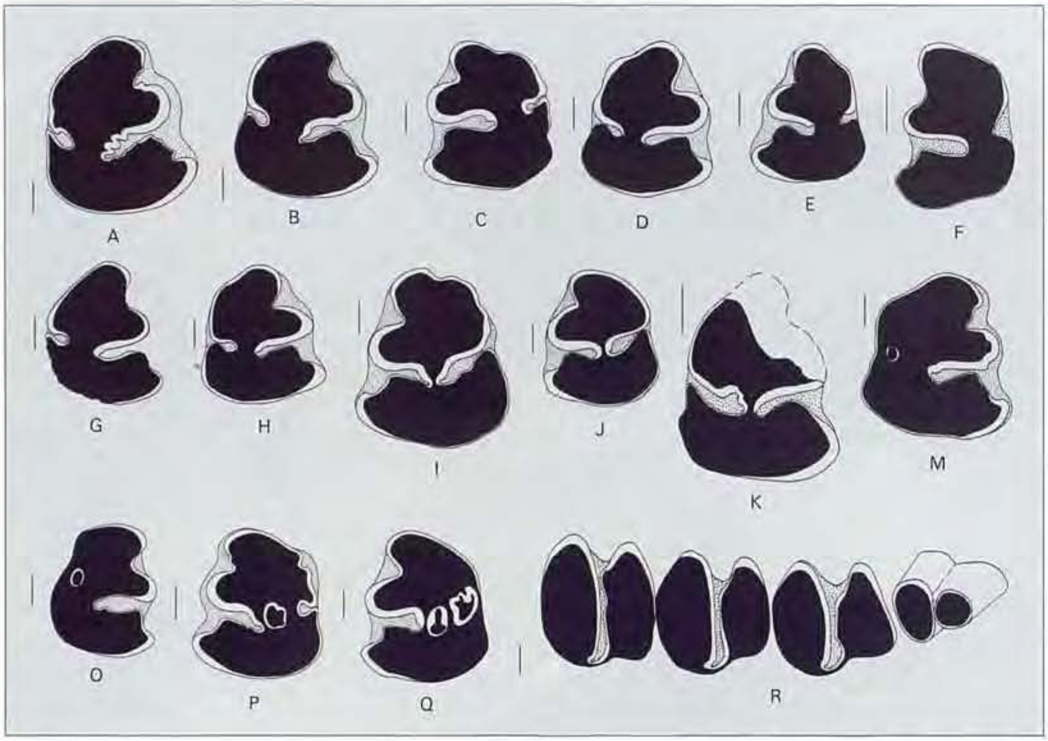

Fig. 5. A-Q: terceros premolares inferiores del conejo gigante de Menorca; R: P_4 -M_3.Escala gráfica: 1 mm. Dibujo de J. Quintana.

Fig. 5. *A-Q: P_3 of the giant rabbit from Menorca; R: P_4 - M_3. Scale: 1 mm. Drawing by J. Quintana.*

Fig. 5. *A-Q: tercers premolars inferiors del conill gegant de Menorca; R: P_4 - M_3. Escala gràfica: 1 mm. Dibuix J. Quintana.*

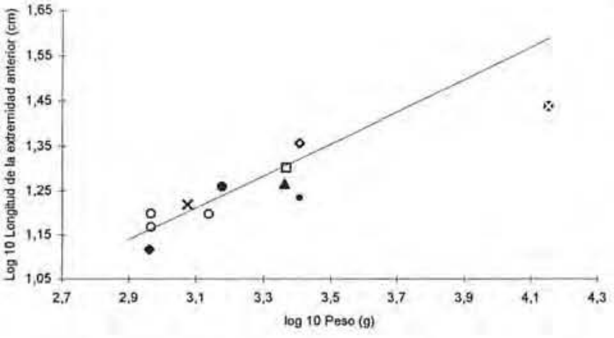

Fig. 6. Representación alométrica de la longitud de la extremidad anterior en el conejo gigante de Menorca (cruz blanca inclinada) y algunos lepóridos actuales (circulo blanco: *Oryctolagus cuniculus*; círculo negro grande: *Bunolagus monticularis*; circulo negro pequeño: *Pentalagus furnessi*; cruz negra inclinada: *Sylvilagus floridanus*; cuadrado negro pequeño inclinado: *Sylvilagus audubonii*; triángulo negro: *Pronolagus randensis*; cuadrado blanco grande: *Lepus granatensis*; cuadrado blanco pequeño inclinado: *Lepus californicus*).

Fig. 6. *Graph of logarithmic values of forelimb length against body weigth in the giant rabbit from Menorca (white sloping cross) and some extant leporids (white circle:* Oryctolagus cuniculus*; big black circle:* Bunolagus monticularis*; little black circle:* Pentalagus furnessi*; black sloping cross:* Sylvilagus floridanus*; little black sloping square:* Sylvilagus audubonii*; black triangle:* Pronolagus randensis*; big white square:* Lepus granatensis*; little white sloping square:* Lepus californicus*).*

Fig. 6. *Representació al·lomètrica de la longitud de l'extremitat anterior del conill gegant de Menorca (creu blanca inclinada) i alguns lepòrids actuals (cercle blanc:* Oryctolagus cuniculus*; cercle negre gros:* Bunolagus monticularis*; cercle negre petit:* Pentalagus furnessi*; creu negra inclinada:* Sylvilagus floridanus*; quadrat negre petit inclinat:* Sylvilagus audubonii*; triangle negre:* Pronolagus randensis*; quadrat blanc gros:* Lepus granatensis*; quadrat blanc petit inclinat:* Lepus californicus*).*

plantigradía de la mano en el conejo gigante es un carácter que lo diferencia claramente del resto de lepóridos.

El estudio de las características del brazo de palanca del músculo *teres major*, de la línea de acción del músculo tríceps y de la ventaja mecánica de la extremidad anterior parecen indicar que la extremidad anterior mostraba, en el conejo gigante, una mayor flexión a nivel del codo y un movimiento más lento y potente. La mano plantígrada debió estabilizar la extremidad anterior durante la marcha, al contrarrestar los movimientos laterales en las articulaciones del hombro y del codo.

EXTREMIDAD POSTERIOR

Como en el caso de la extremidad anterior, el conejo gigante de Menorca muestra una extremidad posterior un 25 % más corta en comparación con otros lepóridos (Fig. 8). Los metatarsos son los huesos que muestran una mayor reducción en su longitud (Tabla 2). Además, en el fémur existe un cambio de orientación y una mayor superficie de la cabeza femoral (Fig. 9); el isquium es más corto y muestra una mayor anchura de la tuberosidad y de la tábula isquiática (Fig. 10).

El pie del conejo gigante es muy corto y ancho (Fig. 11). El estudio morfológico y el realizado mediante el análisis de funciones discriminantes, según la metodología utilizada por Carrano (1997) (en la que se han tenido en cuenta 12 parámetros diferentes) indican claramente la naturaleza plenamente plantígrada del pie del conejo gigante de Menorca. El pie plantígrado de este taxón lo separa netamente del resto de lepóridos corredores. En los lepóridos actuales, el pie adopta diferentes

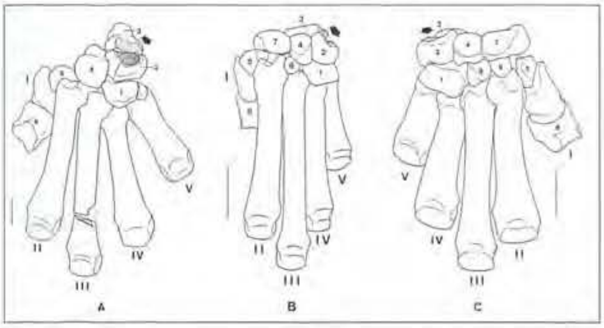

Fig. 7. Huesos del carpo y del metacarpo del conejo gigante de Menorca (A), *O. cuniculus* (B) y *Pentalagus. furnessi* (C). 1: hamatum; 2: triquetrum; 3: pisiforme; 4: lunatum; 5: trapecio; 6: falange proximal del dedo pulgar; 7: escafoideo; 8: capitatum; 9: trapezoideo. La flecha indica la foseta para la epífisis distal de la ulna. Escala gráfica: 5 mm. Dibujo de J. Quintana.

Fig. 7. Carpal and metacarpal bones of the giant leporid from Menorca (A), O. cuniculus *(B) and* Pentalagus furnessi *(C). 1: hamate bone; 2: triquetrum bone; pisiform bone; 4: lunate bone; 5: trapezius bone; 6: proximal phalanx of digit 1; 7: scaphoid bone; 8: capitate bone; 9: trapezoid bone. The arrow indicates the cavity for the distal epiphysis of the ulna. Scale: 5 mm. Drawing by J. Quintana.*

Fig. 7. Ossos del carp i del metacarp del conill gegant de Menorca (A), O. cuniculus *(B) i* Pentalagus. furnessi *(C). 1: hamatum; 2: triquetrum; 3: pisiforme; 4: lunatum; 5: trapeci; 6: falange proximal del dit gros; 7: escafoideu; 8: capitatum; 9: trapezoideu. La fletxa indica la fosseta per a l'epífisi distal de l'ulna. Escala gràfica: 5 mm. Dibuix J. Quintana.*

posturas (plantígradas y digitígradas) a la hora de caminar o correr (Carrano, 1997).

El acortamiento de la extremidad posterior y la plantigradía del pie en el conejo gigante de Menorca son dos características claramente contrarias a la locomoción basada en la velocidad, desarrollada a partir de la elongación de los huesos distales de la extremidad, y en la que se minimiza al máximo el rozamiento de las zonas que contactan con el suelo. Los cambios observados en la cabeza del fémur y en el isquium ponen de manifiesto la mayor importancia relativa de los movimientos mediolaterales frente a los movimientos sagitales en la extremidad posterior.

COLUMNA VERTEBRAL

Las principales modificaciones en la columna vertebral del conejo gigante de Menorca se localizan en las tres últimas vértebras torácicas y en todas las vértebras lumbares. A diferencia de los lepóridos típicamente corredores, el cuerpo vertebral del conejo gigante es muy corto; en las vértebras lumbares, el proceso espinoso ocupa una posición más vertical y caudal (Fig. 12). El conejo gigante muestra, además, una mayor separación entre los procesos mamillares de la última vértebra torácica y en las primeras vértebras lumbares. Por otra parte, la separación entre el proceso espinoso y el proceso costal, y entre los procesos costales disminuye desde la primera hasta la séptima vértebra lumbar; en cambio, la separación entre el proceso mamillar y el proceso costal aumenta desde la primera hasta la séptima vértebra lumbar.

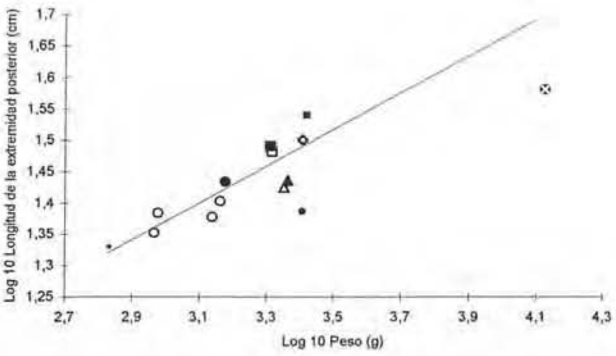

Fig. 8. Representación alométrica de la longitud de la extremidad posterior en el conejo gigante de Menorca (cruz blanca inclinada) y algunos lepóridos actuales (círculo blanco: *Oryctolagus cuniculus*; círculo negro grande: *Bunolagus monticularis*; círculo negro pequeño: *Pentalagus furnessi*; cuadrado negro pequeño inclinado: *Sylvilagus audubonii*; triángulo negro: *Pronolagus randensis*; triángulo blanco: *Pronolagus rupestris*; cuadrado blanco grande: *Lepus granatensis*; cuadrado negro grande: *Lepus capensis*; cuadrado negro pequeño: *Lepus saxatilis*; cuadrado blanco pequeño inclinado: *Lepus californicus*.

Fig. 8. Graph of logarithmic values of hindlimb length against body weigth in the giant rabbit of Menorca (white sloping cross) and some extant leporids (white circle: Oryctolagus cuniculus*; big black circle:* Bunolagus monticularis*; little black circle:* Pentalagus furnessi*; little black sloping square:* Sylvilagus audubonii*; black triangle:* Pronolagus randensis*; white triangle:* Pronolagus rupestris*; big white square:* Lepus granatensis*; big black square:* Lepus capensis*; little black square:* Lepus saxatilis*; little white sloping square:* Lepus californicus.

Fig. 8. Representació al·lomètrica de la llargària de l'extremitat posterior al conill de Menorca (creu blanca inclinada) i alguns lepòrids actuals (cercle blanc: Oryctolagus cuniculus*; cercle negre gros:* Bunolagus monticularis*; cercle negre petit:* Pentalagus furnessi*; creu negra inclinada:* Sylvilagus floridanus*; quadrat negre petit inclinat:* Sylvilagus audubonii*; triangle negre:* Pronolagus randensis*; triangle blanc:* Pronolagus rupestris*; quadrat blanc gros:* Lepus granatensis*; quadrat negre gros:* Lepus capensis*; quadrat negre petit:* Lepus saxatilis*; quadrat blanc petit inclinat:* Lepus californicus*).*

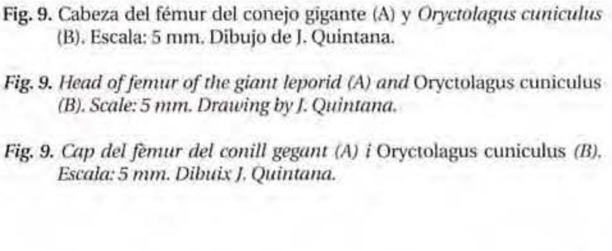

Fig. 9. Cabeza del fémur del conejo gigante (A) y *Oryctolagus cuniculus* (B). Escala: 5 mm. Dibujo de J. Quintana.

Fig. 9. Head of femur of the giant leporid (A) and Oryctolagus cuniculus *(B). Scale: 5 mm. Drawing by J. Quintana.*

Fig. 9. Cap del fèmur del conill gegant (A) i Oryctolagus cuniculus *(B). Escala: 5 mm. Dibuix J. Quintana.*

Resulta también muy significativo la reducción del proceso costal en la séptima vértebra lumbar. Tal cambio está claramente relacionado con la posición de esta vértebra en relación a las alas del ilium: en el conejo gigante de Menorca, el ángulo entre la pelvis y el conjunto formado por el sacro y la séptima vér-

Conejo gigante de Menorca									
		Epífisis proximal		Epífisis distal		Diámetro mínimo diáfisis		Diámetro zona media diáfisis	
	Longitud	D.T.	D.A.P.	D.T.	D.A.P.	D.T.	D.A.P	D.T.	D.A.P
Radio	-44,31	*	-26,94	-22,63	+	-8,65	+	-43,84	+22,43
Ulna	-46,18	?	?	?	?	?	?	+61,37	+34,71
Húmero	-26,72	-	-	+17,79	-	-	-	?	?
2º metacarpo	-36,31	+	*	+	-	*	-	?	?
3º metacarpo	-45,59	-	-	*	-15,92	-	-	?	?
4º metacarpo	?	-	+			-	-	?	?
5º metacarpo	-43,79	-	-19,10	*	-	+24,68	+	?	?
1ª falange	-28,90	*	-17,09	*	-	+	-	?	?
2ª falange	+	-	*	*	+	+	*	?	?
3ª falange	+	?	?	?	?	?	?	?	?

Pentalagus furnessi									
		Epífisis proximal		Epífisis distal		Diámetro mínimo diáfisis		Diámetro zona media diáfisis	
	Longitud	D.T.	D.A.P.	D.T.	D.A.P.	D.T.	D.A.P.	D.T.	D.A.P
Radio	-28,14	+	*	-	+	-	+	-20,38	+
Ulna	-28,54	?	?	?	?	?	?	+	+
Húmero	-12,55	-	*	+	-	-	+	?	?
2º metacarpo	-21,65	+	+13,27	+	+	+	+	?	?
3º metacarpo	-20,90	+	+	+	+	+	+	?	?
4º metacarpo	?	+	+	?	?	+	+	?	?
5º metacarpo	-35,10	+	+	+	+	+26,20	+26,73	?	?
1ª falange	-27,45	+16,08	+	+	+	+24,06	+	?	?
2ª falange	-11,46	+	+	+19,47	+	+28,41	+	?	?
3ª falange	+20,66	?	?	?	?	?	?	?	?

Tabla 1. Cambios alométricos en la extremidad anterior en el conejo gigante de Menorca comparados con los de *Pentalagus furnessi*. Los cambios más significativos vienen expresados en porcentajes, tanto negativos (reducción de la longitud o el diámetro) como positivos (aumento de la longitud o el diámetro). Cuando no se expresan porcentajes, las longitudes o los diámetros quedan incluidos dentro del rango de variación de los lepóridos con los que han sido comparados. En este caso, los valores pueden quedar por debajo (-), por encima (+) o coincidir (*) con la recta de regresión.

Table 1. Allometric changes in the forelimb of the giant rabbit compared with the allometric changes in Pentalagus furnessi, *the Amami rabbit (Japan). The negative and positive percentages express the reduction and the increase in the length or diameter of bones. When the percentages are not expressed, the lengths and diameters are included in the variation rank of the extant leporids. In this case, the values are placed under (-), on (+) or coincide (*) with the allometric line.*

Taula 1. Canvis al·lomètrics a l'extremitat anterior del conill gegant de Menorca en comparació amb els de Pentalagus furnessi. *Els canvis més significatius venen expressats en percentatges, tant negatius (reducció de la longitud o del diàmetre) com positius (increment de la longitud o el diàmetre). Quan no s'expressen percentatges, les longituds o els diàmetres resten inclosos al rang de variació dels lepòrids amb els que han estat comparats. En aquest cas, els valors poden quedar per sota (-), per damunt (+) o coincidir (*) amb la recta de regressió.*

tebra lumbar (el denominado ángulo sacropélvico) es menor al que muestra, por ejemplo, *O. cuniculus* (Linnaeus, 1758), de forma que la séptima vértebra lumbar queda encajada entre las dos alas del ilium (Figs. 13, 14).

El conjunto de cambios sufridos por las vértebras torácicas y lumbares ponen claramente de manifiesto importantes modificaciones en los músculos flexores y extensores de la columna vertebral, viéndose especialmente favorecidos los movimientos laterales y de flexión en sentido ventral, especialmente en la zona torácica distal y lumbar.

CONCLUSIONES

Si bien el estudio del P_3 del conejo gigante de Menorca establece una estrecha relación con el género continental *Alilepus*, las modificaciones esqueléticas, tanto a nivel craneal como poscraneal permiten incluir este taxón en un nuevo género, aún pendiente de descripción.

El estudio de la columna vertebral y las extremidades del conejo gigante de Menorca pone claramente de manifiesto las diferencias existentes en relación con los lepóridos típicamente continentales, cuya locomoción está basada en la

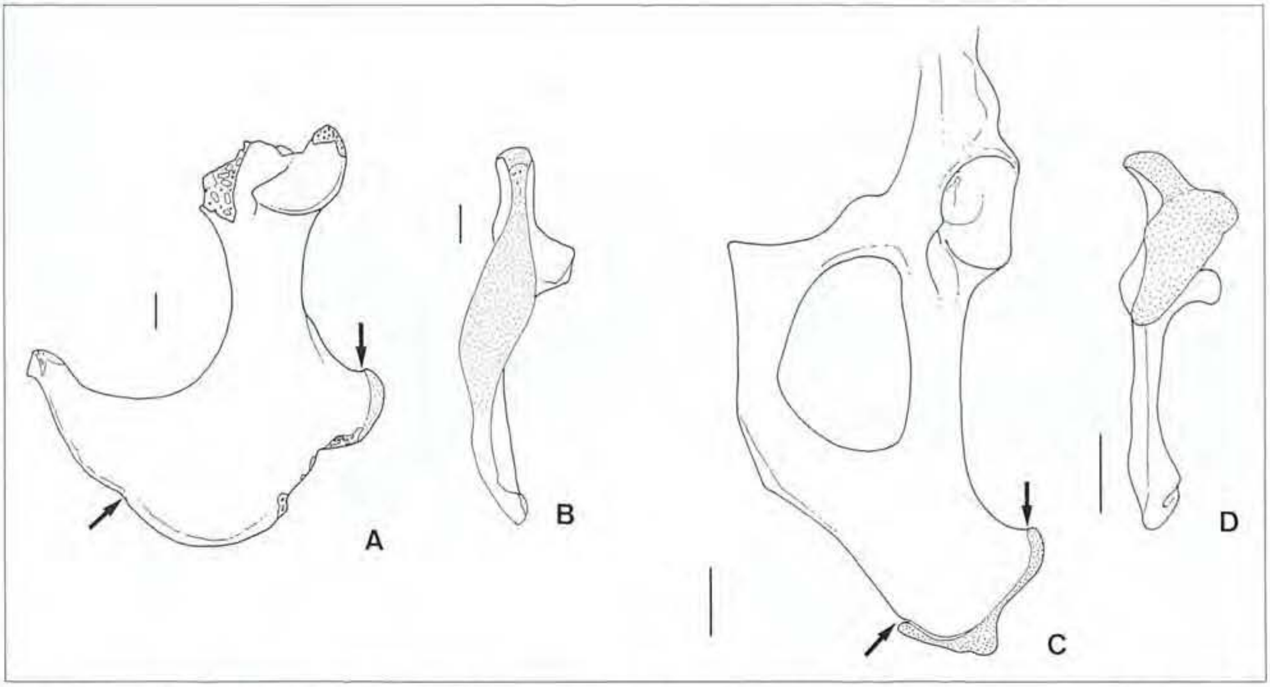

Fig. 11. Desarrollo de la tuberosidad isquiática en el conejo gigante de Menorca (A: vista ventral; B: vista caudal) y en *Oryctolagus cuniculus* (C: vista ventral; D: vista caudal). Las flechas y el punteado indican los límites de la tuberosidad isquiática. Escala: 5 mm. Dibujo de J. Quintana.

Fig. 11. Development in the plate of the ischiadic bone in the giant rabbit (A: ventral view; B: caudal view) and Oryctolagus cuniculus *(C: ventral view; D: caudal view). The arrows and the dotted zone indicates the ischiadic tuber limits. Scale: 5 mm. Drawing by J. Quintana.*

Fig. 11. Desenvolupament de la tuberositat isquiàtica al conill gegant de Menorca (A: vista ventral; B: vista caudal) i a Oryctolagus cuniculus *(C: vista ventral; D: vista caudal). Les fletxes i el puntejat indiquen els límits de la tuberositat isquiàtica. Escala: 5 mm. Dibuix J. Quintana.*

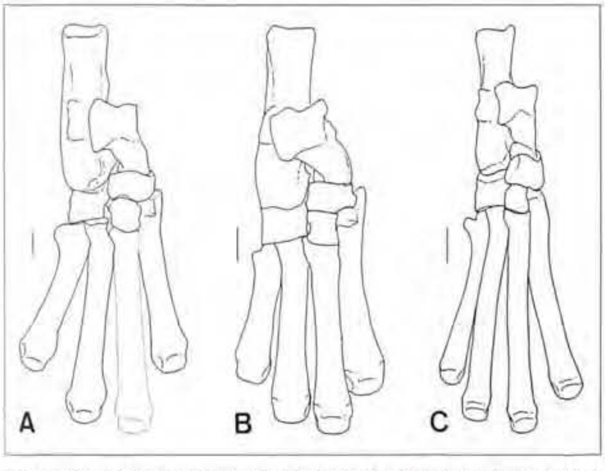

Fig. 10. Pie del conejo gigante de Menorca (A), *Pentalagus furnessi* (B) y *Oryctolagus cuniculus* (C). Escala: 5 mm. Dibujo de J. Quintana.

Fig. 10. Foot of the giant rabbit (A), Pentalagus furnessi *(B) and* Oryctolagus cuniculus *(C). Scale: 5mm. Drawing by J. Quintana.*

Fig. 10. Peu del conill gegant de Menorca (A), Pentalagus furnessi *(B) i* Oryctolagus cuniculus *(C). Escala: 5 mm. Dibuix J. Quintana.*

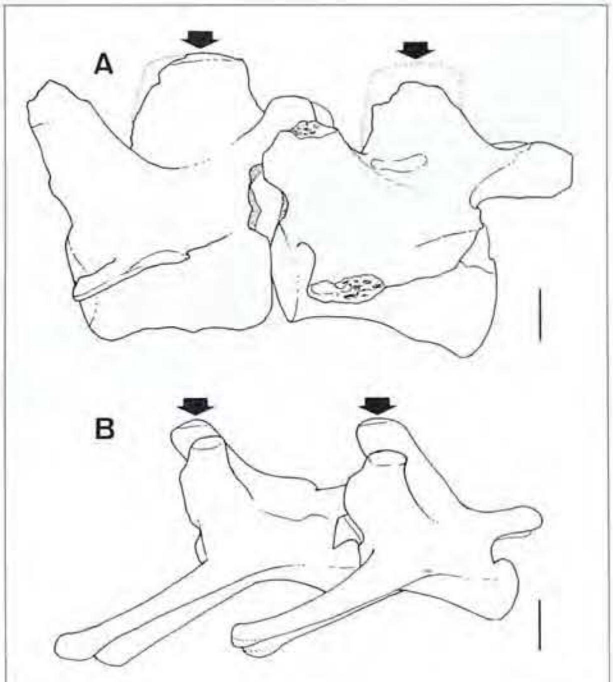

Fig. 12. Inclinación de los procesos espinosos en el conejo gigante de Menorca (A) y *Oryctolagus cuniculus* (B) en las vértebras lumbares. Escala: 5 mm. Dibujo de J. Quintana.

Fig. 12. Spinous processes inclination in the giant rabbit (A) and Oryctolagus cuniculus *(B) in the lumbar vertebrae. Scale: 5 mm. Drawing by J. Quintana.*

Fig. 12. Inclinació dels processos espinosos al conill gegant de Menorca (A) i Oryctolagus cuniculus *(B) a les vèrtebres lumbars. Escala: 5 mm. Dibuix J. Quintana.*

velocidad. La marcada curvatura de la columna vertebral frente a la reducida capacidad de extensión de la misma, la reducción de la longitud de las extremidades, la marcada flexión de las mismas y la plantigradía de pies y manos indican claramente un tipo de locomoción lenta y potente, en la que cobran especial importancia los movimientos medio-laterales frente a los movimientos sagitales de las extremidades. En este sentido, la locomoción del conejo gigante de Menorca sería semejante a la de algunos grandes roedores plantígrados.

Conejo gigante de Menorca									
		Epífisis proximal		Epífisis distal		Diámetro mínimo diáfisis		Diámetro zona media diáfisis	
	Longitud	D.T.	D.A.P.	D.T.	D.A.P.	D.T.	D.A.P.	D.T.	D.A.P
Ilium	-	?	?	?	?	?	?	?	?
Isquium	-24,85	?	?	?	?	?	?	?	?
Acetábulo	+21,04	?	?	?	?	?	?	?	?
Fémur	-31,65	?	?	-	?	?	?	-15,89	-23,57
Tibia	-29,80	-	-20,40	*	-21,86	-	-11,29	?	?
Calcáneo	-	?	?	?	?	?	?	?	?
Astragalo	-19,99	?	?	?	?	?	?	?	?
2º metatarso	-56,45	-	-39,44	*	-	*	-	?	?
3º metatarso	-47,84	-	-32,07	-	*	-	-24,80	?	?
4ª metatarso	-45,51	-	-18,98	*	-	-18,44	-15,65	?	?
5º metatarso	-52,41	-19,01	-25,25	-	-	*	-26,69	?	?
1ª falange	-38,64	*	-25,80	-	*	+27,14	-	?	?
2ª falange	-18,15	-	-	-	-	-	-	?	?
3ª falange	-	?	?	?	?	?	?	?	?

Pentalagus furnessi									
		Epífisis proximal		Epífisis distal		Diámetro mínimo diáfisis		Diámetro zona media diáfisis	
	Longitud	D.T.	D.A.P.	D.T.	D.A.P.	D.T.	D.A.P.	D.T.	D.A.P
Ilium	+	?	?	?	?	?	?	?	?
Isquium	-	?	?	?	?	?	?	?	?
Acetábulo	+	?	?	?	?	?	?	?	?
Fémur	-20,87	?	?	+	?	?	?	-	*
Tibia	-22,13	+	-10,77	+	-	+	-16,73	?	?
Calcaneo	-	?	?	?	?	?	?	?	?
Astragalo	-	?	?	?	?	?	?	?	?
2º metatarso	-59,68	+	*	+	*	-16,59	-	?	?
3º metatarso	-36,49	+	-	+	+	+	-	?	?
4ª metatarso	-37,39	+	*	+	+	+	-	?	?
5º metatarso	-41,66	+	-	+	-	+	-	?	?
1ª falange	-36,49	+	+	+	*	+33,33	+	?	?
2ª falange	-32,80	+	+	+	*	+7,64	+41,17	?	?
3ª falange	+15,09	?	?	?	?	?	?	?	?

Tabla 2. Cambios alométricos en la extremidad posterior en el conejo gigante de Menorca comparados con los de *Pentalagus furnessi*. Los cámbios más significativos vienen expresados en porcentages, tanto negativos (reducción de la longitud o el diámetro) como positivos (aumento de la longitud o el diámetro). Cuando no se expresan porcentages, las longitudes o los diámetros quedan incluidos dentro del rango de variación de los lepóridos con los que han sido comparados. En este caso, los valores pueden quedar por debajo (-), por encima (+) o coincidir (*) con la recta de regresión.

Table 2. Allometric changes in the hindlimb of the giant rabbit compared with the allometric changes in Pentalagus furnessi, *the Amami rabbit (Japan). The negative and positive percentages express the reducction and the increase in the length or diameter of bones. When the percentages are not expressed, the lengths and diameters are included in the variation rank of the extant leporids. In this case, the values are placed under (-), on (+) or coincide (*) with the allometic line.*

Taula 1. Canvis al·lomètrics a l'extremitat posterior del conill gegant de Menorca en comparació amb els de Pentalagus furnessi. *Els canvis més significatius venen expressats en percentatges, tant negatius (reducció de la longitud o del diàmetre) com positius (increment de la longitud o el diàmetre). Quan no s'expressen percentatges, les longituds o els diàmetres resten inclosos al rang de variació dels lepòrids amb els que han estat comparats. En aquest cas, els valors poden quedar per sota (-), per damunt (+) o coincidir (*) amb la recta de regressió.*

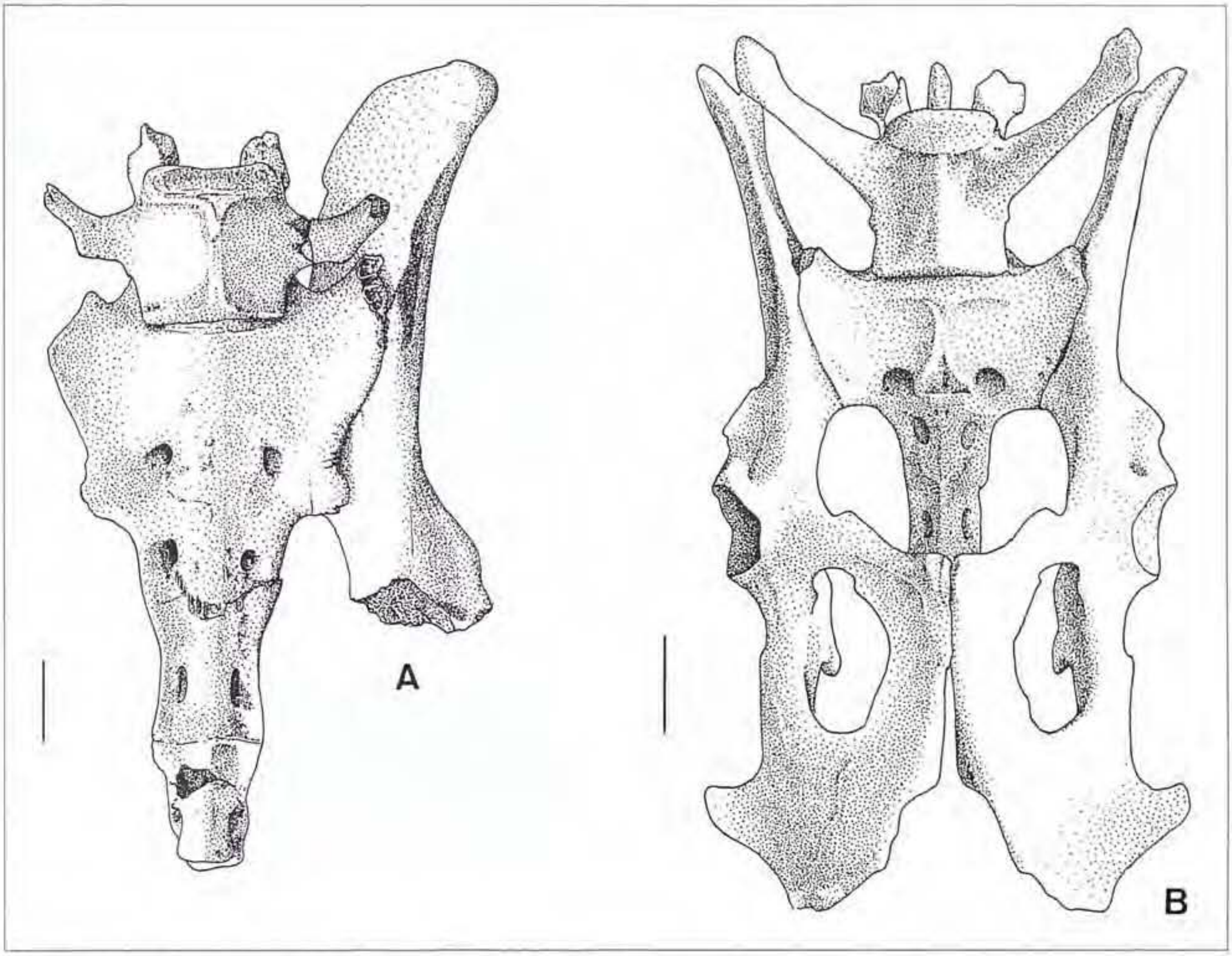

Fig. 13. Posición de la séptima vértebra lumbar en relación con las alas del ilium en el conejo gigante de Menorca (A) y en *Oryctolagus cuniculus* (B) en visión ventral. Escala: 5 mm. Dibujo de J. Quintana.

Fig. 13. Position of the seventh lumbar vertebrae in relation to the wing of ilium in the giant rabbit (A) and Oryctolagus cuniculus *(B) in ventral view. Scale: 5 mm. Drawing by J. Quintana.*

Fig. 13. Posició de la sèptima vèrtebra lumbar en relació amb les ales de l'ilion al conill gegant de Menorca (A) i a Oryctolagus cuniculus *(B) en visió ventral. Escala: 5 mm. Dibuix J. Quintana.*

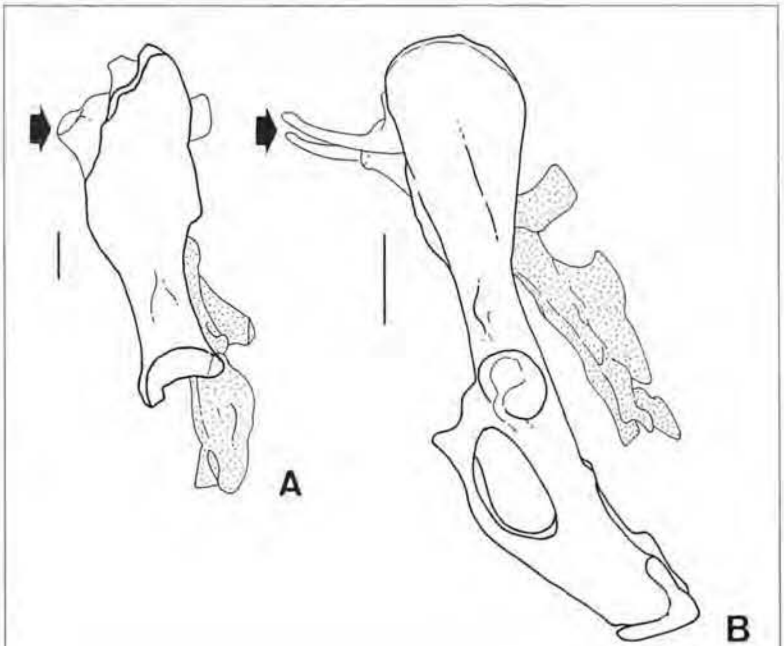

Fig. 14. Posición de la séptima vértebra lumbar (flecha) y del sacro (punteado) en relación con la pelvis en el conejo gigante de Menorca (A) y en *Oryctolagus cuniculus*, visión lateral. Escala: 10 mm. Dibujo de J. Quintana.

Fig. 14. Position of the seventh lumbar vertebrae (arrow), sacrum (dotted) in relation with the pelvis in the giant rabbit (A) and Oryctolagus cuniculus *(B), lateral view. Scale: 10 mm. Drawing by J. Quintana.*

Fig. 14. Posició de la setena vèrtebra lumbar (fletxa) i del sacre (puntejat) respecte la pelvis al conill gegant de Menorca (A) i a Oryctolagus cuniculus, *visió lateral. Escala: 10 mm. Dibuix J. Quintana.*

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29

HOLOCENE EXTINCTION OF ENDEMIC MAMMALS OF THE MEDITERRANEAN ISLANDS: SOME METHODOLOGICAL QUESTIONS AND AN UPDATE

Damià RAMIS & Josep Antoni ALCOVER

RAMIS, D. & ALCOVER, J.A. 2005. Holocene extinction of endemic mammals of the Mediterranean islands: some methodological questions and an update. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 309-318.

Resum

L'objectiu d'aquesta contribució consisteix en millorar el coneixement de les causes i mecanismes relacionats amb l'extinció dels mamífers insulars endèmics a la Mediterrània durant l'Holocè, mitjançant l'anàlisi de les cronologies disponibles per a aquests fets. Aquesta aproximació és aplicada als taxa de Xipre, Creta, Còrsega-Sardenya i Mallorca-Menorca.

Es fan servir criteris de fiabilitat per tal d'establir un marc cronològic sòlid, acurat, per a la presència i absència a cada territori. La cronologia per a la presència dels endemismes és inferida a partir de les datacions absolutes directes obtingudes sobre col·làgen d'ossos d'aquestes espècies, tenint en compte les seves limitacions temporals a cada cas. Les cronologies derivades de la presència de restes faunístiques a contextos estratigràfics datats per altres medis són evitades, si és possible, a causa de potencials edats diacròniques. A la discussió s'introdueixen exemples d'aquestes distorsions potencials procedents d'excavacions mallorquines. Els indicadors per a la desaparició dels endemismes s'obtenen a partir de la seva absència a contextos estratigràfics (dipòsits arqueològics normalment). Aquesta anàlisi permet establir els intervals cronològics per als processos d'extinció a cada territori.

Els resultats són comparats amb les cronologies fiables per a la irrupció humana a cada illa. La manca de sincronia per a les extincions i la seva estreta relació amb la presència humana inicial a la majoria dels casos provoca el rebuig de causes estrictament ambientals com a explicació d'aquestes extincions. En ser analitzades les extincions dels mamífers de mida gran i mitjana, es pot trobar una estreta correlació amb l'edat inferida d'arribada dels humans moderns, encara que no s'ha documentat fins ara un solapament clar dels dos fets. En canvi, no es pot trobar el mateix patró en el cas de la desaparició dels petits mamífers. Mentre es documenta un llarg solapament temporal entre humans i petits mamífers a Còrsega-Sardenya i Creta (on *Crocidura zimmermanni* encara hi és present), l'extinció a les Balears i a Xipre sembla haver estat molt més sobtada, i la coexistència amb els humans primerencs encara no ha estat documentada.

Paraules clau: Illes mediterrànies, Extinció, Arribada humana.

Abstract

The aim of this contribution consists of improving the knowledge of the causes and mechanisms related to the extinction of endemic insular mammals in the Mediterranean during the Holocene, through an analysis of the chronologies available for such events. This approach is applied to the taxa from Cyprus, Crete, Corsica-Sardinia and Mallorca-Menorca.

Reliability criteria are used in order to establish a solid, accurate chronological framework for their presence and absence in each territory. The chronology for the presence of endemics is inferred from direct absolute ages obtained from bone collagen of these species, taking into account their potential limitations in each case. Chronologies derived from the occurrence of faunal remains from stratigraphic contexts dated by other means are avoided where possible due to potential diachronic ages. Examples for these potential distortions coming from Mallorcan excavations are introduced in the discussion. Indicators for the disappearance of endemics are obtained from their absence in dated stratigraphic contexts (usually archaeological deposits). This analysis enables us to establish chronological intervals for these extinction events in each territory.

The results are compared to the reliable chronologies for human irruption in each island. The lack of synchrony for the extinctions and their close relationship to early human presence in most cases precludes strictly environmental causes for such extinctions. When the extinctions of large and medium-sized mammals are analysed, a close correlation can be found with the inferred time for modern human arrival, although a clear overlapping between these two events has not yet been recorded. However, the same pattern cannot be found for the disappearance of small mammals. While great overlapping is recorded between humans and small mammals in Corsica-Sardinia and Crete (where *Crocidura zimmermanni* is still present), the extinction in the Balearics and Cyprus seems to have been much more sudden, and their coexistence with early humans has not yet been recorded.

Key words: Mediterranean islands, Extinction, Human arrival.

INTRODUCTION

Research on the chronology of human arrival and the extinction of endemic mammals in the Balearic Islands archipelago has been carried out during these last years by the present authors. Here, a comparison of the results obtained for Mallorca (and the other Gymnesic Islands) will be made with the data available for the other large Mediterranean islands — that is, Corsica-Sardinia, Crete, and Cyprus — in order to look for potential patterns of faunal extinction.

The species will be divided into two groups: large and medium-sized mammals on the one hand and small mammals on the other (Table 1). If a single species shows a specific behaviour within one of these groups then it will be individualized, if not, each species will be considered as following the same general pattern within the group in which it is included.

METHODS

A chronological framework for the extinction of endemic mammals and for human arrival to all the aforementioned islands will be established. These chronologies will be outlined essentially from direct radiocarbon datings and from stratigraphic relationships. Hence, the last evidence for occurrence and the earliest indicators for absence of endemic species will be considered. In most cases the latter will come from the earliest archaeological deposits. That is, the most ancient human presence involves the first evidence for the absence of endemics in most cases.

Following conventions, dates coming from the calibration of radiometric results appear as 'cal BC' or 'cal AD'. They are expressed on the basis of their 2σ statistical ranges. All of them have been calibrated following the program OxCal v3.5 (Bronk Ramsey, 2000). Uncalibrated radiocarbon ages are presented as 'BP'. Calendar dates not coming from radiocarbon analyses are expressed as 'BC' or 'AD'.

The use of radiocarbon datings in order to infer the chronology of certain events involves different limitations and potential distortions which are widely introduced in specific literature (e.g., Spriggs, 1989; Anderson, 1991; Spriggs & Anderson, 1993; Housley *et al.*, 1997; Tuggle & Spriggs, 2000; Zilhão, 2001). Several methodological procedures will be applied in order to avoid potential distortions of real ages for palaeontological or archaeological events. In the present work, the use of reliability criteria follows the proposals explained in previous publications (Alcover *et al.*, 2001; Ramis *et al.*, 2002).

Here, only two of these main features will be commented on the basis of examples recorded by the present authors in the excavation of Cova des Moro: (1) the presence of differently aged materials in the same sedimentological layer; and (2) distortions of the real age based on the results given by dating of associated long life-based samples.

In Cova des Moro (stratigraphic unit 406), 13 remains of *Eliomys morpheus* and 6 of *Asoriculus hidalgoi* have recently been recovered (2001-2002, unpublished results) through systematic sieving. Additionally, remains of *Eliomys quercinus* and *Apodemus sylvaticus* have also been identified in this faunal assemblage. Pottery types belonging to two different prehistoric phases have been recorded in this archaeological level. Firstly, those belonging to the earliest phase are characteristic undecorated types, which appear to be related to the incised Bell Beaker pottery from several other archaeological sites in the island. This characteristic pottery element is present in Mallorca during the uppermost part of the III millennium and possibly the lowermost part of the II millennium cal BC (Coll, 2001). Secondly, the main bulk of the material is chronologically attributed to the end of the II millennium cal B.C. or the beginning of the next one, on the basis of the presence of the same pottery types in the habitation structures of this period (e.g., Pons, 1999; Salvà, 2001). Two different AMS ^{14}C datings were obtained for this stratigraphic unit, both based on collagen from two introduced bovid bone samples —Beta-155645: 3750±40 BP (2290-2030 cal BC) and Beta-162619: 2860±50 BP (1190-900 cal BC). These results are consistent and confirm those obtained through the analysis of the archaeological

	Large and middle-sizedmammals	Small mammals
Mallorca-Menorca-Cabrera	*Myotragus balearicus* (*)	*Eliomys morpheus* (*) *Asoriculus hidalgoi* (*)
Corsica-Sardinia	*Megaceros cazioti* (*) *Cynotherium sardous* (*)	*Rhagamys orthodon* *Thyrrhenicola henseli* *Asoriculus corsicanus / similis* *Prolagus sardus* (*)
Crete	*Hippopotamus creutzburgi* (*) *Elephas creutzburgi*	*Mus minotaurus*
	Candiacervus sp.	*Crocidura zimmermanni*
Cyprus	*Phanourios minutus* (*)	*Mus* I
	Elephas cypriotes	*Mus* II

Table 1. Analysed species and islands. (*)=Taxa with direct radiocarbon ages available.

Taula 1. *Espècies i illes analitzades. (*)=Taxa amb dates radiocarbòniques directes disponibles.*

materials. AMS ^{14}C dating on an *Eliomys morpheus* bone was carried out in order to check the assumed coetaneity between the endemic small mammal remains and the archaeological deposit where they had been found. The result obtained was Beta-162613: 12250±80 BP (13500-11800 cal BC). This date indicates that the *Eliomys morpheus* remains from Cova des Moro, and probably also the *Asoriculus hidalgoi* remains, pre-date the archaeological context from which they were recovered (Ramis *et al.*, in press).

This first example illustrates the risk of chronologies not obtained from the materials themselves, but from their contextual association with other items with chronological implications. Stratigraphic association is helpful to the study of evolution and extinction patterns, but some possible limitations must be taken into account. The factors involved in the formation of a deposit are very numerous and diverse, and the taphonomic analysis offers some limitations to discern exactly the precedence of every single remain.

Secondly, a new instance of how charcoal-based radiocarbon dating can distort the real age of a feature has been recorded in Cova des Moro. A thin ash and charcoal layer containing introduced fauna and some flaked pebbles was first dated through the radiocarbon analysis of a charcoal sample (Calvo *et al.*, 2001). The result obtained was UtC-7877: 3961±41 BP (2580-2300 cal BC). In order to check the validity of this age, a jaw of a domestic caprine from the same layer was also dated through radiocarbon analysis, Beta-162615: 3420±50 BP (1880-1530 cal BC), that is yielding an age between 420 and 1050 years later than the former one (Ramis *et al.*, in press).

RESULTS

Mallorca-Menorca-Cabrera

Earliest human presence

After reviewing the evidence for the assumed early human presence in the Balearics, it was concluded that the first arrival in the Gymnesic Islands occurred in the III millennium cal BC (Alcover *et al.*, 2001; Ramis *et al.*, 2002). Currently, the most ancient archaeological contexts of the island of Mallorca date back to the end of the III millennium cal BC and are related to the Bell Beaker cultural tradition. The chronological evidence comes from Cova des Moro (Calvo *et al.*, 2001; Ramis *et al.*, in press), Coval Simó (Coll, 2001) and Ca na Cotxera (Calvo & Guerrero, 2002). A dating from this last site, KIA-17389: 3770±30 BP (2290-2040 cal BC), provides the earliest reliable *terminus ante quem* for human presence in Mallorca, demonstrating this to be previous to 2040 cal BC.

The earliest chronological datum from the island of Menorca was obtained in the burial place of Biniai Nou (Plantalamor & Marquès, 2001). The dating which demonstrates the earliest human presence is UtC-8949: 3745±35 BP (2290-2030 cal BC), obtained on human bones.

Currently, the archaeological evidence available for the earliest human presence in Cabrera derives from surface findings, in some caves of the island, of some pottery types (Trias, 1974) which can be placed roughly around 1000 cal BC. Recently, some new fragments have been discovered which are related to other pottery types (Riera, pers. com.) which in the Mallorcan and Menorcan reliable contexts are dated within the last third of the III millennium cal BC and the first half of the next one.

Apparently, and with some caution derived from the limitations of the archaeological record, no significant differences can be traced as to the earliest human presence in each island of the Gymnesic archipelago.

Large and medium-sized fauna

Traditionally, the *Myotragus* bone-based radiocarbon dating BM-1408: 4093±392 BP (3700-1600 cal BC) had been considered as the most recent evidence for the survival of this species in Mallorca (Burleigh & Clutton-Brock, 1980). Nevertheless, the reliability of this dating has been recently called into question (van Strydonck *et al.*, 2005). Leaving aside this date, the result from Cova Estreta (Encinas & Alcover, 1997), UtC-5171: 5720±60 BP (4720-4400 cal BC), can be considered as the most recent chronology for *Myotragus* presence in Mallorca. Evidence for later survival of this endemic caprine has been obtained recently from the other two Gymnesic Islands. A *Myotragus* specimen from Cova des Penyal Blanc, in Cabrera (Alcover *et al.*, 1997), yielded the result UtC-6517: 4785±40 BP (3650-3380 cal BC), while the dating Beta-177237: 5060±40 BP (3970-3760 cal BC) was obtained on another bone from Pas den Revull, in Menorca (Quintana *et al.*, 2003). The available chronology for *Myotragus* survival in each of the three Gymnesic Islands does not differ significantly, although it is a little earlier for Mallorca. Considering this fact and the geographic proximity of these islands, they will be considered here as a whole. Hence, the evidence from Cabrera, which demonstrates that *Myotragus* was living there after 3650 cal BC, will be considered as representative also for Mallorca.

Small mammals

The most recent available ^{14}C age for *Eliomys morpheus* in Mallorca is UtC-5175: 6357±44 BP (5480-5250 cal BC), obtained from collagen of bones collected at Cova Estreta (Encinas & Alcover, 1997). Therefore, *Eliomys morpheus* disappeared from Mallorca later than 5480 cal BC. The only available ^{14}C age for *Asoriculus hidalgoi* in Mallorca is Beta-163133: 4280±50 BP (3030-2690 cal BC), obtained on collagen from bones collected at Cova des Garrover (Bover *et al.*, submitted). This allows us to conclude that, with a $p > 95.45$ %, *Asoriculus hidalgoi* disappeared from Mallorca later than 3030 cal BC.

Some evidence related to the disappearance of both species can be mentioned. Both are absent from the most ancient archaeological sites, in which the introduced *Eliomys quercinus* and *Apodemus sylvaticus* remains have been found. Microfaunal analyses are available from some of the most ancient archaeological contexts — e.g., Coval d'en Pep Rave (Coll, 1981) or Coval Simó and Ca na Cotxera (unpublished); all of which show the absence of endemic mammals, while *Eliomys querci-*

nus and *Apodemus sylvaticus* (two human-introduced rodent species) are present in some of these deposits. Systematic sieving was applied in the case of the first two sites mentioned (excavations of 1980 and 1998-2001, respectively), while this aspect could not be confirmed for the recovery of the faunal assemblage from the open-air site of Ca na Cotxera (excavation of 1968). Additionally, no documentation of the presence of autochthonous small mammals has been recorded in younger archaeological deposits from Mallorca. The case of an assumed relationship in Cova des Moro (Ramis *et al.*, in press) has already been commented.

Corsica-Sardinia

Earliest human presence

There are several claims for human presence on these islands during the Lower and Middle Palaeolithic, based on certain characteristics of human remains (Spoor & Sondaar, 1986), faunal evolution dynamics (Sondaar, 1987), unstratified lithic industries (Martini & Ulzega, 1992), or taphonomic aspects of faunal assemblages (Klein Hofmeijer, 1996; Bonifay *et al.*, 1998; Bonifay, 2001); although most authors do not consider the evidence to be conclusive (Vigne, 1989; Cherry, 1992; Spoor, 1999; Pérez Ripoll, 2002). The earliest evidence for anatomically modern humans in Corsica and Sardinia belongs to the beginning of the Holocene, and is culturally placed in the Mesolithic. It is represented by several Corsican cultural assemblages from the caves or rock-shelters of Araguina-Sennola (Lanfranchi & Weiss, 1972), Curacchiaghju (Lanfranchi, 1967), Strettte II (Magdeleine, 1985), Torre d'Aquila (Magdeleine, 1995) and Monte Leone (Vigne *et al.*, 1998); and from layer 2 of Grotta Su Corbeddu in Sardinia (Sondaar *et al.*, 1984). Absolute chronology is available for all these sites, but was obtained through radiocarbon dating of long life samples (charcoal) or *Prolagus* bones. Human consumption of *Prolagus* is well attested in Corsica and Sardinia (Vigne & Desse-Berset, 1995), but the trouble with dating unmodified *Prolagus* remains could arise if the selected specimens came from a natural level and had been re-deposited in an archaeological layer later on.

Although these questions introduce some inaccuracy as to the exact age of the assemblages, the chronologies obtained for the Mesolithic in Corsica and Sardinia (placed mainly within the range between the X and VII millennia cal BC) do not differ significantly from that of the same period in the surrounding mainland. In order to select a *terminus ante quem* for human arrival, and taking into account the aforementioned factors, here *Prolagus* bone-based datings will be preferred to those obtained on charcoal samples. These come from two different sites (Su Corbeddu and Monte Leone). Both the most ancient and the most recent probabilistic chronological intervals obtained from these datings come from Monte Leone and, respectively, are AA-18111: 9750±175 BP (9800-8600 cal BC) and AA-18108: 8050±60 BP (7300-6700 cal BC). Thus, it would derive that human presence in Corsica could be previous to 8600 cal BC, while a slightly more conservative opinion would consider the event previous to 6700 cal BC.

Large and medium-sized mammals

The most recent age for the survival of *Megaceros cazioti* comes from Grotta su Corbeddu in Sardinia (Klein Hofmeijer, 1996) with the result UtC-241: 11980±140 BP (13400-11500 cal BC). A similar result was obtained on *Cynotherium sardous* remains from the site of Castiglione 3, in Corsica (Salotti *et al.*, 2000) —Ly-965(OXA): 11760±110 BP (13200-11400 cal BC). The last evidence for endemic megafauna survival in Corsica and Sardinia also comes from Grotta su Corbeddu (Klein Hofmeijer, 1996), and consists of the radiocarbon dating made on a *Cynotherium sardous* bone which displayed the result UtC-2583: 11350±100 BP (11850-11050 cal BC).

Small mammals

Direct dating on Corsican/Sardinian small-sized endemics is available for *Prolagus sardus*. The sites of Grotta Su Corbeddu and Monte Leone yield this information, as previously pointed out. This proves the survival of *Prolagus* until later than 7300 cal BC. However, the record from Monte di Tuda indicates the survival of the four autochthonous small mammals until Classic Antiquity (Vigne, 1992; Vigne & Valladas, 1996). Nevertheless, it must be noted that the fossil age does not derive from direct dating but from stratigraphic association to other materials.

Crete

Earliest human presence

There is well attested evidence for Mesolithic (X-IX millennia cal BC) navigation in the Aegean (Perlès, 1979; Sampson, 1998). It cannot be excluded that Crete was reached during this period, and evidence supporting this hypothesis may arise in the future (Broodbank & Strasser, 1991). Yet, currently, the most ancient chronological evidence for human presence on the island is sensibly later, coming from the inferior level of Knossos, which belongs to the Aceramic Neolithic period, dated to the late VII or VI millennium cal BC (Evans, 1971). Specifically, the dating BM-436: 7740±140 BP (7050-6250 cal BC) constitutes the earliest reliable date for human presence on the island, because of its short life source (wheat), and shows that the event is previous to 6250 cal BC

Large and medium-sized fauna

There is, as yet, no complete agreement on the faunal episodes for the Cretan Pleistocene, and several proposals based on the paleontological record are available. de Vos (2000) defends the existence of eight Cervidae species, belonging to the genus *Candiacervus*, from the radiation of a unique ancestor. Other authors differ in the number of species and also more than one radiation is recognized. Pleistocene megafauna also consisted of an elephant (*Elephas creutzburgi*) and a hippopotamus, both of reduced size (*Hippopotamus creutzburgi*).

Hamilakis (1996) asserted that little attention has been paid to the research of endemic faunal extinctions and, additionally, a series of direct absolute dating has not been possible due to the lack of collagen in most samples. Currently, there is only one absolute age for the endemic fauna of the Late glacial or later. This was obtained on a hippo bone from Katharo Basin and displayed the result 12135±485 BP (13800-11200 cal BC), with no reference available of the laboratorium (Bachmayer & Zapfe 1985). Nevertheless, Reese *et al.* (1996: 47), on the basis of a personal communication of the original authors, point out that this result may be highly erroneous due to a possible deficiency in the dated sample. In the absence of any other chronological evidence, and taking into account its dubious reliability, this dating will be considered provisionally here as indicating the presence of large endemic mammals on Crete later than 13800 cal BC.

Small mammals

There is no evidence, due to the lack of record, as to the survival of the endemic *Mus minotaurus* after the first human arrival to Crete (e.g., Vigne, 1999). Nevertheless, *Crocidura zimmemanni* is one of the few examples of small mammals from the true Mediterranean islands to survive until the present day, although its distribution seems to have been reduced to the Cretan inner mountain area since Minoan time (*ca.* 3000 cal BC), with the arrival of *Crocidura suaveolens* and *Suncus etruscus* (Reumer, 1996).

Cyprus

Earliest human presence

Claims for Mesolithic hunter-gatherers in Cyprus near 10000 cal BC (e.g., Simmons & Wigand, 1994; Wigand & Simmons, 1999) have been made on the interpretation of the record from Akrotiri-Aetokremnos (e.g., Simmons, 1991; 1999). However, several opinions consider this record to be a natural fossil assemblage (e.g., Bunimovitz & Barkai, 1996; Olsen, 1999; Pérez Ripoll, 2002). Their arguments seem more compelling to the present authors. Thus, the most ancient record for human presence on Cyprus belongs to the IX millennium cal BC and corresponds to the Early Aceramic Neolithic assemblages from the sites of Kalavasos-Tenta (Todd, 2002), Parekklisha-Shillourokambos (Guilaine, 1996; 2003; Guilaine *et al.*, 2000; Guilaine & Briois, 2002) and Kissonerga-Mylouthkia (Peltenburg *et al.*, 2000; 2002). Out of all this information, the dating OxA-7460: 9315±60 BP (8740-8320 cal BC), from the last site, obtained on a short life sample (barley), shows the earliest reliable *terminus ante quem* for human presence on the island, that is, 8320 cal BC.

Large and medium-sized fauna

The Late Quaternary megafauna from Cyprus consisted of two dwarf species, an elephant (*Elephas cypriotes*) and a hippopotamus (*Phanourios minutus*). Several dates obtained with AAR and ESR methods are available from different sites, falling within the final millennia of the Pleistocene and the beginning of the Holocene. However, as the reliability of these results has been questioned (Reese, 1996; Wigand & Simmons, 1999) they will not be taken into account here. The other group of absolute datings for the Cyprian endemic large mammals consists of the data from Akrotiri-Aetokremnos (Wigand & Simmons, 1999). Several problems have been noted on the dated bones from this site, derived from variable contamination of the samples and from the dated organic fraction. Dates obtained on other materials (sediment, shell, charcoal) are also problematic. So, it can be concluded that a precise conversion of the radiocarbon dating into calendar ages is not possible in this case. The authors suggest that the deposit was formed in a short time (some centuries maybe) about 10000 cal BC (Wigand & Simmons, 1999). Only one of the radiocarbon dates on fossil remains was obtained on the collagen fraction. The sample was a *Phanourios* bone from an altered stratum, which offered the result TX-5976B: 9420±550 BP (10700-7300 cal BC). Provisionally, this date will be considered as representative for the chronology of the endemic megafauna presence on Cyprus, given that the result was obtained through the radiocarbon dating of the collagen fraction and is compatible with the propounded chronology for the deposit (Wigand & Simmons, 1999). Consequently, this dating indicates that the *Phanourios* extinction on Cyprus occurred later than 10700 cal BC.

Small mammals

In Cyprus, two *Mus* species are the only small autochthonous mammals recorded during the Late Pleistocene and Early Holocene. After human establishment on the island, the presence of *Mus* was first identified in pre-ceramic levels from Khirokitia, in the VII millennium cal BC. On the basis of metrical analysis it was inferred that these remains could belong to one of the two endemic species, larger than *Mus musculus*, which had reached the island in later times (Davis, 1989). But, recently, two different *Mus* species have been recorded in the Kissonerga-Mylouthkia site, in pre-ceramic levels dated from the late IX and VIII millennium cal BC. One of them has been identified as the domestic mouse (*Mus musculus domesticus*), while some doubts persist as to the attribution of the other to one of the endemic species or, alternatively, to the mainland *Mus macedonicus* (Cucchi *et al.*, 2002).

DISCUSSION AND CONCLUSIONS

Relevant relationships can be established when comparing the chronology for the last occurrences of the endemic mammals on each of the islands analysed and, on the other hand, the first well attested record for human presence in these territories.

As previously known, the extinctions of large and medium-sized mammals on the Mediterranean islands are not synchronous (e.g., Vigne, 1987; 1999). Their last recorded occurrence and the earliest evidence for absence yield the intervals within which each extinction event must be placed. These intervals overlap in all cases except for *Myotragus*. Its extinction in the Balearics has been proved to be several millennia later than that of equivalent species in the other large Mediterranean islands.

It is important to note here that the heterochrony of such extinctions is closely related to the heterochrony of the human colonization of the large Mediterranean islands (Ramis & Alcover, 2004). The first human presence in the large Mediterranean islands is not synchronous: there is a huge gap between the early cultural evidence in Mallorca (and the Gymnesics in general) and the islands of the Central and East Mediterranean (Fig. 1).

Thus, a close relationship between human arrival and the large and medium-sized fauna in each large Mediterranean island can be strongly suggested. As a result, humans emerge as the most plausible agent for the turnover of large and medium-sized fauna during the Holocene and, given the lack of overlapping, each extinction event seems to have been very sudden. The factors that are better adapted to such a scenario are: (1) overhunting (e.g., Martin, 1984) and (2) introduction of alien diseases (MacPhee & Marx, 1997). However, currently there is no reliable evidence to test such possibilities.

Concerning the extinction of the small endemic mammals, a very different relationship arises. Two different patterns can be observed (Fig. 2). A long coexistence between humans and small endemic mammals is recorded in Corsica-Sardinia and Crete. According to several authors (Reumer, 1996; Vigne *et al.*, 1997), a low-intensity pattern tending to extinction can be applied in these cases. This has been propounded especially for Corsica (e.g., Vigne, 1990; 1999; Vigne & Valladas, 1996; Vigne *et al.*, 1997), but extended in some cases to the whole Mediterranean islands (e.g. Vigne & Alcover, 1985; Vigne, 1987).

According to Vigne (1987; 1999), the effect of human hunting on the small endemic mammals through the Mesolithic and the Neolithic would have been a modification of the evolutionary tendency of the different species, with a size diminution. The role played by the introduction of new predators is considered as non relevant by this author, since the small mammals should have been adapted to hunting pressure by Pleistocene predator birds. The arrival of new competitors, like *Rattus rattus* (recorded on the island since the end of I millennium cal BC), is considered as a cause of the reduction of the population size and of the restriction of the distribution to woody areas. The final extinction of

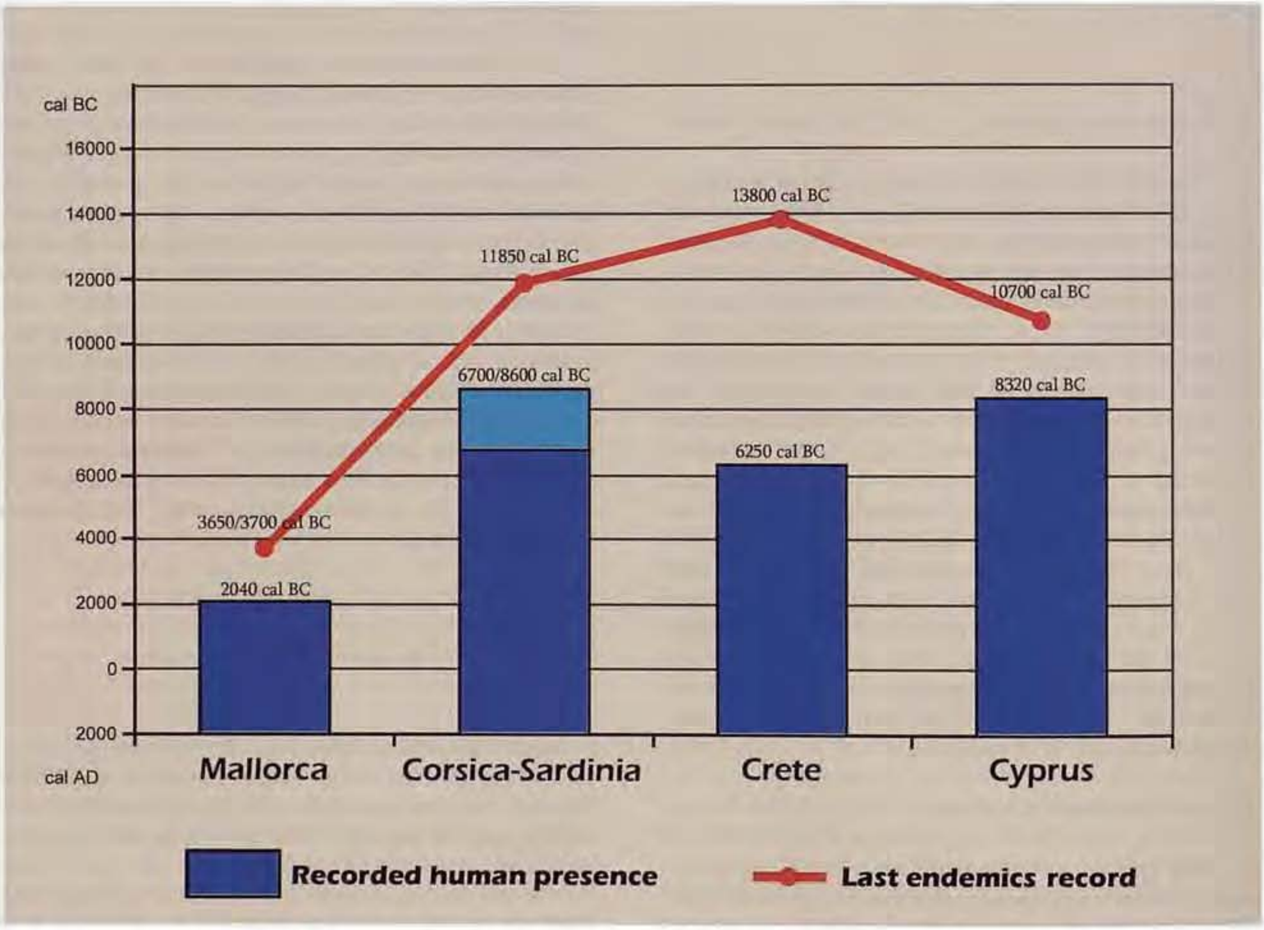

Fig. 1. Graphic comparison of the Mediterranean islands considered here, with the representation of the last available chronological record for **large and medium-sized** endemic mammals and, on the other hand, the period with recorded human presence in such territories.

Fig. 1. *Comparació gràfica de les illes mediterrànies considerades, amb la representació del darrer registre cronològic disponible per als mamífers endèmics de* ***mida gran i mitjana*** *i, d'altra banda, del període amb presència humana documentada a cada territori.*

these species would have taken place between I millennium AD and the beginning of the next one, as a result of the deforestation of their last habitats during Late Antiquity and the Early Middle Ages. In short, the extinctions of the endemic Corsican micro-mammals would be the final point of a gradual recession process motivated by the combined effect of the presence of new competitors and human modification of the environment (Vigne *et al.*, 1997).

Alternatively, a sudden extinction happens in the Gymnesics and Cyprus (the islands with a more intense isolation during the Plio-Pleistocene). Overhunting does not seem to be a key factor affecting the extinction of small sized mammals from Mallorca and Cyprus. Hence, the introduction of new diseases emerges as a possible explanation. This hypothesis bears some similarities with the proposal for extinction of autochthonous small mammals in the Caribbean islands as a result of the introduction of new pathogens. MacPhee & Iturralde-Vinent (2000) suggest the close relationship between the extinction of most of the small mammals from the Antilles, after coexisting with humans for several millennia, and the arrival of rats (*Rattus rattus*) from the Old World, possibly carrying new diseases.

The explanation of such different patterns is a matter for future research. The low-intensity pattern for extinction is applied to the species from islands with faunal incorporations during the Pleistocene, while the sudden extinction pattern corresponds to animals from islands with a much more extended period of isolation. The possibility that the Pleistocene arrival of new terrestrial vertebrates to Corsica-Sardinia (Sondaar, 1987) and Crete (van der Made, 1996) involved some genetic adaptations to the insular endemics, which made them more resistant to mainland pathogens, remains as a hypothesis to be tested.

Dating alone cannot solve the problem of the cause of faunal extinctions, but can be useful to test the different possible explanations (Brook & Bowman, 2002). Given the current impossibility to analyse the Late Quaternary extinctions in the Mediterranean through alternative sources, the use of chronological records constitutes a good approach to focus the event. The possibility that future research records of fossil remains dated to the last moments of species survival and evidence for coexistence with humans will improve our knowledge of the topic and allow us to test the hypotheses here propounded.

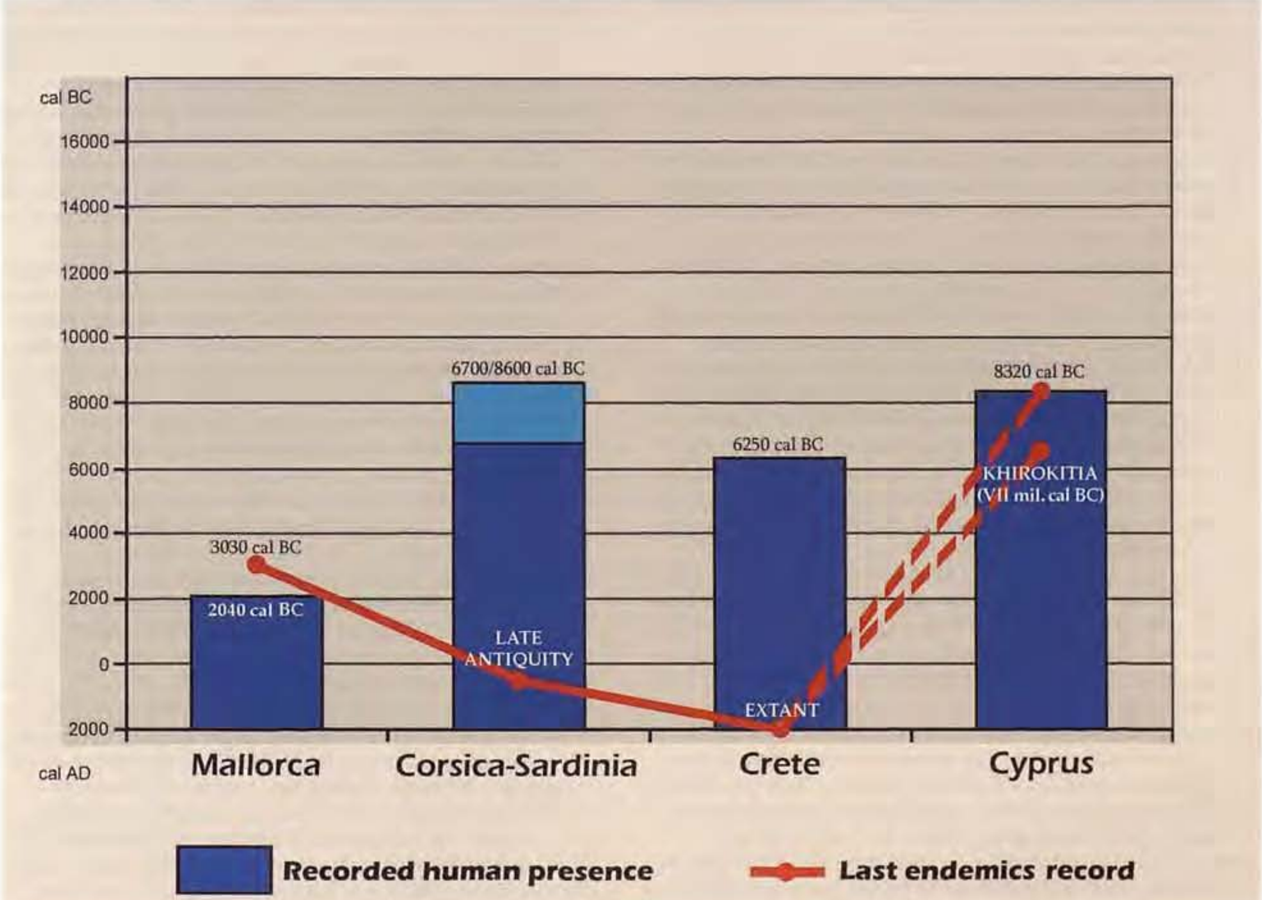

Fig. 2. Graphic comparison of the Mediterranean islands considered here, with the representation of the last available chronological record for **small-sized** endemic mammals and, again, the period with recorded human presence in such territories.

Fig. 2. Comparació gràfica de les illes mediterrànies considerades, amb la representació del darrer registre cronològic disponible per als mamífers endèmics de ***mida petita*** *i, novament, del període amb presència humana documentada a cada territori.*

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First results on the fossilization of Dwarf Hippo skeletal remains from Aghia Napa, Cyprus

Elizabeth T. Stathopoulou

Stathopoulou, E. 2005. First results on the fossilization of Dwarf Hippo skeletal remains from Aghia Napa, Cyprus. *In* Alcover, J.A. & Bover, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 319-324.

Resum

El 2001 la Universitat d'Atenes va començar l'excavació paleontològica d'un jaciment situat a Aghia Napa, Xipre, en col·laboració amb el Departament de Prospeccions Geològiques de Xipre. Aquest jaciment ha lliurat una rica col·lecció de restes esquelètiques d'hipopòtams nans del Quaternari Superior. L'objecte d'aquest treball rau en estudiar l'estat de conservació dels materials com a resultat de la seva fossilització. El material triat prové de les excavacions realitzades els dos darrers anys i consisteix en ossos i dents. La fossilització sembla haver afectat la histologia del material estudiat, mentre que la cristal·lització i la química sembla que l'han afectat menys. En general, els materials no s'han vist molt afectats pels processos causats per la interacció entre les restes del sistema esquelètic i el sòl.

Paraules clau: Fossilització, ossos, Hipopòtams nans, Aghia Napa, Xipre, Quaternari.

Abstract

During the year 2001, Athens University began palaeontological excavations at a site situated in Aghia Napa, Cyprus in collaboration with the Geological Survey Department of Cyprus. This site has given a rich collection of skeletal remains of Dwarf Hippos from the Upper Quaternary. The object of this paper is to study the state of preservation of the material as a result of fossilization. The material chosen was derived from the excavations realized during the last two years and consists of a number of bones and teeth. Fossilization seems to have mostly affected the histology of our material, while the crystallinity and the chemistry are less affected. In general our material has not been strongly affected by the procedures caused by the interaction of the system skeletal remain-soil.

Keywords: Fossilization, bones, Dwarf Hippopotamus, Aghia Napa, Cyprus, Quaternary.

Introduction

The site

The fossiliferous *Hippopotamus* locality of Aghia Napa was formed when the roof of a natural cave-shelter collapsed on a bone bearing layer. The first excavations at the Aghia Napa locality began in June 2001. It was the first scientifically controlled palaeontological excavation to be realized in Cyprus by a Greek-Cypriot palaeontological team. Since, 4 excavation periods of 2 weeks each have been completed and have brought to light more than 5000 fragmented or complete bones. Eventually, it became possible to uncover a very rich, mostly undisturbed fossiliferous layer that was more than one-meter thick. This layer was full of skeletal remains in excellent state of preservation.

The site includes bones from an endemic hippopotamus that lived on Cyprus during the Upper Quaternary. The first dating attempts by the method C^{14} were negative due to the lack of collagen. (Maniatis, 2003; pers. com.). Absolute dating by other methods is still expected.

More than 50 animals are already documented and a significant percentage of juveniles are present (6-7%). Biometrically the material belongs to one size group, which belongs to the known group of the endemic hippopotamus of Cyprus that is the *Phanourios minor* Group (Boekschoten & Sondaar, 1972; Houtekamer & Sondaar, 1979).

The accompanying fauna includes micromammals, birds and a small carnivore still not completely prepared and studied. A few deer phalanges are present but up to now they have only been found in the disturbed layers.

Disturbance of human origin is found in various areas of the shelter but is very recent. The site has been partly excavated without a scientific methodology about 60-70 years ago, causing significant and irregular disturbance. Otherwise, there is still no evidence to support an extinction of the hippopotamus due to humans during the Late Pleistocene or the earlier stages of Holocene, as it has been suggested from Aetokremnos (Simmons, 1999, 2001).

Fossilization

Fossilization, which is better described as diagenesis, is a highly complex phenomenon that depends on a number of geochemical parameters. It includes all post mortem alterations that eventually lead to the preservation of skeletal material through geological time. It has been intensely studied during the last decades (Piepenbrink, 1989; Hedges & Millard, 1995; Stathopoulou, 2000; Stathopoulou & Theodorou, 2001; Hedges, 2002).

Diagenesis can be recognized by a number of alterations that occur at different stages from the time of death and may concern the organic component of bone, the inorganic mineral fraction in means of recrystallization, uptake of certain cations, ionic exchange etc and the infilling with secondary mineral phases. Microbial activity is also very important, since it seems to lead to the gradual degradation of bone, which is easily interpreted by the alteration or the loss of histological detail.

All hard tissues found in fossils (bone, enamel, dentine) consist of a heterogeneous, complicated dynamic system which consists of a dense framework of organized fibrils of collagen and a type of biological apatite (poorly crystallized hydroxylapatite ($Ca_{10}(PO_4)_6(OH)_2$) which also contains a certain amount of carbonate and thus is called carbonate hydroxylapatite (Posner, 1985; Person *et al.*, 1995). This fact makes it obvious that in order to study diagenesis one must look into all the mentioned procedures in turn and in detail.

The object of this paper is to study the state of preservation of the material as a result of fossilization.

MATERIAL AND METHODS

The material chosen was derived from the excavations realized during the last two years and consists of ten long bones (parts or fragments of femora, tibias, humeri, etc.: AN-10 up to AN-19) and six teeth (two molars: AN-1, AN-4, two canines: AN-2, AN-5, two incisors: AN-6, AN-7). Some of the bone samples may be seen in Fig. 1.

Fig.1. Some of the dwarf hippo bones used in this study.

Fig. 1. Alguns dels ossos d'hipopòtams nans emprats a aquest estudi.

In this paper emphasis is given to the preservation of the internal microstructure of the material, the observation of which was realized via optical and scanning microscopy. Thin sections as well as small fragments of compact bone were prepared in order to be observed by polarizing light microscopy and a JEOL JSM-5600 scanning electron microscope.

Some first information concerning the mineralogical and chemical composition was also reached by X-ray Diffractometry (SIEMENS D500 Diffractometer with secondary graphite monochromator and CuKa radiation) and X-ray microanalysis (OXFORD LINK™ ISIS™ 300-Energy Dispersive X-Ray microanalysis -EDX) while the presence of secondary mineral phases was looked into as well.

The crystallinity index was determined by the XRD technique according to the method proposed by Person *et al.* (1995), in order to make some first speculations on how intense dissolution and recrystallization has been while other important ratios such as Ca/P were estimated to assist us conclude on the fossilization status of our material.

RESULTS AND DISCUSSION

Histology

Studying the bone samples through a polarizing microscope, one may observe that the characteristic features of bone (osteons, intersistial and internal-external circumferential lamella, cement lines, lacunae and canaliculi) seem to be quite destroyed with areas of healthy osteons found mostly around the bone marrow cavity. Four zones seem to be present from the marrow cavity outwards. 1. Area of healthy osteons with all characteristic features present (Fig. 2). 2. Area of osteons with few obvious features (Fig. 3, 4). 3. Area of totally destroyed microstructure. 4. Area with remains of osteons. These areas are not present in all samples in this pattern but in general one could say that the histology is quite affected by diagenetic procedures.

The histology index measured according to Hedges & Millard (1995) varies from 1-2 (0: no original histology visible, 5: <5% affected, histology identical to fresh bone).

Observation with the SEM revealed further details concerning microstructure where it was still present, such as the lacunae and canaliculi and the structure of lamella, the network of the haversian canals, their internal surfaces, the crystals that are found within etc. We were able to observe generally few healthy areas of bone (Fig. 5, 6) and most areas revealed remnants of basic microstructure, mostly due to the very intense microbial activity. The usual image of these bones under the SEM was that of a complicated network of voids, tunnels and areas of intact bone.

The microstructure of dentine and enamel does not show any alterations due to diagenesis as expected and all characteristic features are present. One may observe the Hunter-Schreger lines in enamel (Fig. 7, 8), which characterize hippo teeth and also the enamel prisms and their characteristic patterns (Fig. 9). Dentinal tubules are seen in dentine with no evidence of diagenetic alterations concerning histology (Fig. 10, 11).

Fig. 2 Area of bone with well-preserved osteons, as observed via optical microscopy.

Fig. 2. *Àrea d'os amb osteons ben conservats, tal com s'observen mitjançant microscopia òptica.*

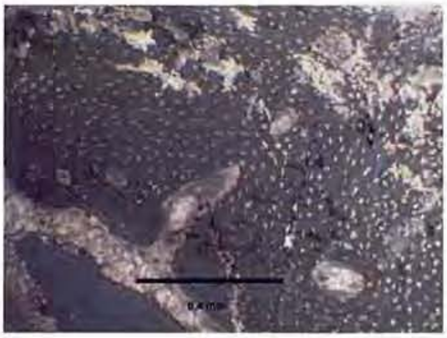

Fig. 3. Lacunae as seen in healthy osteons (optical microscopy).

Fig. 3. *Lacunae tal com s'observen als osteons sans (amb microscopia òptica).*

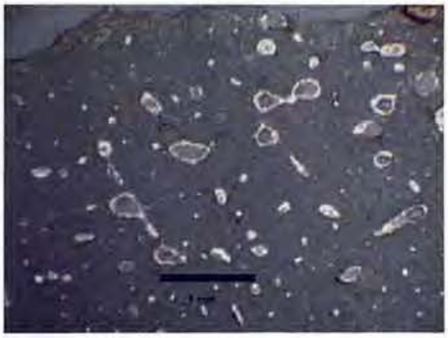

Fig. 4. Area of compact bone with only the haversian channels present as it was seen through the optical microscope.

Fig. 4. *Àrea d'ós compacte amb només els canals haversians present, tal com s'observa mitjançant microscopia òptica.*

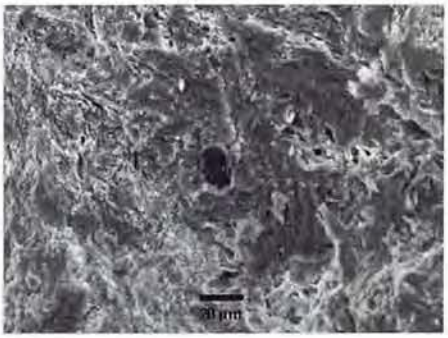

Fig. 5. One of the osteons to be seen under the SEM.

Fig. 5. *Un dels osteons a veure mitjançant el SEM.*

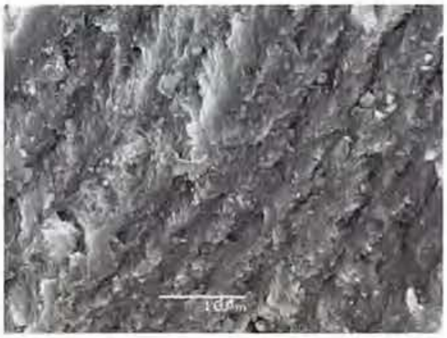

Fig. 6. Lamella as seen in healthy osteons under the SEM.

Fig. 6. *Lamella tal com es veuen als osteons sans mitjançant el SEM.*

Microbial attack is a common phenomenon in fossil bones and is produced by a variety of microorganisms (bacteria, cyanobacteria, fungi and protozoans of amoebic type) (Hackett, 1981; Soudry & Nathan, 2000). Bone tunneling is commonly considered as the result of the dissolution of the mineral and organic matrices of the bone by fungal metabolic acids (Piepenbrink, 1989).

Microbial activity is present in all bone samples but not in any tooth samples. This activity is found as voids and canals of relatively small diameter (about 0,5 microns). The activity is found in the form of small gatherings or total coverage of the samples (Figure 12-14), while one may see early stages of activity as well as totally destroyed areas or secondary activity amongst the voids of a previous occurrence. The organisms that have caused the characteristic images are still not well defined, but the size of the produced voids leads us to believe that they could be bacteria or fungi.

Infilling of voids

The only secondary mineral phase present in voids of our samples is Calcite. It is found in all bone samples, in some dentine samples (from canines and small amounts in molars) but in no enamel samples. Calcite is found in fractures, voids left by the decomposition of organic matter, such as the haversian canals, the lacunae etc, the marrow cavity. The crystals differ according to the size and shape of the void-fracture in which they are found.

Dissolution and recrystallization

Crystallinity refers to the degree of order within the crystal lattice. A quantitative estimation of crystallinity for bone apatites from their XRD spectra is given by the crystallinity index (C.I.), which was estimated according to Person *et al.* (1995). The C.I. of the biological apatites studied vary between 0,13 and 1,36 (Table 1, 2).

Fresh bone theoretically gives 0,00. The closest values to that are given by our dentine samples, while bone lies between the value of fresh bone and the C.I. of enamel samples. The bone values vary between 0,17 and 0.5 and give an average of 0,3, dentine does not seem to differ amongst the different types of teeth and gives an average of 0,15, while enamel seems to present higher values in canines than molars. Enamel consists of a totally crystalline apatite and gives an average of 1,2.

Chemical Composition changes

The bone and teeth material consist of Carbonate hydroxylapatite and there are no significant signs of F present. There is a differentiation of the Ca/P ratios, and possible ionic exchanges with the environment have also occurred. The average chemical composition of all samples can be found in Table 3 & 4. One may observe that the most common elements apart from Ca and P are Si, S and Na, K. Enamel is also richer in Cl. The Ca/P ratio for fresh bone is 2,14 and for the mineral Hydroxylapatite 2,16. The ratios measured in our bone samples are quite higher than 2,14; varying between 2,38 and 2,80 and giving an average of 2,5. Dentine gave a Ca/P of 2,39 and enamel an average of 2,13, which is very close to fresh bone.

	AN-10	AN-11	AN-12	AN-13	AN-14	AN-15	AN-16	AN-17	AN-18	AN-19	AVERAGE
C.I. (bones)	0.50	0.30	0.35	0.30	0.29	0.26	0.17	0.32	0.27	0.25	0.3

Table 1. Average Crystallinity indexes of studied bone samples.

Taula 1. *Indexs de cristal·linitat promig de les mostres estudiades d'ossos.*

CONCLUSIONS

Bone shows serious diagenetic changes, especially in terms of histology. Microbial activity is abundant and has caused the partial destruction of its structure. Enamel is the hardest tissue and shows great endurance during fossilization. On the other hand, dentine is more like bone and more vulnerable to diagenetic procedures. Often there is microbial activity in dentine, similar to bone, though not in our case (Stathopoulou *et al.*, in press). Enamel has not shown any such forms.

In means of crystallinity enamel is closest to the mineral hydroxylapatite. On the contrary dentine has behaved more like bone, since it is closer to bone concerning its mineral and organic contents and crystal size.

Contamination of bone in the ground takes both physical and chemical forms. The porous structure of bone tissue is susceptible to infiltration by foreign materials. The contaminants result from either precipitation from groundwater or physical incorporation of materials in the bone. Ca, for example can be introduced by the precipitation of Calcite in ground water. Inclusions, such as quartz are included in bone as solid grains. Na and Mg are an associated pair that is present due to metabolic and dietary factors and tend to leach out through time while Al, Mn, Fe, Mg may come from enrichment from soil contaminants (Price *et al.*, 1992). The average Ca and P values in most of our bone samples are higher and lower than those in fresh bone respectively and their ratio could indicate an increase in Ca due to the intrusion of Calcite in the bone voids or/and a loss of P perhaps due to its depletion.

Fig. 7. Longitudinal section of an incisor, observed through optical microscopy. One may observe the Hunter-Schreger lines.

Fig. 7. *Secció longitudinal d'una incisiva, observada mitjançant mi-croscopia òptica. Es poden observar les línies de Hunter-Schreger.*

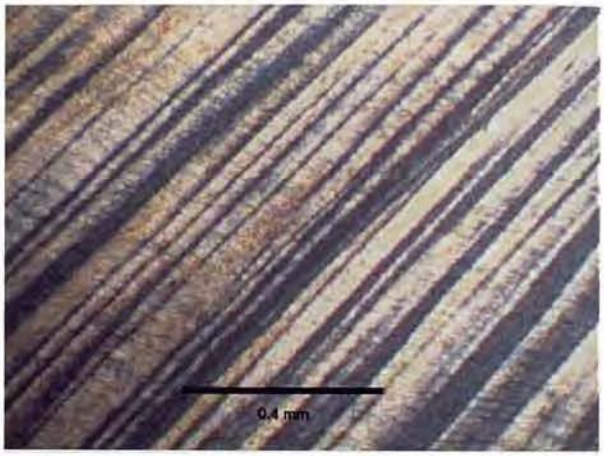

Fig. 8. Transverse section of an incisor (optical microscopy). One may observe the Hunter-Schreger lines in the enamel.

Fig. 8. *Secció transversal d'una incisiva, observada mitjançant microscopia òptica. Es poden observar les línies de Hunter-Schreger a l'esmalt.*

Fig. 9. Enamel prisms as they appear in a transverse section of a molar (SEM images).

Fig. 9. *Prismes d'esmalt tal com apareixen a una secció transversal d'un molar (imatges del SEM).*

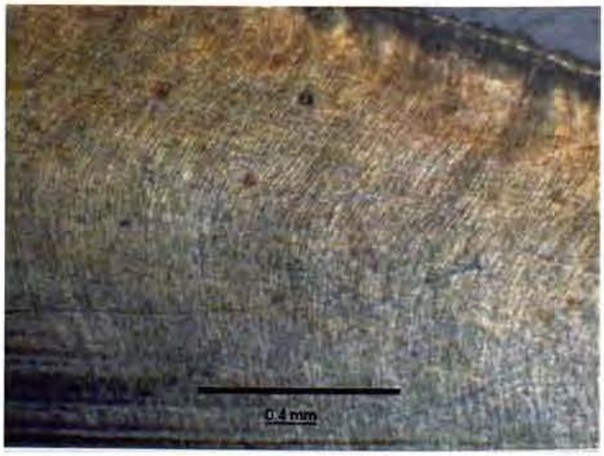

Fig. 10. Longitudinal section of a canine, one may observe the primary curvatures of the dentinal tubules (optical microscopy).

Fig. 10. *Secció longitudinal d'una canina. Es poden observar les corbatures primàries dels túbuls dentinals (mitjançant microscopia òptica).*

C.I. *average*	molars	canines	incisors	Average value
dentine	0.16	0.16	0.13	*0.15*
enamel	1.05	1.36	Not measured	*1.2*

Table 2. Average Crystallinity indexes of studied dentine and enamel samples.

Taula 2. Index de cristal·linitat promig de les mostres d'esmalt i dentina estudiades.

Most bone and dentine voids are filled with Calcite, making the material compact and strong.

As we have already mentioned this is only a preliminary study and further work is to be realized in the near future. Based on these first results, one may say that diagenesis in Aghia Napa appears mostly as a destruction of histology in bones, and a few changes in the chemistry of our material and the crystallinity. Compared to bone material from various Greek sites one may observe that the C.I. and the Ca/P are quite lower. This means that the material from Aghia Napa is less crystalline and closer to fresh bone, and less affected by Ca increase and P depletion. In few words, less affected by the procedures caused by the interaction of the system skeletal remain-soil.

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Fig. 11. Dentinal tubules as they are seen in a fragment of tooth dentine (SEM image).

Fig. 11. Túbuls de dentina com es veuen a un fragment de dentina de dent (miatge SEM).

Fig. 12. Microbial activity in bone (SEM image).

Fig. 12. Activitat microbiana a un os (imatge SEM).

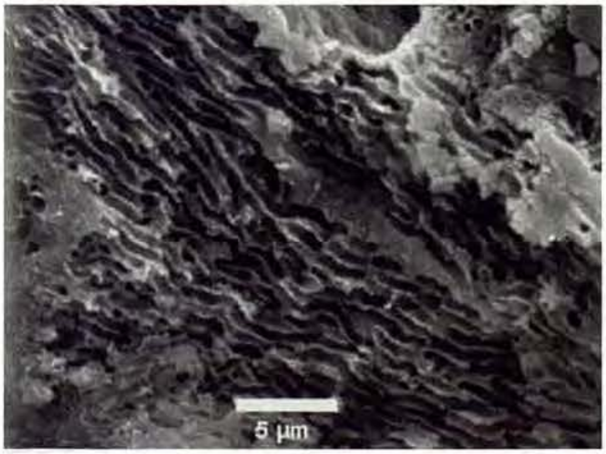

Fig. 13. Microbial activity, found as canals (SEM image).

Fig. 13. Activitat microbiana, trobada com canals (imatge SEM).

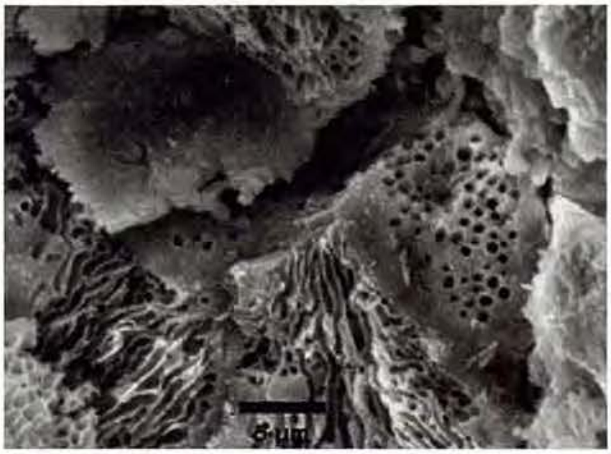

Fig. 14. Microbial activity as a combination of round voids and canals (SEM images).

Fig. 14. Activitat microbiana com una combinació de buits arrodonits i canals (imatges SEM).

	AN-10	AN-11	AN-12	AN-13	AN-14	AN-15	AN-16	AN-17	AN-18	AN-19	AVERAGE
O	38.7	37.7	37.0	36.5	38.9	39.3	39.6	39.8	38.8	39.3	*38.6*
Na	0.1	0.4	0.1	-	0.3	0.6	0.5	0.1	0.5	0.5	*0.3*
Mg	0.1	-	-	-	-	0.1	0.2	0.1	0.2	-	*0.1*
Al	-	-	-	-	0.2	0.1	0.2	0.1	0.3	0.1	*0.1*
Si	0.3	0.2	0.4	0.2	0.3	0.2	0.3	0.2	0.6	0.3	*0.3*
P	17.7	17.5	17.8	17.6	17.3	16.4	16.9	17.2	15.3	16.2	*17.0*
S	0.2	0.4	0.2	0.4	0.3	0.2	0.1	0.1	0.3	0.3	*0.3*
K	0.1	0.1	0.2	-	-	-	0.1	0.1	0.1	0.1	*0.1*
Cl	-	-	-	-	-	-	-	-	0.1	0.1	*-*
Ca	41.9	41.8	43.0	42.8	41.3	42.7	42.0	41.9	43.1	42.7	*42.3*
Ca/P	2.38	2.39	2.42	2.44	2.39	2.6	2.49	2.44	2.8	2.64	*2.5*

Table 3. Average Chemical composition and Ca/P ratios of studied bone samples. Values in percentages.

Taula 3. *Composició química promedi i proporcions Ca/P de les mostres estudiades d'ossos. Dades expressades en percentatges.*

	dentine				enamel		
	molars	*canines*	*incisors*	*AVERAGE*	*molars*	*canines*	*AVERAGE*
O	42.24	41.8	41.5	*41.8*	42.5	40.2	*41.7*
Na	0.4	0.5	0.3	*0.4*	0.5	0.5	*0.5*
Mg	<0.1	-	-	*<0.1*	0.1	-	*<0.1*
Al	<0.1	-	0.1	*<0.1*	0.1	-	*<0.1*
Si	0.2	-	0.1	*0.1*	0.2	0.2	*0.2*
P	16.4	16.1	16.6	*16.4*	17.9	18.0	*18.0*
S	0.3	0.3	0.3	*0.3*	0.2	0.1	*0.2*
Cl	-	0.2	-	*<0.1*	0.3	0.3	*0.3*
K	-	-	<0.1	*<0.1*	0.1	0.2	*0.2*
Ca	39.3	38.3	39.6	*39.2*	37.7	39.4	*38.0*
Fe	-	-	-	*-*	0.1	-	*<0.1*
Ca/P	2.4	2.39	2.39	*2.39*	2.1	2.18	*2.13*

Table 4. Average Chemical composition and Ca/P ratios of studied tooth samples. Values in percentages.

Taula 4. *Composició química promig i proporcions Ca/P de les mostres estudiades de dents. Dades expressades en percentatges.*

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THE POSTCRANIAL OF THE DEER *HOPLITOMERYX* (PLIOCENE; ITALY): ANOTHER EXAMPLE OF ADAPTIVE RADIATION ON EASTERN MEDITERRANEAN ISLANDS

Alexandra VAN DER GEER

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Resum

Durant el Pliocè, a l'illa de Gargano (costa sudest d'Itàlia) va evolucionar una fauna vertebrada altament endèmica. Aquesta fauna comprenia, entre d'altres, el eriçó gegant *Deinogalerix*, l'òliba gegant *Tyto gigantea*, el hàmster gegant *Hattomys*, i el cèrvol *Hoplitomeryx* amb cinc banyes i canins superiors en forma de sabre (tipus mòsquid). Els materials esquelètics d'*Hoplitomeryx* formen un grup heterogeni, amb quatre classes de talla; dintre de les classes de talla poden estar presents diferents morfotipus. Totes les classes de talla comparteixen els mateixos trets típics d'*Hoplitomeryx*. Aquests són: una banya nasal central i un parell de banyes orbitals en punxa, canines sortints, fusió completa del navicocuboide amb el metatarsià, acanaladura metatarsiana distalment tancada, astràgal sense costats paral·lels, i una ròtula allargada. Les dife-rents classes de talla es troben repartides de forma igual a les fissures excavades, i a llavors no es poden considerar cronotipus. La hipòtesi d'un arxipèlag consistent en diferents illes on a cada una d'elles hi hagués un morfotipus no s'ha pogut confirmar.

La situació de diferents morfotipus coexistint a una illa té un paral·lel amb *Candiacervus* (Pleistocè, Creta, Gràcia). Les opinions sobre la seva taxonomia són diverses, i actualment prevaleixen dos models: un gènere per a vuit morfotipus o, alternativament, dos gèneres per a cinc espècies. El segon model només es basa en les proporcions dels membres, però aquestes són característiques taxonòmiques invàlides per als endemismes insulars, ja que canvien sota la influència de factors ambientals diferents dels continentals. També a *Hoplitomeryx* els morfotipus difereixen en les proporcions dels membres, però en aquest cas resulta improbable que provinguin de diferents ancestres, ja que en aquest cas els ancestres haurien d'haver compartit els trets hoplitomerícids típics. La morfoesfera d'*Hoplitomeryx* és massa coherent com per suposar dos o més ancestres, i indica un origen monofilètic de tots els morfotipus.

En lloc d'això, la gran variació s'explica com a un exemple de radiació adaptativa, que va començar quan l'ancestre miocènic va colonitzar l'illa. L'espectre de nínxols buits degué promoure la seva radiació en diferents tipus tròfics, conduint a una diferenciació d'*Hoplitomeryx*. La manca compartida de mamífers depredadors grans i l'oferta limitada d'aliment a tots els nínxols degué promoure el desenvolupament de trets derivats secundaris a totes les classes de talla.

Paraules clau: Gargano, endemisme, *Candiacervus*, *Cervus astylodon*, fauna de *Microtia*.

Summary

During the Pliocene a highly endemic vertebrate fauna evolved on Gargano Island (south-east coast of Italy), comprising amongst others the giant hedgehog *Deinogalerix*, the giant barn owl *Tyto gigantea*, the giant hamster *Hattomys*, and the prongdeer *Hoplitomeryx* with five horns and sabrelike ('moschid' type) upper canines. The *Hoplitomeryx* skeletal material forms a he-terogenous group, containing four size groups; within the size groups different morphotypes may be present. All size groups share the same typical *Hoplitomeryx* features. These are: one central nasal horn and a pair of pronged orbital horns, protruding canines, complete fusion of the navicocuboid with the metatarsal, distally closed metatarsal gully, a non-parallel-sided astragalus, and an elongated patella. The different size groups are equally distributed over the excavated fissures, and are therefore not to be considered chronotypes. The hypothesis of an archipelago consisting of different islands each with its own morphotype cannot be confirmed.

The situation with several co-existing morphotypes on an island is paralleled by *Candiacervus* (Pleistocene, Crete, Greece). Opinions about its taxonomy differ, and at present two models prevail: one genus for eight morphotypes, or alternatively, two genera for five species. The second model is based upon limb proportions only, but these are invalid taxonomic features for island endemics, as they change under influence of environmental factors that differ from the mainland. Also in *Hoplitomeryx* the morphotypes differ in limb proportions, but here different ancestors are unlikely, because in that case they all ancestors must have shared the typical hoplitomerycid features. The morphosphere of *Hoplitomeryx* is too coherent to assume two or more different ancestors, and indicates a monophyletic origin of all morphotypes.

The large variation is instead explained as an example of adaptive radiation, starting when the Miocene ancestor colonized the island. The range of empty niches promoted its radiation into several trophic types, yielding a differentiation in *Hoplitomeryx*. The shared lack of large mammalian predators and the limited amount of food in all niches promoted the development of secondary features in all size groups (apomorphies).

Keywords: Gargano, endemism, *Candiacervus*, *Cervus astylodon*, *Microtia* fauna.

INTRODUCTION

The Gargano fauna

Once upon a time, the five-horned deer *Hoplitomeryx matthei* Leinders, 1984 (Fig. 1) lived on the Gargano Island, now part of the east coast of South Italy. Its fossilized remains were retrieved in the late sixties and subsequent years (Freudenthal, 1971) from reworked reddish, massive or crudely stratified silty-sandy clays (*terre rosse*), which partially fill the paleo-karstic fissures in the Mesozoic limestone substrate and that are on their turn overlain by Late-Pliocene-Early Pleistocene sediments of a subsequently marine, shallow water and terrigenous origin (Abbazzi *et al.*, 1996). In this way a buried paleokarst (*sensu* Bosak *et al.*, 1989) originated. The fauna from the paleokarst fillings is known as *Microtia* fauna after the endemic murid of the region. Later, after the regression and continentalization of the area, a second karstic cycle started in de late Early Pleistocene, the neokarst, which removed part of the paleokarst fill (Abazzi *et al.*, 1996). In this paper, I focus only on the *Microtia* fauna from the Early Pliocene paleokarst fillings.

Hoplitomeryx was not the only inhabitant of the Early Pliocene palaeoisland; many remains of other vertebrates have been found in the paleokarst fills as well. The other mammals that have been identified and described can be divided into genera and species that are truly endemic to the Gargano only, and species that are more wide-spread. The true endemic genera are the soricid *Deinogalerix* Freudenthal, 1972 with five species, amongst which the giant *D. koeningswaldi* with a skull length of approximately 20 cm (Freudenthal, 1972; Butler, 1980), the murid *Microtia* Freudenthal, 1976, which appears to be the only burrowing murine genus known till now (Parra *et al.*, 1999), and which radiated into at least three lineages of different size, and of which the largest, *M. magna*, has a skull length of about 10 cm (Freudenthal, 1976), the huge glirid *Stertomys laticrestatus* Daams & Freudenthal, 1985, and the hamster *Hattomys* Freudenthal, 1985, with three species. True endemic species, belonging to wider spread genera, are the otter *Paralutra garganensis* (Willemsen, 1983) and the ochotonids *Prolagus imperialis* (Mazza, 1987) and *P. apricenicus* (Mazza, 1987), of which the largest, *P. imperialis*, is larger than any other known *Prolagus* species (Mazza, 1987). The mammals that are also found in other regions are the arvicolid *Apodemus gorafensis* (Ruiz Bustos *et al.*, 1984), and the three hamsters *Cricetulodon*, *Megacricetodon*, *Cricetus* (Freudenthal, 1985).

Fig. 1. The deer *Hoplitomeryx matthei* Leinders, 1984 is characterised by its five horns (one nasal horn and two pronghorns on each orbit). Its fossils are found in the *terre rosse* of the paleokarst fissures of the Gargano (South Italy), associated with other faunal elements, known as the *Microtia* fauna.

Fig. 1. El cèrvol Hoplitomeryx matthei *Leinders, 1984 es caracteritza per tenir cinc banyes (una banya nasal i dues punxes sobre cada òrbita). Els seus fòssils es troben a bretxes paleocàrstiques vermelloses de Gargano (Sud d'Itàlia), associats amb altres elements faunístics, coneguts com a la fauna de* Microtia.

Also the sky above the Gargano was not empty, and was filled with at least the following birds (Ballmann, 1973, 1976): the endemic eagle *Garganoaetus* Ballmann, 1973 with three species, the barn owl *Tyto* with three species, of which the largest, the endemic *T. gigantea* (Ballmann, 1973), was about twice as large as the living *Bubu bubo*, a true owl possibly of the genus *Strix*, and the Eurasian pigeon *Columba omnisanctorum* and gull *Apus wetmorei*.

The age of the Gargano

The age of these fossiliferous sediments is still under discussion (Abbazzi *et al.*, 1996; Zafonte & Masini, 1992; De Giuli *et al.*, 1986). The first datation of the *terrae rossae* was based upon a combination of stratigraphy and microfauna. In these studies, the calcarenite overlying the karst system is considered to have been deposited during the Tortonian, or Vallesian - early Turolian Mammal Age (Freudenthal, 1971, 1976; D' Alessandro *et al.*, 1979), and therefore the fissure deposits were supposed to range from late Vallesian (MN 10) to early Turolian (MN 11), which was confirmed by the microfaunal evolutionary stage in the view of Freudenthal (1971, 1972, 1976). A younger age than in first instance is assumed by De Giuli & Torre (1984a, 1984b) and De Giuli *et al.* (1985, 1986, 1987), who propose the Late Turolian (Messinian, MN 13), or early Ruscinian (MN 14) as period during which the endemic fauna evolved. Freudenthal (1985) also adjusts his earlier estimation to the Messinian, on the basis of the cricetids. Other studies are based exclusively on faunal elements, such as Ballmann (1973), who gives a post-quem age of Late Aragonian, MN 7/8 on the basis of avifauna. De Giuli *et al.* (1986) give a post-quem date of latest Turolian (MN 13) on the basis of the occurrence of a true *Apodemus (A. gorafensis)*, a widely distributed taxon in the Early Pliocene onwards (Martín Suarez & Mein, 1998); the first *Apodemus* occurs in the Eastern Mediterranean at the beginning of the Late Miocene (Koufos, 2001). De Guili *et al.* (1985) consider Monte Gargano as part of a larger structural unit, the so-called Apulo Dalmatic Realm, which gradually got disrupted and submerged from the earliest Miocene to the Early Pleistocene, with a temporary major regression in the earliest Pliocene or Messinian, and a smaller, local regression in the Middle Pliocene (*Globorotalia* gr. *crassaformis* zone; Valleri, 1984), documented by field geological data, which resulted in the almost complete submersion of the foreland in the Late Pliocene - Early Pleistocene (De Giuli & Torre, 1984a; De Giuli *et al.*, 1985; Valleri, 1984). During the Pleistocene, the regional uplift caused the emergence and continentalization of the foreland (Ricchetti *et al.*, 1992). The Messinian-earliest Pliocene regression is considered probably the time of the last large fauna immigration (Torre, 1986). A detailed biogeostratigraphic study is made by Abbazzi *et al.* (1996), who define eight units, ranging from late Miocene to Middle Pleistocene. The oldest unit (1) is a facies of residual red silty clays, *terre rosse*, which are the fillings of the paleokarst. The next five units are breccia facies, with successive *Globorotalia punticulata* and *G. inflata*, of which the second is rich in mollusks, including marine taxa. The next unit is terrigenous, and consists of sands and pelites with marine mollusks. The last, eight unit is again a filling, now of the neokarst, represented by alternating finely stratified sands and pelites. Unit 1, containing the *Microtia* fauna with endemic taxa, is assigned a Late Miocene - Early Pliocene age, whereas Unit 7 coincides with the Plio-Pleistocene boundary; Unit 8 contains a late Villafranchian fauna, and is therefore assigned a late Early Pleistocene age. During the neokarst cycle, most of the fillings of the Paleokarst were washed out and/or reworked (Abbazzi *et al.*, 1996), which makes proper stratigraphic and evolutionary approaches extremely risky. Unit 1 is found in many sites spread over the region, whereas Unit 8 is constricted to Pirro Nord and Cava Dell' Erba (community of Apricena), the area where F16 and F17 are assigned to the Unit 1 finds. It is not completely clear if the marine Tortonian sediments effectively overlie the fossiliferous horizon, and furthermore, the study is local (quarries between Apricena and Poggio Imperiale), and Abbazzi *et al.* (1996) strongly advise not to extrapolate the stratigraphic data to a larger scale, for example the entire Gargano area, due to the complexity of the stratigraphic relationships in the Gargano, in which extremely dynamic paleogeographic conditions were governed by structural activity. In other words, the only observation that remains valid is that the Unit 1 endemic *Microtia* fauna predates the Unit 8 latest Villafranchian fauna, but the absolute age is still unclear.

Diagnosis of *Hoplitomeryx*

Leinders (1984) described the cranial and dental material of the Gargano artiodactyls, and established a new cervid family Hoplitomerycidae, a new genus *Hoplitomeryx*, and a new species *matthei*. The most striking characteristic of the Hoplitomerycidae is the presence of five horns (Fig. 1), of which one projects between the eyes on the caudal part of the nasals. The other four arise in pairs above the orbit, and can be considered pronged horns, hence the name prongdeer was suggested (Van der Geer, in press). Other characters are a large bulla tympanica, a non-pneumatized skull roof, the large, flaring and sabre-like upper canines, lack of P1 and P2 inf., a non-molarized P4 inf., a variable degree of hypsodonty, and an M3 inf. with large, bicuspid third lobe. *Hoplitomeryx* had a short, massive snout, more anteriorly positioned orbits, and a double lacrimal orifice on the rim of the orbit. Some artiodactyl material (amongst others, an orbital horncore, a fused metatarso-cubonavicular, and some molars) discovered in the Turolian (Late Miocene) Scontrone fauna (Maiella, Abruzzo National Park, Central Italy) has also been attributed to *Hoplitomeryx* (Mazza & Rustioni, 1996; Rustioni *et al.*, 1992).

The postcranial elements of *Hoplitomeryx* have not been described yet in full detail, but they are remarkably homogenuous in their morphology. They show many typical endemic features, such as the fusion of the navico-cuboid with the metatarsus, described as a functional adaptation by Leinders & Sondaar (1974), shortening of some metapodials as described for *Myotragus* (Sondaar, 1977) and in one case the fusion of both malleoli with the tibia, which has till now been reported only for one other species: *Myotragus* (Bover, 2003; Bover *et al.*, this volume). Other diagnostic features are the non-parallel sided astragalus (Van der Geer, 1999) and the extremely elongated patella (Van der Geer, in press); these are explained as a return to a less derived condition, favored by the absence of predators and the lack of abundant food (Van der Geer, in press).

The size of the *Hoplitomeryx* postcranial material is on the contrary less homogenuous, and seems to form a heterogenous group, containing at least four size classes. The sizes are not restricted to specific fissures, and an equally distribution over the fissures instead seems to be more the case. In most fissures, more than one size is represented. Due to the often fragmentary character of the material, and the relative scarcity of the material, it is at the moment not possible to recognize all size classes in each limb element, in particular the largest sizes. Large specimens are always incomplete, and as a remarkable detail, the largest size is represented by juveniles only. The total number of size groups is therefore a combination of the groups defined per limb element,

In this article only the metapodals are described in more detail, as an illustration of the process of adaptive radiation, which is supposed to be the underlying drive behind the speciation of *Hoplitomeryx*. The other limb bones follow the same pattern, and will be dealt with in a future paper.

Explanation of increased size range

The increased size range with separate size groups as observed in endemic insular taxa is usually explained in terms of allopatric speciation, which implies the existence of an archipelago, e.g. the famous Darwin's Finches on the Galápagos Islands. The Pliocene island Monte Gargano (Italy) has been considered part of a larger archipelago (Apulo-Dalmatic Realm) in relation to the micromammals (De Giuli & Torre, 1984; De Giuli *et al.*, 1985, 1987) and the ochotonid *Prolagus* (Mazza, 1987) to explain the presence of several sister taxa that evolved in a relatively short time. Another explanation is the occurrence of more than one invasions, e.g. as suggested for the deer *Candiacervus* on Crete (Kuss, 1975; De Vos, 1984, however cf. De Vos, 1996, 2000; Capasso Barbato, 1992; Caloi & Palombo, 1996) and the rodents on the Monte Gargano (Freudenthal, 1976).

In the archipelago hypothesis, it does not explain sufficiently why sister taxa are found together on one and the same island. In the multiple invasion hypothesis, it is no explanation as to where and why this new sister taxon evolved. In both cases it is not clear why the sister taxa wait with migration untill full speciation has taken place.

What we see is only the end result, consisting of a range of taxa, closely related; when the variety is large and the genetic distance small, the term flock is used (e.g. Greenwood, 1974; Echelle & Kornfield, 1984, and references therein). The radiation into morphotypes can be compared to the medium scale, medium term radiations (e.g. the radiation of the antlered deer in Eurasia), and on its turn with the large scale, long term radiations (e.g. the radiation of the marsupials in South America and Australia; Woodburne & Case, 1996). The main driving force in all cases is the urge to occupy free ecological niches. The resulting speciation can be explained best in terms of sympatric speciation (De Vos & Van der Geer, 2002).

MATERIAL

Hoplitomeryx

For the description are used: 47 adult metatarsals, 6 juvenile metatarsals, 55 adult metacarpals, all RGM numbers; stored at Naturalis, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; 3 unnumberd metatarsals (field numbers P77/4, F8 and 25.9.83 Fina F9), and 1 unnumbered metacarpal (field number P77/4), all four stored at Museum of Geology and Paleontology, University of Florence, Italy)

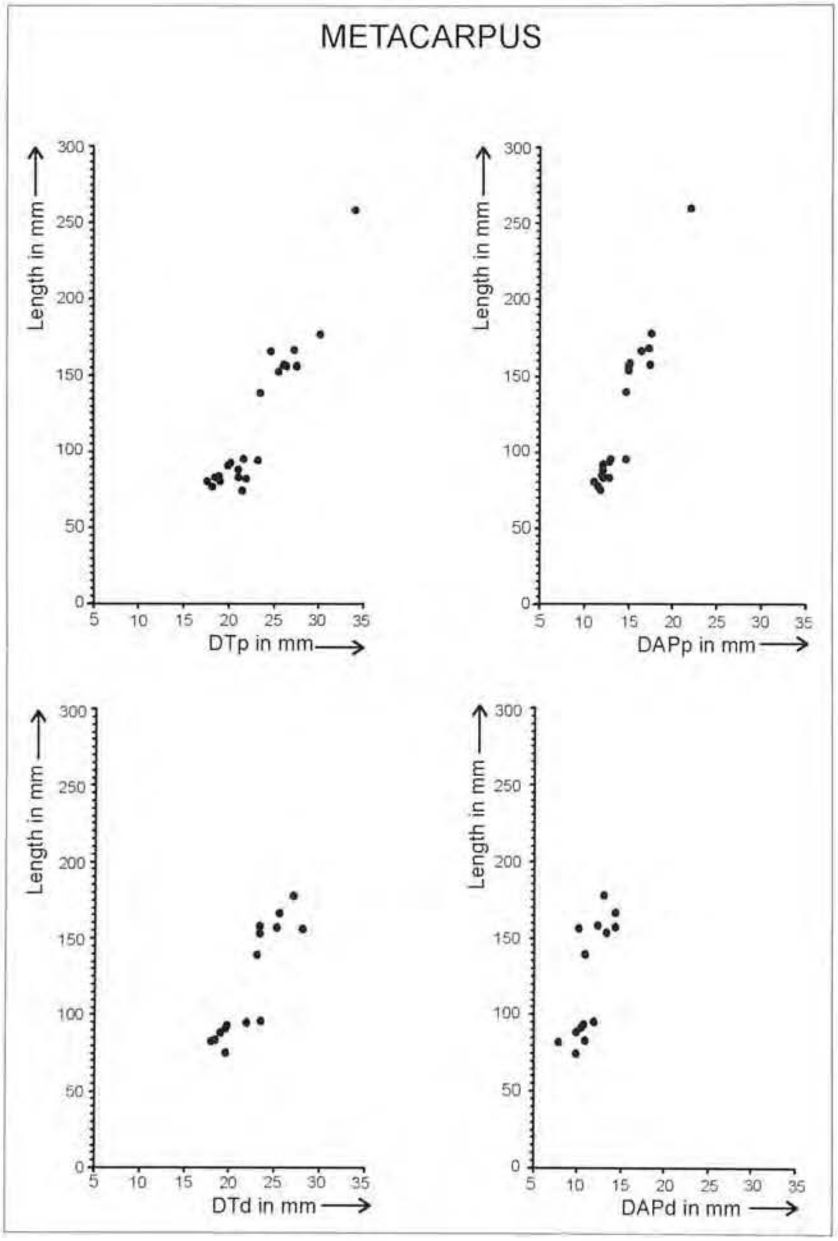

Fig. 2. The four different massivity diagrams of adult metacarpals of *Hoplitomeryx* show three (massivity proximal end) or two (massivity distal end) size groups. DTp = proximal width; DAPp = proximal depth; DTd = distal width; DAPd = distal depth.

Fig. 2. *Els quatre diagrames de massivitat diferent de metacarpians adults d'*Hoplitomeryx *mostren tres (extrem proximal de massivitat) o dues (extrem distal de massivitat) classes de talla. DTp = amplària proximal; DAPp = fondària proximal; DTd = amplària distal; DAPd = fondària distal.*

Comparison material

The following species have been used for comparison, in alphabetical order:

Alces alces (Fairbanks, Alaska, Rancholabrean; F:AM BX276 and 2 others, drawer with F:AM 8309-1933, n=6); *Antilocapra americana* (North America, recent; FMNH 14239, FMNH 57217, FMNH 74239); *Axis axis* (Pleistocene, Java; Coll. Dubois, nos. 5376, 5593, 6089, 6258, 9853, 9861); *Blastomeryx* (Trinity River; F:AM CRO 60-1752); *Candiacervus* size 2 (Liko Cave, Crete, Pleistocene; LiB n=20, LiC n=20, Li-C n.n. complete leg); *Cervalces* (Rancholabrean, Alaska; F:AM 527); *Cervus elaphus* (Rancholabrean, Alaska; drawer with F:AM 34672, n=5); *Cervus kendengis* (Pleistocene, Java; Coll. Dubois nos. 6459 and 6471); *Cranioceras granti* (Clarendonian, Nebraska; F:AM 31716, n=7); *Eumeryx culminis* (Mongolia, Middle Rupelian; AMNH 19147, cast of type); *Ovis aries* (n=5, own collection); *Rangifer tarandus* (Fairbanks, Alaska, Rancholabran; F:AM A 591 (complete postcranial skeleton), drawer with A 473 (n-12), drawer with F:AM 120-6244 (n=8), and F:AM 2204-1951).

THE *HOPLITOMERYX* METACARPUS

Introduction

Metacarpals of *Hoplitomeryx* have been recovered from the following fissures in the Gargano, in alphabetical order: Chiro 1, Chiro 2, Chiro 4, Chiro 10B, Chiro 12, Chiro 14b, Chiro 27, Chiro 29, Chiro D1, Chiro D3, Falcone 2A, Fina D, Fina H, Fina K, Fina N, Gervasio 1, Nazario 4, Pizzicolli 4, Pizzicolli 12, S. Giovannino, S. Giovannino Low, Trefossi 2A, Trefossi F26.

To determine full-grown stage, the pattern as described for *Dama dama* (after Pöhlmeyer, 1985) is followed. At birth the distal epiphysis is unfused, and consists of two separate condyles. At the end of the sixth month the two condyles are fused. At 20 months the distal epiphysis starts to fuse with the diaphysis, and at the end of the second year this fusion is complete. *Megaloceros cazioti* (="*Megaceroides*" *cazioti*, *Dama cazioti*) follows the same pattern (Klein-Hofmeijer, 1996), and the same appears to be true for *Candiacervus* size 1 (= *Candiacervus ropalophorus*) (Biskop, 1978). It is therefore reasonable to accept the same pattern for *Hoplitomeryx*, but not necessarily with the same growth speed. Specimens without distal end cannot be determined on ontogenetic stage, and are therefore discarded from the size estimations.

Metacarpal size

Measured are maximal length, proximal width and depth, and distal width and depth. Length is measured from the most proximal end of the proximal articulation till the distalmost end of the trochlea. Proximal depth (DAPp) and proximal width (DTp) are both the maximum values as measured on the articulation area. Distal depth (DAPd) and distal width (DTd) are both the maximum values as measured on the distal epiphysial fusion line. Measurements on the distal articulation itself, the trochlea, are found to be too subjective, and in many cases impossible due to fragmentation.

Length of the adult *Hoplitomeryx* metacarpals appears to vary between about 74,4 mm and 259 mm (average 118,7 mm). Proximal depth varies between 9 mm and 22 mm (average 13,8 mm); proximal width (DTp) between 12 mm and 34 mm (average 22,3 mm). Distal depth (DAPd) varies between 9,2 mm and 18,2 mm (average 11,8 mm); distal width (DTd) between 18 mm and 31,5 mm (average 21,8 mm).

In the massivity diagrams of the adult specimens, three groups can be discerned (Fig. 2; Fig. 3). The low number of larger, complete specimens may lead to artificial groups, which as a consequence would disappear if more specimens could be measured. A fourth group is not represented by an adult specimen, but by a juvenile trochlea, which is significantly larger than any of the adult specimens, with a DAPd 22,2 mm and a DTd 36,6 mm (for the adult range, see above).

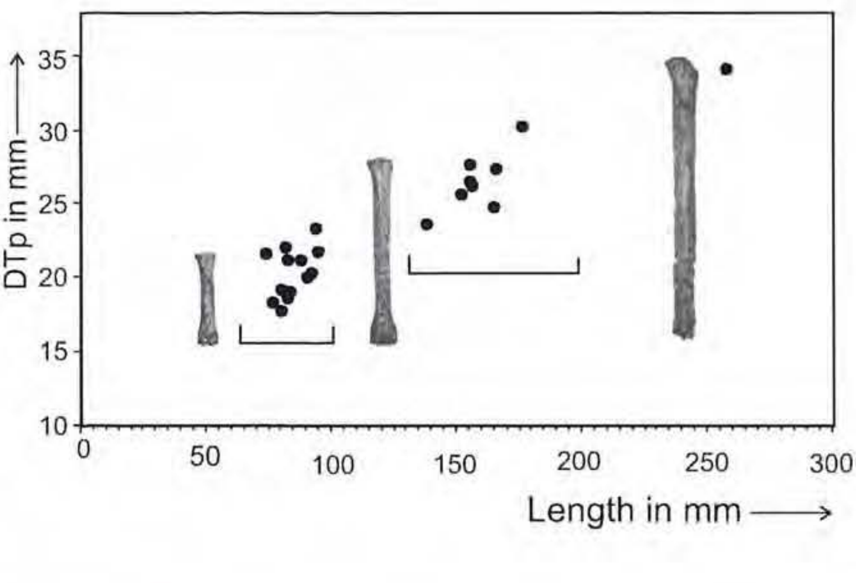

Fig.. 3. Proximal massivity (transversal diameter against length) clearly shows three size groups. The smallest specimens are laterally compressed at midshaft, while the larger specimens are straight.

Fig. 3. La massivitat proximal (diàmetre transvers respecte la llargària) mostra clarament tres classes de talla. Els espècimens més petits estan clarament comprimits enmig de la canya, mentre que els espècimens més grans són rectes.

The massivity indexes (DT/L) gradually increases from large to small specimens, as is also observed in *Candiacervus* (after De Vos, 1979), but run a bit ahead, in other words, the smaller specimens are relatively more massive. Another observation is that in the diagram with DAPp/L plotted against DTp/L, two clouds can be discerned, which shows that the smaller specimens are more square than the larger specimens, which are clearly more broad (DT) than deep (DAP). The smallest specimens are therefore not only shortened, but also more square in cross-section.

Four sizes groups can be discerned within the available material, based upon the maximum length. These groups are the following, from small to large:

Size 1. Length varies between 74,4 mm and 95 mm with an average of 85,5 mm (N=14). Proximal depth (DAPp) varies between 11 mm and 14,6 (average 12,1 mm), proximal width (DTp) between 17,6 mm and 23,2 mm (average 19,9 mm). Distal depth (DAPd) varies between 10 mm and 12 mm (average 10,9 mm), distal width (DTd) between 18,3 mm and 23,4 mm (average 20,2 mm). The average distal massivity DTd/L is 0,24.

The length of this size group corresponds to that of *Cervus astylodon* size G3 (range 80-89 mm) of Kume (Ryukyu Islands, Japan; after Matsumoto & Otsuka, 2000), and to *Candiacervus* size 1 (range 88,4-114,1 mm; after De Vos, 1979). The distal massivity corresponds to that of *Candiacervus* sizes 1 and 2 (range 0,21-0,24).

Size 2. Length varies between 139 mm and 177 mm with an average of 158,9 mm (N=8). Proximal depth (DAPp) varies between 14,6 mm and 17,5 mm (average 16,0 mm), proximal width (DTp) between 23,5 mm and 30,1 mm (average 26,4 mm). Distal depth (DAPd) varies between 10,3 mm and 14,4 mm (average 12,7 mm), distal width (DTd) between 23,0 mm and 28,0 mm (average 25,0 mm). The average distal massivity DTd/L is 0,16.

The length of this size group corresponds to that of *Candiacervus* size 3 (range 131,0-144,2 mm; after De Vos,

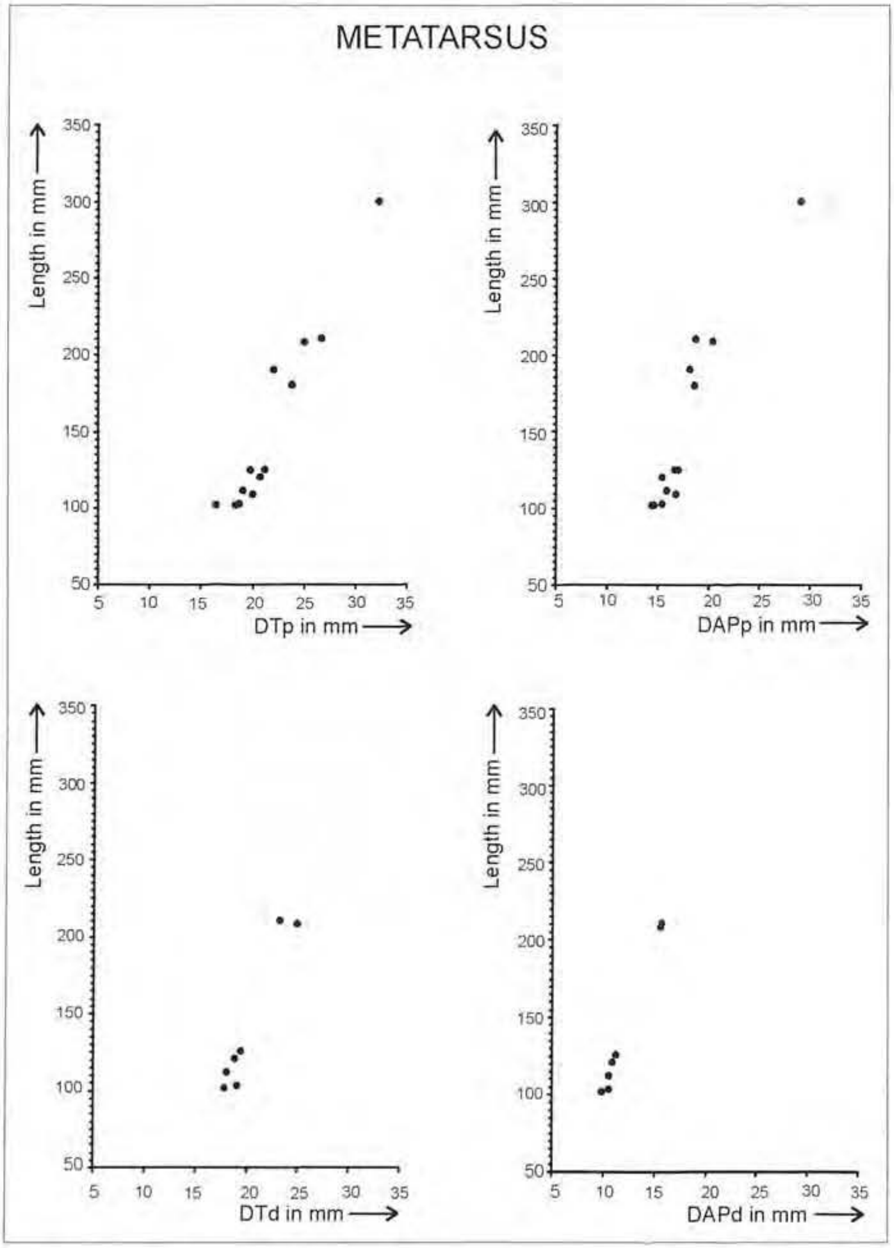

Fig. 4. The four different massivity diagrams of adult metatarsals of *Hoplitomeryx* show three (massivity proximal end) or two (massivity distal end) size groups. DTp = proximal width; DAPp = proximal depth; DTd = distal width; DAPd = distal depth.

*Fig. 4. Els quatre diagrames de massivitat diferent de metatarsians adults d'*Hoplitomeryx *mostren tres (massivitat de l' extrem proximal) o dues (massivitat de l'extrem distal) classes de talla. DTp = amplària proximal; DAPp = fondària proximal; DTd = amplària distal; DAPd = fondària distal.*

1979), to that of *Cervus astylodon* size G1 (140 mm; after Matsumoto & Otsuka, 2000) from Ryukyu Islands, Japan, and to that of the living Japanese deer *Cervus nippon keramae* (range 140-155 mm; after Matsumoto & Otsuka, 2000). The distal massivity corresponds to that of *Candiacervus* sizes 4 and 5 combined (range 0,14-0,17), to *Cervus elaphus* (0,15-0,17), and *Rusa unicolor* (0,16).

Size 3. The length of specimens of this size group may be about 259 mm (only one specimen), with a proximal depth (DAPp) of 19,5-22 mm (two specimens), and a proximal width (DTp) of about 33,4-34 mm (two specimens). Distal depth is about 18,2 mm, and distal width about DTd 31,5 mm, but there is only one specimen available. The distal massivity DTd/L would then be about 0,12, which corresponds to *Capreolus capreolus* (0,12-0,13).

The length of this size group seems to correspond to the size of *Candiacervus* size 5 (range 262 mm-284 mm; after Kotsakis *et al.*, 1976), but the proximal and distal diameters are lower, for example the proximal DT is about 38 mm (after Capasso Barbato, 1988, table 7)

Size 4. This size group is not represented by measurable adult specimens, but its existence is without doubt, as the largest juvenile trochlea epiphysis is already clearly larger than any adult trochlea. The specimen in question has already at this stage (no fusion started yet) a distal depth (DAPd) of 22,2 mm, and a distal width (DTd) of 36,6 mm. This size corresponds probably to that *Candiacervus* size 6, but no metacarpals were found. However, the increase in DTd of the metatarsal between size 5 and 6 is about 20% (calculated with data from Kotsakis *et al.*, 1976); it is logic to assume that the same takes place in the DTd of the metacarpal, too. In *Hoplitomeryx* an increase of 20% can be observed in the metacarpal DTd from size 3 to size 4. For the moment I therefore compare *Hoplitomeryx* metacarpals of size 4 to *Candiacervus* size 6.

Morphology of the metacarpal

The morphology of the metacarpus shows some uniform features, shared by all *Hoplitomeryx* specimens, but also some differences. The shared characters are the following. The groove on the dorsal surface for the interosseus muscle covers the proximal one third of the shaft or the proximal two third. The trochlea of *Hoplitomeryx* is inclined as in deer, with the lateral trochlea extending further than the medial one, or straight as in bovids, with the lateral and medial trochlea extending equally far.

The *Hoplitomeryx* specimens are, however, not homogeneous in the configuration of the proximal articulation, and four morphotypes can be discerned if we take the features into account with which cervids are distinguished from bovids (*sensu* Heintz, 1970). These morphotypes are irrespective of size, and are the following:

Morphotype 1. The crest ends in the central fossa, and makes an angle of about 30 degrees with the dorsopalmar axis. The fossa lies more or less central, and makes no contact with the palmar surface. This pattern is not only typical for *Cervus* (Heintz, 1970), but is also found in the other modern cervoids *Antilocapra americana* and *Rangifer tarandus*, and even in the very distantly related *Cranioceras granti*. The crest may be continued palmar of the fossa, as in some *Axis axis* (Coll. Dub. no. 5593).

Morphotype 2. The separating crest ends in central fossa, and runs more or less dorso-palmar following the DAP-axis; the fossa lies central, and the contact area between the lateral and medial articulation is minimal. The difference with morphotype 1 is the angle of the crest compared to the DAP-axis; it may be thus nothing more than a variety of the typical cervoid pattern, in which the lateral component increased in importance (= weight bearing). This configuration is typical for the Tokunoshima-type of *Cervus astylodon* from Ryukyu Islands, Japan (Matsumoto & Otsuka, 2000), and is also seen in *Alces alces* and *Cervalces*. The crest may be continued palmar of the fossa, as in *Cervalces*. In some specimens, the fossa borders the palmar surface.

Morphotype 3. The crest runs parallel to the border of the fossa, and ends somewhere within the lateral facet. The crest runs more or less dorso-palmar along the DAP-axis, and the fossa borders the palmar surface. This pattern is seen in the Kume-type of *Cervus astylodon*.

Morphotype 4. The crest runs parallel to the border of the fossa, along the DAP-axis, and ends at the palmar surface, as in bovids. In a way this morphotype is an elaboration of the former type. This pattern is seen in the Okinawa-type *of Cervus astylodon*, and is typical for bovids, e.g. *Gazellospira torticornis* (Heintz 1970: 33, fig.26), *Ovis aries* and *Myotragus balearicus*.

THE *HOPLITOMERYX* METATARSUS

Introduction

Metatarsals of *Hoplitomeryx* have been recovered from the following fissures in the Gargano, in alphabetical order: Chiro 10c, Chiro 23, Chiro 28, Chiro 28a, Chiro 29, Chiro 30, Chiro D1, Chiro D3, F8, Fina F9, Fina N, Gervasio 1, Nazario 1, Nazario 3, Nazario 4, Pizzicoli 1, Pizzicoli 4, Pizzicoli 12, Posticchia 1B, Posticchia 5, S. Giovannino, S. Giovannino Low, Trefossi 1.

To determine the ontogenetic stage of the metatarsals, the fusion pattern as described for *Dama dama* (after Pöhlmeyer, 1985) are followed. At time of birth the distal epiphysis is unfused, and consists of two separated condyles. At the beginning of the fourth month they become fused, and at month 22 the distal epiphysis fuses with the diaphysis. The pattern of fusion is confirmed by the data for *Megaloceros cazioti* (Klein-Hofmeijer, 1996), and by *Candiacervus cretensis* from Gerani layer 4: there are specimens with two separated condyles, larger specimens with a single distal epiphysis, and again larger specimens with a visible fusion line.

For the time of fusion of the navicocuboid with the metatarsal, no data for other insular species are available. It appears that in *Hoplitomeryx* this fusion takes place already before the fusion of the distal epiphysis with the shaft. This is evidenced by RGM 178.258 (Chiro 3) and RGM 178.534 (Nazario 3), where the distal epiphysis is still unfused, and the fusion line between navicocuboid and metatarsal already hardly visible, to the degree as seen in adult specimens. The earliest developmental stage is represented by RGM 178.261 (Chiro 3) and RGM 178.659 (Fina K), where the condyles are separated and no fusion has yet taken place with the cubonavicoid. At this stage the proximal articulation is developed as in *Dama dama*, which means that the lateral and medial facet are developed,whereas the other two facets are not.

Metatarsal size

Measured are maximal length, proximal width and depth, and distal width and depth. Length is measured from the top of the internal point of the cubonavicular element (which is in all cases firmly fused to the cannon bone, with no trace of a fusion line in adults), till the distalmost end of the trochlea. Proximal depth (DAPp) and proximal width (DTp) are both the maximum values as measured on the cubonavicular part. Distal depth (DAPd) and distal width (DTd) are both the maximum values as measured on the distal epiphysial fusion line. Measurements on the distal articulation itself, the trochlea, are found to be too subjective, and in many cases impossible due to fragmentation.

The length of the *Hoplitomeryx* metatarsal varies between about 420 and 102 mm (average 174 mm). Proximal depth varies between 13,1 mm and 29,1 mm (average 16,4 mm); proximal width (DTp) between 16,5 mm and 32,3 mm (average 20,6 mm). Distal depth (DAPd) varies between 9,9 mm and 17,1 mm (average 12,2 mm); distal width (DTd) between 16,9 mm and 26,0 mm (average 20,2 mm).

All measurements fall within a large range, especially those of the smaller half of the collection, but with some discontinuities; three or two groups can be discerned in the scatter diagrams (Fig. 4). The low number of complete specimens may lead to artificial groups, which as a consequence would disappear if more specimens could be measured.

The massivity indexes (DT/L) gradually increase from large to small specimens, as is also observed in *Candiacervus* (after De Vos, 1979).

The shapes (DAP/DT) of the distal and proximal ends show a gradual change along the size scale. The smaller the specimens, the more square they become; in other words, the ends remain more or less the same while the length decreases. If we divide the shape by maximal length, it appears that this allometric ratio runs a bit behind along the length scale: the smallest specimens have a relatively slightly larger DAPp than the largest specimens, and at the same time a relatively smaller DAPd.

The size groups are the following, from small to large:

Size 1. Length varies between 102 mm and 125 mm, with an average of 112,2 mm (N=8). The massivity proximal varies between 0,16 and 0,18 (average 0,17), and distal between 0,16 and 0,19 (average 0,17). The length of this group corresponds to that of *Candiacervus* size 1 (range 110 mm-131 mm, without the cubonavicular bone; after De Vos, 1979), but also includes smaller specimens than ever found in *Candiacervus*. Such small specimens, and even smaller ones, occur in *Cervus astylodon* from Ryukyu Islands, Japan, where the smallest length is 76 mm (after Matsumoto & Otsuka, 2000). A distal massivity of 0,16-0,19 is also found in *Rangifer tarandus* and *Candiacervus* sizes 1 to 3 (after De Vos, 1979).

Size 2. Length varies between 180 mm and 210 mm, with an average of 199,6 (N=5). The massivity proximal varies between 0,12 and 0,13 (average 0,13), and distal between 0,11 and 0,12 (average 0,12). This size class is comparable to *Candiacervus* size 3 of De Vos (1979), which has a metatarsal length (without cubonavicular) of 180 mm. It is also comparable to *Megaloceros cazioti*, which has a metatarsal length between 185 mm and 217 mm, without the cubonavicular (after Klein Hofmeijer, 1996). A distal massivity of 0,11-0,12 is also found in *Capreolus capreolus*, *Moschus* and *Candiacervus* size 6 (after De Vos, 1979).

Size 3. This size class is not represented by a complete specimen, but is likely to be present, seen the presence of a large proximal part of about one and a half times that of the former size (rgm 178.553). The estimated length would than be about 300 mm., but this is only true in case this proximal part belongs to a full grown individual. The massivity proximal is 0,11, distal it is unknown. This size is, tentatively, comparable to that of *Candiacervus* size 5 of De Vos (1979), which has a metatarsal length (excl. cubonavicular) of about 304 mm (after Kotsakis *et al.*, 1976).

Size 4. This size class is not represented by an adult specimen, but the juvenile shaft rgm 425.055 exceeds the largest available specimen, and is already its unfused stage twice as large. The estimated full grown length therefore is at least 420 mm. The massivity proximal is unknown, distal it is about 0,08. This size is comparable to that of *Candiacervus* size 6, which has a length (excl. cubonavicular) of about 406 mm (after Kotsakis *et al.*, 1976).

Morphology of the cannon bone

All *Hoplitomeryx* full-grown metatarsals, without exception, show a complete fusion with the navicocubocuneiform, elongated specimens as well as shortened specimens. As such, complete fusion can be considered a synapomorphic character of all morphotypes of *Hoplitomeryx*. This is unique, as in other described island artiodactyls this is not the case. The percentage of total fusion is 0% in *Megaloceros cazioti* from Sardegna, Italy (after Klein-Hofmeijer, 1996), 0% in *Cervus astylodon* from the Ryukyu Islands, Japan (after Matsumoto & Otsuka, 2000), both species Late Pleistocene, 6% in *Candiacervus ropalophorus* (= *C.* size 1) from Gerani 4 Cave, Crete (De Vos, 1979). In *Myotragus balearicus* this percentage differs according to locality and age: 40% in Cova de Son Maiol, 50% in Cova de Llenaire, which are both late Late Pleistocene, 60% in Cova des Moro and 80% in Cova de Moleta, which are both Holocene (Moyá-Solá, 1979:89).

In proximal view, there is a difference between the *Hoplitomeryx* specimens as regards the configuration of the fossae. Three configurations seem to be present. Two fossae can be present, where the fossae are located in the non-articulatory surface, interno-dorsal of both facets. One single fossa can be present, located within the lateral facet. No fossae can be present. The first configuration is seen in some bovids, e.g. *Ovis*; the third configuration is observed in deer (e.g. *Candiacervus* size 2 from Liko, Crete; *Rangifer tarandus*), dromomerycids (*Cranioceras granti*), but also in *Myotragus balearicus*. The second configuration is new, and maybe a variation of the first type.

In general, the morphology of the distal articulation is strikingly similar in all *Hoplitomeryx* specimens, irrespective of size. In all specimens the trochlea is complete, whereby the condyls extend slightly further on plantar side than on dorsal side. In almost all specimens the lateral condyl extends clearly further distal than medial condyl; as an exception they extend equally far. In almost all specimens the condyls are parallel to each other; in exceptional cases they diverge or converge. The lateral surface of the distal epiphysis is always diverging.

The same distal articulation is seen in *Axis axis*. In *Rangifer* the extension varies from clearly further to not at all. In *Alces alces* there is hardly an extension or not at all. In *Cervus kendengis* (Pleistocene, Java) the lateral condyl extends further than the medial condyl (Coll. Dubois nos. 5406, 6501, 6502), or they extend both equally far (Coll. Dubois no. 6982). *Hoplitomeryx* follows a *Cervus* pattern, including the rare exceptions.

All *Hoplitomeryx* specimens have a square cross-section, laterally compressed, and most specimens miss a clear volar sulcus. The smallest specimens have a convex plantar surface. The same shape can be observed in *Cervus kendengis, Axis axis, Candiacervus.*

As to the development of the muscular groove at the plantar surface, there is a gradual range from moderate robust with a weak or even indistinct muscular groove till robust with a pronounced muscular groove. The majority of specimens is moderate robust, and only about one third of the specimens shows the pronounced groove. There is no relation between development of the groove and length.

In all *Hoplitomeryx* specimens the medial ridge along the sulcus interosseus is higher than the lateral border, ranging from only slightly higher to clearly higher. In rare cases the development is so strong that the medial border is even convex at about one third from the proximal end.

In *Axis axis* from Java and *Candiacervus* size 2 from Liko Cave, Crete, the medial border is only slightly higher than the lateral border. In *Rangifer tarandus* the medial border is clearly higher than the lateral border.

The gully on the dorsal surface of the shaft of the metatarsal bone is distally closed in all *Hoplitomeryx* specimens, as typical for deer (Heintz, 1963). This is not only true for the genus *Cervus*, but already for the very early relative *Eumeryx*, which otherwise differs a great deal from eucervoids. The closed gully is also found in *Antilocapra*, and in the telemetacarpal cervoids (*Blastomeryx, Rangifer, Alces*).

In all *Hoplitomeryx* specimens the dorsal gully is pronounced, and extends proximally till somewhere in the cubonavicular, in any case at a point proximally of the fusion between metatarsal and the cubo-navicular bone. In cervids as a rule, the gully ends in the fossa just proximal of the distal epiphysis in cervids, whereas the gully continues till the end in bovids (Heintz, 1963). This is confirmed by *Rangifer tarandus*, but not by *Candiacervus* size 2 from Liko Cave, Crete; in the latter the gully also extends till the proximal articulation. In *Antilocapra americana* the gully also extends till the proximal end.

Size groups

To summarize, in both the metacarpals and the metatarsals of *Hoplitomeryx* four size groups are discerned, which are comparable in size, from small to large, to the Cretan deer *Candiacervus* size 1, size 3, size 5 and size 6, as we saw above.

Remarks on the chronology

The four size groups and the different morphotypes are equally distributed over the excavated fissures, and are therefore not considered chronotypes. The hypothesis of an archipelago consisting of different islands each with its own morphotype, cannot be confirmed on the basis of *Hoplitomeryx*. For example, shortened metatarsals are found in Posticchia 5 and Nazario 4, whereas normal sized metatarsals are found in S. Giovannino (both upper and low) and Fina N. The former two fissures are supposed to be of an older age than the latter (Freudenthal, 1976; De Giuli, 1986; Abbazzi *et al.*, 1993). Metacarpals, too, cannot consolidate the idea of chronology, as the shortened specimens are from Gervasio, and the normal specimens from S. Giovannino (both upper and lower) and Nazario 4. Gervasio is supposed to be older than the latter two fissures. Normal-sized metacarpals and shortened metatarsals are found together in Nazario 4. Also the astragalus contradicts the given chronology (Van der Geer, 1999). If we take the fitting bones into consideration, we see that a Chiro D1 tibia fits a Gervasio astragalus, a Gervasio tibia fits a Fina N astragalus, and finally that a Gervasio astragalus, a Chiro D1 tibia, a S. Giovannino metatarsal but also a Chiro 28 metatarsal fit perfectly well. Their time distance cannot have been very large. The only way to accept the rodent-based chronology is a fully developed radiation in *Hoplitomeryx* already in an early stage.

Other examples

The situation with several co-existing morphotypes on an island finds already a perfect parallel in the Gargano itself: all mammalian and avian taxa appear to be represented by three to five species, different in size and/or morpology. If all fissures would have contained only one species at the time, a morphological change during the ages would be the most parsimonous solution. That is, however, not the case, as the majority of fissures yields more than one species of each genus.

Is the situation with co-existing size groups unique for the Gargano? No, it is not unique at all, but appears to be just another example of what happens on islands of all times. Where the mainlands host a range of genera and species, the islands host a range of species and morphotypes. A good example is provided by the Pleistocene deer *Candiacervus* of Crete. A huge amount of fossils have been recovered, so that statistics are useful. It appears that *Candiacervus* bones show a statistically significant large variation, so that six size groups can be reliably distinguished (De Vos, 1979). The taxonomical phramework (for a complete overview, see Dermitzakis & De Vos, 1987 and De Vos, 2000), is still under discussion, and two theories prevail concerning its phylogenetic status: one monophyletic genus *Candiacervus* (De Vos, 2000), or two paraphyletic genera *Megaloceros* and *Cervus* (Capasso Barbato, 1988; 1992) or *Megaceroides* and ?*Pseudodama* (Caloi & Palombo, 1996). Irrespective of the taxonomical problems, the eight Cretan deer types in any case differ clearly too much to assume a similar ecological niche; more likely is the hypothesis of different niches. On the ground of body proportions, molar morphology and wear pattern, the specialist trophic niches occupied by the eight taxa might, tentatively, be summarized as follows: grassy food or prickly bushes on a rocky hill (*Candiacervus* sizes 1 and 2), grasses on a steppe-like plain (*Candiacervus* size 3), leaves and branches in a forest, like red deer (*Candiacervus* size 4), leaf-like food and soft bushes in a forested terrain with many obstacles (*Candiacervus* sizes 5 and 6) (De Vos & Van der Geer, 2002).

It is strange that theories based on radiation instead of on linear evolution are only reluctantly accepted for mammals. A factor may be the absence of a good testing facility. For fishes for example this is much easier: experiments not only in vitro but also in vivo can be done, and the process behind changes can be followed step by step. A lot of research has been done on the haplochromine cichlid fishes of the East African Great Lakes. These fishes can be compared to colonizers of a new island, as they entered a new and still unoccupied lake. Lake Victoria was filled about 14,000 years ago, due to the creation of the Rif Valley, which started to arise from 750,000 years ago. Immediately after the formation of the lake, a host of adaptive zones became available. The entering of a zone with free niches gave the cichlids the possibility to radiate beyond the degree seen in related cichlids. The haplochromine species flock of Lake Victoria is a good example of recent speciation, which took place in less than 200.000 years (Meyer *et al.*, 1990). The rapid adaptive radiation resulted in a wide range of trophotypes (Fryer & Iles, 1972; Greenwood, 1974; Barel *et al.*, 1977; Witte, 1981; Keenleyside, 1991). Initially they differed little from their immediate reverine ancestors, and there is no evidence of significant new morphological changes that facilitated their differentiation into many trophic levels; rather they capitalised on a biological versatility already present (Liem & Osse, 1975). The cichlids were obviously capable of a much higher rate of speciation than were other fish in the East African Great Lakes, and were able to differentiate into many different trophic levels with a minimum of morphological change (Carroll, 1997). It resulted mainly in differences in the mouth, which gradually became adapted to different types of food: detritus, fishes, shells, crabs, insects, phytoplankton, zooplankton.

For taxonomy, such radiations as seen in the cichlids are a disaster, as taxonomy deals with fixed, clearly defined subunits of the observable world, whereas in reality such a species flock approaches a continuum. The taxonomical problems become evident through the many revisions and reconsiderations of the classification of the haplochromine cichlids (e.g. Greenwood, 1981; Witte & Witte-Maas, 1981; Hoogerhoud, 1984; Van Oijen, 1991). This reminds us of the taxonomical problems with *Candiacervus*, with Darwin's finches, and maybe soon with *Hoplitomeryx*, as soon as more material has been described in full and scholars start to fit it into a phylogenetic scheme.

DISCUSSION AND CONCLUSION

In *Hoplitomeryx* the four size groups differ in limb proportions, as is the case in *Candiacervus* from Crete and *Cervus astylodon* from Ryukyu Islands, Japan. In the case of *Hoplitomeryx* the assumption of different ancestral genera is unlikely, because in that case the separate ancestors must have shared the typical hoplitomerycid features. The morposphere of *Hoplitomeryx* is too coherent to assume two or more different ancestors.

The large variation could be explained through adaptive radiation (as in Darwin's finches on the Galápagos), that gradually evolved after the Miocene pre-antler stage cervoid entered the island. The range of empty niches promoted the radiation into several trophic types, and caused the differentiation in *Hoplitomeryx*. The lack of large mammalian predators and the limited amount of food in all niches promoted the fast development into morphotypes. This is demonstrated by Darwin's finches, which are limited in numbers primarily by their food supply in the absence of predators; in such a case, adaptations in feeding methods are likely to be of special importance in determining the survival of the species, and the absence of predators may well have accelerated their adaptive radiation (Lack, 1947: 114). An alternative hypothesis explaining the occurrence of several sympatric species is that of multiple speciation on an archipelago of relatively close islands, with a later island merging. This can be excluded on geological grounds (Abbazzi *et al.*, 1996).

Interspecific competition for food and area is therefore at the present stage of knowledge the only reasonable hypothesis to explain the different size groups observed for the *Hoplitomeryx* groups. This appears also to be true for some mainland rodent communities (Dayan & Simberloff, 1994; Parra *et al.*, 1999), so why not for larger mammals, such as cervoids. As a matter of fact, different species of Cervidae occurring in the same mainland habitat under natural conditions are, as a rule, of considerable different size. In the case of exception to this rule, for instance *Rucervus duvauceli* and *Rusa unicolor* in some parts of India, the species occupy different ecological niches or in some cases a slightly different habitat (Van Bemmel, 1973: 295).

If we explain the different size groups of *Hoplitomeryx* and *Candiacervus* as the outcome of an adaptive radiation in an area with originally empty ecological niches, we automatically assume a narrow genetic base for the whole genus, in contrast to a mainland genus like *Cervus*.

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32

THE MOUNTING OF A SKELETON OF THE FOSSIL SPECIES *CANDIACERVUS* SP. II FROM LIKO CAVE, CRETE, GREECE

Alexandra van der Geer, John de Vos, George Lyras & Michael Dermitzakis

van der Geer, A., de Vos, J., Lyras, G. & Dermitzakis, M. 2005. The mounting of a skeleton of the fossil species *Candiacervus* sp. II from Liko Cave, Crete, Greece. *In* Alcover, J.A. & Bover, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 337-346.

Resum

S'ha muntat un esquelet del cérvol pleistocènic endèmic de Creta per a la nova exhibició del Museu de Geologia de la Universitat d'Atenes. Aquest cérvol difereix de tots els cérvols continentals vivents i extingits, principalment en les seves proporcions. Les mesures i comparacions confirmen aquesta observació, però això no és prou com per a que el públic general se n'adoni del seu impacte. Per contra, un esquelet muntat deixa clar que aquest cérvol tenia uns membres considerablement escurçats, especialment els metàpodes, mentre que la llargària del cos, o la llargària de la columna vertebral, eren més aviat normals. La impressió global és més propera a la d'un bòvid nan insular, com ara *Myotragus*, que a la d'un cérvol petit, tal com *Axis axis*.

El primer problema a resoldre fou la selecció de material. Ja que mai s'ha trobat un esquelet articulat complet, se n'ha de fer un de compost. Amb aquest motiu, només es varen seleccionar ossos de la classe de talla II (de Vos, 1979 ; Dermitzakis & de Vos, 1987) provinents d'un nivell d'una cova (cova de Liko, estrat B). D'aquesta manera es garanteix un interval geològic estret. Tot seguit, es varen mesurar tots els espècimens disponibles, i es va calcular el promig per a tots els elements. D'acord amb això, es va triar l'exemplar de cada element que més s'apropava a la mitjana calculada. Les peces dretes i esquerres havien de ser de la mateixa mida i robustesa, i els elements contigus havien de casar anatòmicament. Només en alguns casos s'ha hagut de recórrer a triar algun element que faltava a partir d'un nivell diferent, però mai a partir d'una cova diferent i mai a partir d'una classe de talla diferent. S'ha prioritzat la mida, la robustesa i l'ajustament anatòmic, i després que els ossos fossin complets i el color. Hi havia alguns peus articulats disponibles, encara que de mida i robustesa diferents, que s'han emprat per determinar les proporcions correctes i la posició correcta entre les falanges individuals, i els ossos carpians i tarsians. La mateixa cosa fou vàlida per a la columna vertebral. Per a l'establiment de la postura es van fer servir cérvols vivents com a comparació; per a l'extrapolació dels teixits tous (discos intervertebrals, cartílags de les articulacions) també es va recórrer al model dels cérvols vivents.

De cara a amagar els bastiments de suport, es va inserir dins els ossos una armadura metàl·lica interna fent forats i fitxant-la amb goma de poliuretà. S'ha fabricat l'esquelet complet en parts modulars bones d'ajuntar pel seu transport fàcil a la mostra. Parts absents petites (principalment processos vertebrals, parts costals i les ales pèlviques) s'han reconstruït amb apoxy, en base a altres elements disponibles de *Candiacervus* de la cova de Liko o per interpolació del millor ajustament entre dues parts absents. Les traces de la matriu original han estat estretes, per a una impressió millor del material fòssil. Per completar l'esquelet s'ha fet una rèplica del crani de l'espècimen tipus de la classe de talla II de de Vos (1979) i una rèplica de l'espècimen tipus del banyam tipus I de de Vos (1984).

Paraules clau: Pleistocè, endemisme, cérvol, reconstrucció, esquelet muntat.

Summary

For the new exhibition in the Museum of Palaeontology and Geology of the University of Athens a skeleton of the endemic Pleistocene Cretan deer was mounted. This deer differs from all known recent and extinct mainland deer, mainly in its proportions. Measurements and comparisons confirm this observation, but are not enough to make the public realize its impact. A mounted skeleton on the contrary makes it at once clear that this deer had considerably shortened limbs, especially the metapodals, whereas the body length and the vertebral column length are rather normal. The overall impression is closer to that of an insular dwarf bovid like *Myotragus* than to that of a small deer such as the spotted deer (*Axis axis*).

The first problem to be tackled was the selection of the material. Since a complete articulated skeleton has never been found, a composite had to be made. For this purpose, only bones of size class II (de Vos, 1979; Dermitzakis & de Vos, 1987) coming from one layer of one cave (Liko Cave, layer B) were selected. In this way a narrow geological range was assured. Subsequently, the available specimens were measured, and of all elements the average size was calculated. Accordingly, of each element the specimen that came the most close to the calculated average was selected. Left and right had to be of exactly the same size and robustness, and adjoining elements had to fit anatomically. Only in some cases a missing element had to be chosen from a different layer (layers C and D), but never from a different cave, and never from a different size class. Priority was first given to size, robustness and anatomical fitting, and next to completeness and colour. Several articulated feet were available, although of the wrong size or robustness, which were used in determining the right proportions and right stance between individual phalanges, tarsal and carpal bones. The same was valid for the vertebral column. For postural aspects, living deer were used as comparison; for extrapolation of soft tissue (intervertebral disks, articulation cartilage) also living deer stood model.

In order to keep the supporting fabrication as hidden as possible, an internal metal armature was inserted in the bones through drilled holes and fixed with polyurethane glue. The complete skeleton is fabricated in ready-to-assemble modular parts for easy transportation and reassembly on the spot. Minor missing parts (mainly vertebral processes, costal parts and the pelvic wings) have been reconstructed in epoxy putty, based on other *Candiacervus* elements from Liko or by interpolating the best fit between two existing parts. For a better impression of the fossil material, traces of the original matrix were left on the bones. A cast of the skull of the type specimen of size II of de Vos (1979) and a cast of the type specimen of antler type 1 of de Vos (1984) were made to complete the skeleton.

Keywords: Pleistocene, endemic, deer, reconstructing, mounted skeleton.

INTRODUCTION

Recently, the Museum of Palaeontology and Geology of the University of Athens reorganized its exhibition completely, in accordance to the latest insights in palaeontology and climatology. The pattern of the new exhibition follows the patterns of global climatological changes throughout time. These climatological changes had a great impact on the palaeoenvironment and were the cause of extinctions and evolutionary changes in many mammalian species. One of the clearest examples is the extinction of the endemic island deer of Crete, *Candiacervus*. Once this deer roamed the island, and was represented by eight morphotypes as a result of adaptive radiation, distributed over six size classes and three antler morphotypes, from small to large classified as *C. ropalophorus*, *C.* spp. II (a, b and c), *C. cretensis*, *C. rethymnensis*, *C.* sp. V, and *C.* sp. VI (classification following de Vos, 1979, 1984, 2000). Other taxonomies (e.g. Capasso Barbato, 1989; Caloi & Palombo, 1996) recognize five species, but these opinions are not followed here, furthermore, taxonomic problems are irrelevant for the reconstruction at the moment. At the end of the Pleistocene the climate gradually became warmer; at the same time the island became smaller by a sea level rise. This resulted in a drastic decrease in number and species richness of the Cretan deer. At present it is known to us only by its fossilized bones.

Bones alone, however, have no high educational value in a modern exhibition, so a reconstruction of the complete animal appeared necessary. How else to show the public that this endemic creature really looked so completely different from the deer we know, even if we include an island deer like *Cervus marianus* from Philippines? A mere assemblage of bones is not enough to stress the essential different nature of the Cretan deer; this can be done only with the help of a complete skeleton. Unfortunately such a skeleton was never found, so the only way is to reconstruct a skeleton out of individual elements, assemble them in a feasible, life-like articulation, and reconstruct a possible mode of locomotion and other postural aspects. We choose to assemble a skeleton out of size II elements, all adult and male. In the exhibition the skeleton is placed on the model of a small island. In order to stress the different habitat of the Cretan deer from the mainland species, we let it stand on the higher level of a rocky cliff. The skeleton is mounted with its head turned towards the spectator, so that both antlers are shown in their full length and a certain contact with the visitor is created.

Fig. 1. Cave Liko (northwestern Crete) contained a large amount of *Candiacervus* bones, mainly of size II. With the exception of only a few articulated parts, the fossils came from disarticulated individuals.

Fig. 1. La cova Liko (nord-oest de Creta) contenia una gran quantitat d'ossos de Candiacervus, *principalment de la classe de mida II. Amb l'excepció d'unes poques parts articulades, els fòssils provenen d'individus desarticulats.*

METHOD

Selecting elements

First of all, we want to show a species that shows the characteristic endemic feature of the shortened legs. Only size classes I, II and III as defined by de Vos (1979) (= *C. ropalophorus*, the three spp. II, and *C. cretensis*) come therefore into consideration. Of these three taxonomical units, we choose not to build the largest or the smallest size, as in such a way a rather exceptional individual is built. Therefore sizes I and III were skipped and we proceeded with spp. II, of which there are three types, but all with the same size (estimated withers height about 50 cm; de Vos, 2000).

Secondly, the appropriate elements had to be selected. Within spp. II there is a certain amount of individual variation, amongst which an average type should be selected, but at the same time the proportions between the elements should be correct. It appears that the proportions between limb bones of an articulated skeleton can be reliably approached by merely taking the average values of a large enough collection of disarticulated elements; this method has been tested for *Cervus philisi* with 30 disarticulated skeletons and 1 articulated skeleton (Heintz, 1970). For all practical reasons, this means that if we take the average bone from a large collection of disarticulated elements, we approach the correct articulated skeleton close enough to be reliable.

Another choice that has to be made is that of gender. In the case of deer, a male individual is the obvious choice as the antler informs us not only about the deer's taxonomic position, which is good for the visiting scientist, but also it is the most attractive feature for the general public, which happens to be our most important target group.

The excavation at Liko cave (north-western Crete) yielded a large amount of (adult) deer bones (Fig. 1), of which size II is by far the most common: 95,3% (de Vos, 1979). The fossils were from numerous disarticulated individuals, with the exception of a few articulated parts. Fortunately, the number of bones was large enough to apply the abovementioned method. For each bone we calculated the mean value and this made it possible to select within each bone category the specimen with the average measurements. We choose almost entirely from one layer (Liko B), with only a few additional specimens from other layers (Liko C, Liko OD), to assure a narrow geological time range for the selection. After the selection of the average, more or less complete adult specimens, the best fitting specimens were selected from this selection. Most important discriminative factors were, in this order, equal size of left and right side, similarity in robustness of left and right side, completeness, anatomical fitting with proximal element, anatomical fitting with distal element. Anatomical fitting was checked for each combination with a skeleton of a muntjac (chosen for its robustness) and of a spotted deer (chosen for its comparable size). In case a right and a left element were of equal size, equal robustness but one of the two was severely damaged, glued together and lacking major parts of the epiphyseal areas, this specimen was discarded, and quite often also the other specimen as no exact mirrored copy could be found, and we had to start with a fresh combination. To our surprise, many elements fitted so well, not only anatomically but also in colour and fossilization, that most likely they originated from one individual.

Technique

The complete skeleton is fabricated in ready-to-assemble modular parts, which can be reassembled on the final spot. This allows not only easy and comprehensive transportation, but gives at the same time opportunities for minor changes in the future, mainly of course in the posture of the animal. Minor missing parts (mainly vertebral processes, costal parts and the pelvic wings) have been reconstructed in epoxy putty, based on other *Candiacervus* elements from Liko or by interpolating the best fit between two existing parts, again with the spotted deer and muntjac as reference. The reconstructed parts were shaped with a grinder and sand paper, and then painted with water colour to which coarse sand was added. The colour does not approximate too well the real fossil in order to make the reconstruction apparent. The addition of sand gave a sandstone-like texture to the reconstructed parts, which does not distract the eye from the rest of the mount. The reconstructed edges of the neural spines slightly diverge from the smooth curve that should connect their tips. This was done on purpose in order to make clear to the visitors that the mount was made of fossil elements composite out of many individuals. For a better impression of the fossil material, traces of the original matrix were left on the real bones. Because the selected skull is the type specimen of sp. II (see below), it was preferable to keep the original in the research collection. Furthermore, the process of attaching new, more complete antlers to that skull would have resulted in an alternation of the type specimen, which would confuse future researchers. For these reasons we substituted it with a cast. Because of all parts of the skele-

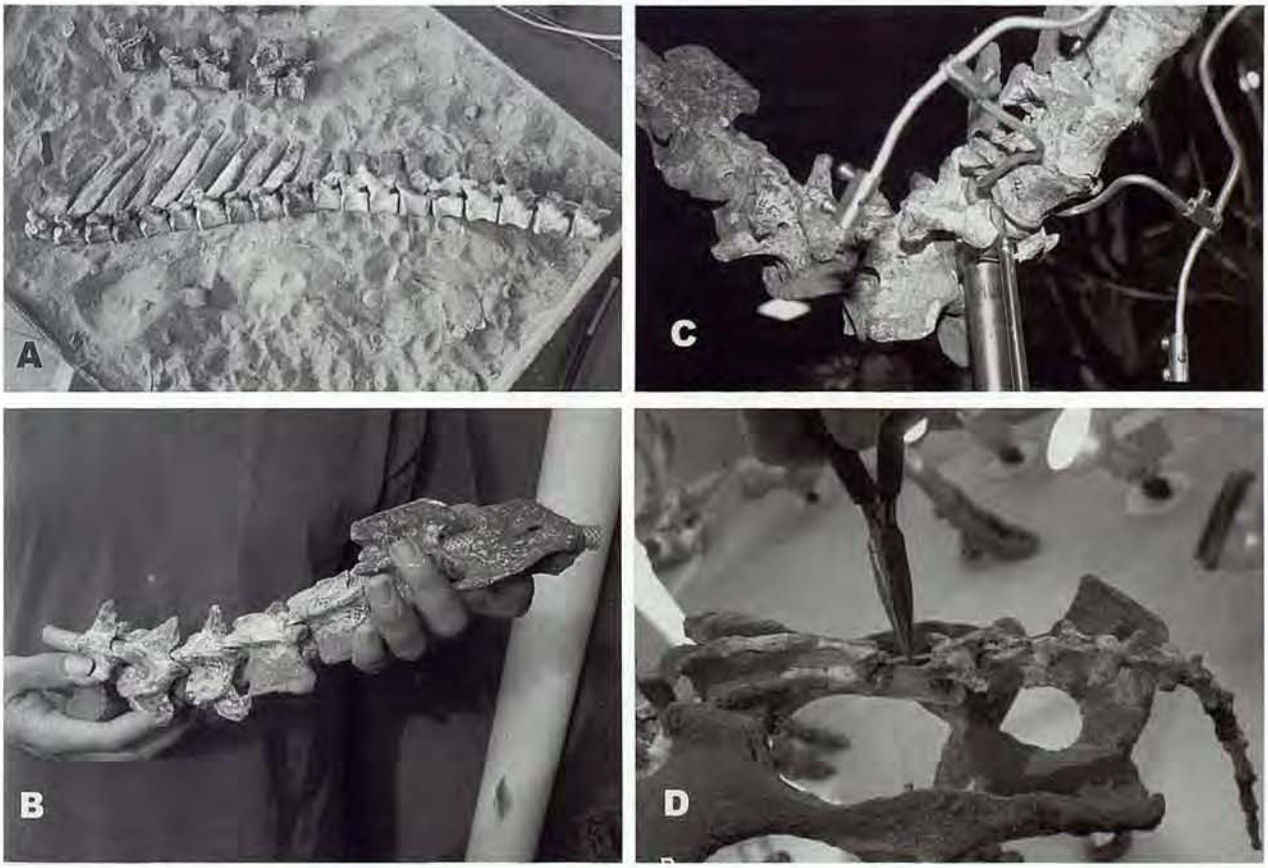


Fig. 2. A. Finding the correct position of the vertebrae of *Candiacervus* with the use of sand failed, because of the very fragile and thin aspect of the transversal processes. **B:** The best approach was that with the help of a flexible tube that was inserted in the vertebral canal (technique Aart Walen). **C:** The front limb bones are hanged as one unit to the skeleton into an armature that holds the scapula. **D:** The hindlimb is attached with a screw through the femoral head that is screwed into a metal plate at the interior side of the pelvis.

Fig. 2. A. L'establiment de la posició correcta de les vèrtebres de Candiacervus *amb l'ús d'arena va fallar, degut a l'aspecte molt fràgil i prim de les apòfisis transverses. **B.** La millor aproximació es va aconseguir amb l'ajut d'un tub flexible que s'inseria al canal vertebral (tècnica Aart Walen). **C.** Els ossos de les cames de davant es pengen com a una unitat a l'esquelet mitjançant un ànima metàl·lica que s'aferra a l'escàpula. **D.** El membre posterior s'uneix amb un pern a través del cap del fèmur que s'enrosca a una placa de metall situada al costat intern de la pelvis.*

ton the head is the most closely examined element by visitors (Madsen, 1973), the cast was realistically painted, contrary to additions to the postcranial elements (see above). Finally replica polyurethane antlers were made to complete the skeleton. We choose to cast the type specimen (Ge4-2870, left) of antler type 1 coming from Cave Gerani 4 and described and figured by de Vos (1984); the right side is a mirrored cast. Although this specimen comes from a different cave (Gerani 4), we think it fit for our reconstruction, based upon the many fragmentary antlers from Liko that correspond exactly to this holotype, not only in morphology but also in size. This means that antler type 1 not only occurred in the Liko population, but was also not rare. In addition, a complete antler was never found in Liko, and a reconstruction with fragments only would be a hazardous operation.

In order to keep the supporting fabrication as hidden as possible, an internal metal armature was inserted in the bones through drilled holes and fixed with polyurethane glue to the bone to prevent damage caused by friction between bone and metal. The hindlimb was attached in this way: a screw through the femoral head was screwed into a metal plate at the interior side of the pelvis at the position of the acetabulum (Fig. 2; Fig. 3). The internal iron rod exits the metatarsals and is placed immediately on the base. The phalanges are placed in front of the iron rod. They are attached together and to the metatarsals with the use of thin electric wires: their PVC cover was inserted in the two bones at the opposite sides of the articulation facets of the diaphysis and the two elements are hold together with the wires' copper core. This ensured a better stability, and prevented too much damage to these small elements. The method of building a fully free skeleton could not be applied in this case because the diameter of the bones of the anterior limbs is too small to drill them safely in order to pass a wide rod. However, the support at the front was necessary because of the huge torque of the heavy skull and backward orientated antlers. So in order to prevent the skeleton from falling forward, we had to install a heavy steel rod between the front feet and the first thoracic vertebra (Fig. 3). The front limb bones were attached to each other with wires and were hanged as one unit to the skeleton with the use of small nuts and bolts (Fig. 2). The ribs are for the larger part sculpted due to strength considerations and the lack of complete bones, and are epoxied and glued to the frame.

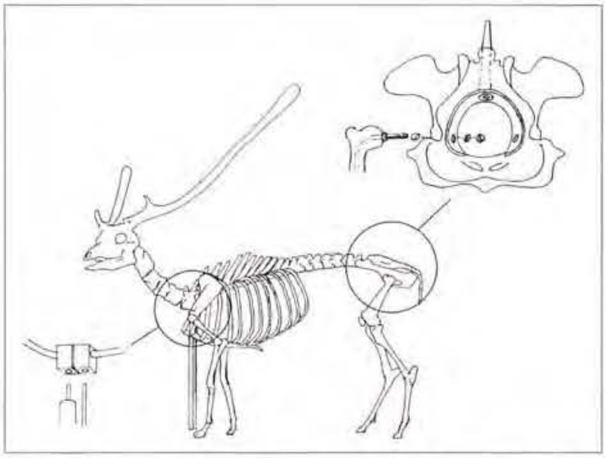


Fig. 3. Detail drawing of the supporting system at the front limb and the attachment system of the hindlimb. **Left:** A heavy steel rod turned out to be inevitable, due to the huge torque of the heavy skull with antlers. It was fixed to the wire through the vertebral canal. **Right:** The femoral head is screwed into a metal plate that is attached to the interior side of the pelvis.

Fig. 3. Dibuix de detall del sistema de suport del membre anterior i del sistema d'unió del membre posterior. ***Esquerra.*** *Una pesada barra d'acer és inevitable, degut al pes de pesat crani amb el banyam. Fou fitxada al fil de ferro de l'interior del canal vertebral.* ***Dreta.*** *El cap del fèmur s'engranpona a una placa metàl·lica situada al costat intern de la pelvis.*

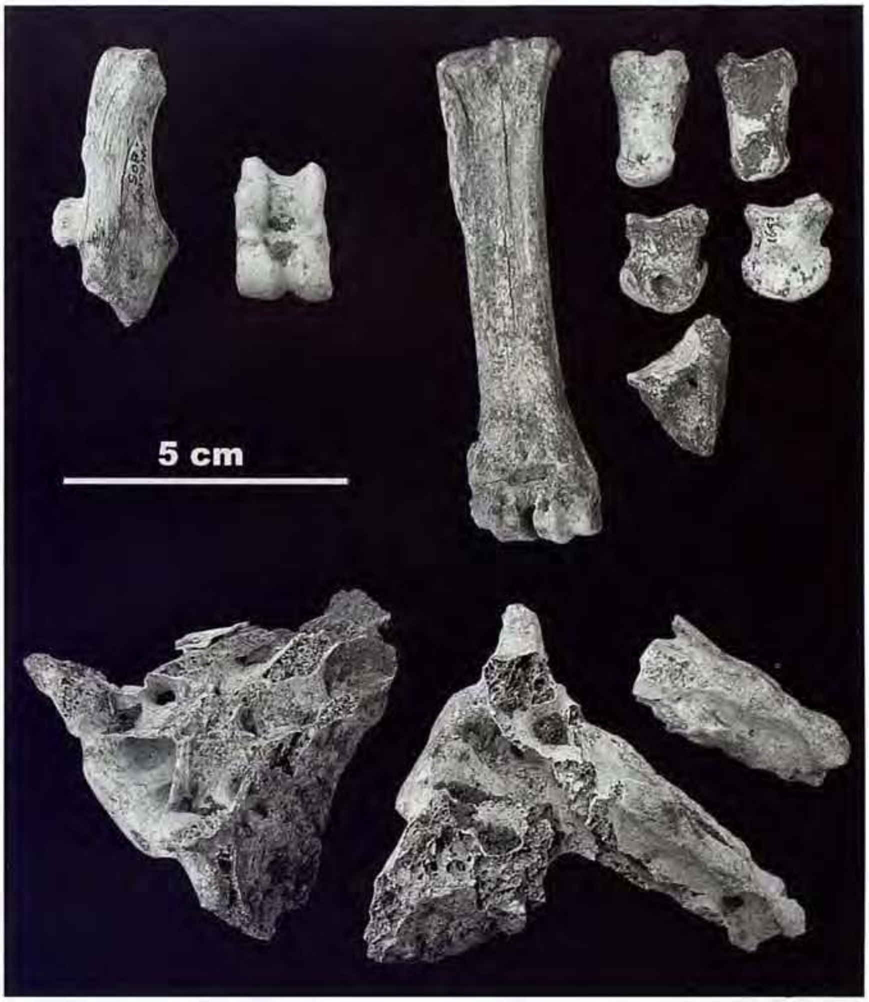
The skeleton is articulated in a life-like, natural pose, which requires choices about the angles of articulation and the ranges of flexion, extension, abduction and adduction. To ensure this, the articular surfaces were studied in detail with living deer as reference, and the best fit or close-packed situation was chosen to assure the rest position of the articulation, with the exception of the front limb and the cervical vertebras. In the case of the phalanges, we checked the resulting position with alive *Dama dama* and x-rays from anatomy handbooks. The front limb is articulated in such a way that the animal steps on an elevation of about

Fig. 4. The selected atlas (ampg (v)1626) and axis (Li-B 2240), which both belong to males, based upon their more robust morphology with much more pronounced muscular attachment areas in comparison to equal sized female specimens.

Fig. 4. L'atles (ampg(v)1626) i l'axis (Li-B 2240) seleccionats, tots dos pertanyents a mascles, segons la seva morfologia més robusta, amb unes àrees d'inserció musculars més pronunciades, en comparació amb espècimens femenins de la mateixa mida.

Fig. 5. **Above, left**: The right calcaneum (Li-B 403) and right astragalus (Li-B 1468) in volar view. **Above, right**: The selection of fitting phalanges was eased by the presence of several associated feet in the collection, of which this is one example. **Below**: As a complete, medium-sized sacrum was not available, it had to be composed out of three damaged specimens.

*Fig. 5. **A dalt, a l'esquerra.** Calcani dret (Li-B 403) i astràgal dret (Li-B 1468) en norma volar. **A dalt, a la dreta.** La tria de falanges que articulessin va acabar gràcies a la presència de diversos peus associats a la col·lecció; aquest n'és un exemple. **A sota.** Com que no es disposava de cap sacre complet de mida mitjana es va haver de recrear un a partir de tres espècimens espanyats.*



10 centimetre. The cervical column is adjusted to an upheld position of the head, which makes in addition a turn of 90 degrees in order to look to the spectator. The best fit for the other vertebras was in first instance approached with the help of a metal rod through the vertebral canal, but this appeared impossible due to the stiff nature of metal: each bending to conform the right curvature between two vertebras caused at the same time an error in another pair of vertebras. Also the method with the use of sand (Fig. 2) failed, as with every corrective movement the transversal processes ran the risk to break off. A far better approach was that with the help of a flexible tube that was inserted in the vertebral canal (Fig. 2), a technique suggested by Aart Walen (pers. comm. 2003). That tube can be considered as a simulation of the neural canal, and it helped us to find the exact anatomical position of the vertebrae. In addition, the vertebrae with the tube inside appeared to be a construction stable enough to allow us to pass the metal rod through the tube itself. After that, the whole construction was fixed with epoxy putty and glue. For the right shape of the vertebral column we further assumed a V-shaped cartilage disk to have been present in the living animal, similar to those seen in recent deer; for this we compared with *Axis axis*, *Rusa unicolor*, *Dama dama* and *Cervus elaphus*). The caudal vertebras were attached to each other and to the sacrum with a system similar to the one that we used for the phalanges.

A final step was to cover all exposed metal or plastic parts of the mount (with the exception of the central metal rod between the anterior limbs). For that purpose we imitated the calcite deposits of Liko cave, by mixing epoxy putty, glue and clay collected from the cave itself.

MATERIAL

All used elements of *Candiacervus* are stored at the University of Athens (Greece), Department of Geology, Section Historical Geology and Palaeontology. The material originates from the 1973 to 1975 excavations at cave Liko (Likotinaras) in the Rethymnon area at the north-western part of the island, carried out by a Dutch team consisting of Hans Brinkerink, John de Vos, David Mayhew under supervision of the late Dr Paul Sondaar (at that time University of Utrecht, The Netherlands). The material collected from Liko comes from the uppermost 75 cm of the cave deposits, attributed to the Late Pleistocene. The material was transported to the Netherlands, cleaned, repaired, numbered (codes Li-B, Li-C, Li-OD), catalogued and measured. During spring 2002, the material was returned to Athens, where it is presently stored and in the process of being renumbered (code AMPG (V)). All materials chosen for the composite skeleton originate practically speaking from one level, level B, with some additions from level C and level OD. All specimens belong to adult individuals.

The living deer used for comparison are all stored at Naturalis, Nationaal Natuurhistorisch Museum, Leiden (The Netherlands), and consist of *Axis axis, Cervus elaphus, Rusa unicolor, Dama dama.* Alive fallow deer (*Dama dama*) were observed in a private zoo (Leidse Hout, Leiden, The Netherlands).

CRANIAL SKELETON

The skull is actually the most important element of the skeleton as it embodies so much of an animal's "personality" (Antón, 2003). The most stringent requirements for the skull, apart from size, are that it belonged to a male, and that it is as complete as possible. This immediately implies that the possibilities are limited. The possibilities increase when we forget about the antlers and the jaws, and substitute them for separately found, unassociated specimens. The possibilities further increase when we include damaged, incomplete skulls into consideration that can easily be filled up with epoxy. The selected skull comes from Liko B (ampg(v) 1734 = Li-B 717).

For the antler, we could select from the three types as known and described for size II (Dermitzakis & de Vos, 1987: fig. 10a-c). None of the antlers, however, was complete; a complete left antler (Ge4-2870) was only known from Cave Gerani 4, described as type specimen for antler type 1. Fortunately this type also occurred in Liko, and indeed many fragmentary antlers were present in the collection which fitted in morphology and size exactly to this type specimen. This warrants the combination of this antler type with the type skull and our postcranial skeleton. The other two antler types are too fragmentary and too incomplete to be a reliable basis for a reconstruction.

The lower jaw constituted an additional problem: age. Not only the size and the robustness have to be similar for right and left, but also the degree of abrasion of the dental elements. The individual age of the right and left jaw should not differ too much.

AXIAL COLUMN

For the atlases, only the robust, presumably male specimens were considered. In the male atlas in living deer, the ventral arch is thicker at the median vertebral entry, in the dorsoventral direction, than the height diameter of the

Fig. 6. Some of the postcranial elements selected for the mounting. **A, B**: The frontlimbs (for numbers, see Table 1). **C:** The right hindlimb (for numbers, see Table 1). **D:** Left cannon bone (Li-B 898). **E:** The exceptionally complete left scapula Li-B 605. **F:** Left femur (Li-B 1325).

Fig. 6. *Alguns dels elements postcranials seleccionats per al muntatge.* ***A, B.*** *Cames anteriors (per als números, veure Taula 1).* ***C.*** *Cama dreta posterior (per als números, veure Taula 1).* ***D.*** *Os canon esquerre (Li-B 898).* ***E.*** *Escàpula esquerra excepcionalment completa (Li-B 1325).*

overlying spinal canal. The most appropriate atlas is specimen ampg(v) 1626 (male; original number Li-B 2219) (Fig. 4). For the axis, a similar approach was taken, with as additional criterion that it should fit the chosen atlas. In the male deer axis, the spinous process is higher than in the female, but in many *Candiacervus* specimens this process is unfortunately broken-off, so features of overall robustness and pronounced muscular scars constitute better criteria. The resulting specimen was Li-B 2240. These atlas and axis can be attributed to males without doubt, at the basis of their more robust morphology compared to equal sized female atlases and axes. The muscular attachment areas are much more pronounced on the first cervical vertebras of all living male deer, due to the heavier skull with appendages.

The procedure for the remaining cervical vertebras was much easier, as they had to fit the preceding vertebra as natural as possible. The only feature to discard some fitting specimens was the obvious lack of robustness, a high degree of damage, or the lack of the caudal articulation. In case a caudal articulation is missing, the procedure of fitting one by one is blocked. The resulting cervical column consists of C3 (Li-B 2273), C4 (Li-B 2289), C5 (Li-B 2313), C6 (Li-B 2343), and C7 (Li-B 2357).

For the thoracic vertebras the procedure was simply continued, resulting in a sequence T1 - T13, unfortunately all unnumbered, though all from Liko B. No already associated specimens of average size could be found in the collection, but of other sizes instead. These associated pairs were used to check the resulting morphology. The same is valid for the lumbar vertebras L1-L6, all unnumbered, all from Liko B. Here a larger associated series, consisting of T12 up to and including L6, was used as reference.

A complete, medium-sized sacrum (in the case of *Candiacervus* consisting of four sacral vertebras) was not available, but it appeared possible to compose one out of three damaged specimens (all unnumbered; Fig. 5) with the use of epoxy to fill up the gaps.

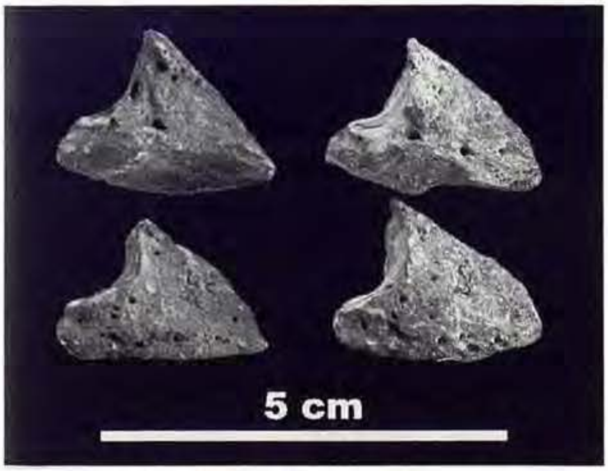


Fig. 7. Posterior third phalanges of *Candiacervus* appear to be lower, slightly shorter, slightly more massive, slightly more pointed, and with a more straight anterior surface than the anterior hooves. In the latter, the anterior surface is more convex.

Fig. 7. Les falanges terceres posteriors de Candiacervus *semblen ser més baixes, lleugerament més curtes, lleugerament més massisses, lleugerament més punxegudes i amb una superfície anterior més recta que les anteriors. A les darreres la superfície anterior és més convexa.*

The caudal vertebras finally appear to be ten in number, Cd1-Cd10, based upon the occurrence of only ten morphotypes among a large collection of caudal vertebras. For an estimation of the degree of size reduction from one tail vertebra to the next one, muntjac and spotted deer were used as reference. All caudal vertebras are unnumbered, and originate from Liko B; associated specimens were lacking.

SCAPULA AND PELVIS

To estimate the average sized scapula, the average measurements of the glenoid cavity are chosen, as almost all scapulae lack the body with the spina. The selected scapulae Li-B 588 (dex) and Li-B 605 (sin) are slightly, though insignifantly, larger, mainly due to the fact that we had to select a robust type, muscular enough to be associated with an individual that has to carry a heavy skull with a long antler of 60 cm. The left scapula Li-B 605 is exceptionally complete (Fig. 6), and is the only size II scapula from Liko B of which the total length can be estimated rather accurate. Missing parts are sculptured in epoxy, based upon the overall size and shape of *Axis axis*, as this deer corresponds best in size to *Candiacervus*.

Complete pelvic girdles are lacking all together. In order to provide a fitting specimen, we selected a pelvis with complete acetabulum (left and right), and a more or less complete ischial wing (left or right), to make contact with the sacrum. Missing parts are sculptured in epoxy. As average measurements those of the acetabulum are chosen, which are done on sight only, as no undamaged acceptable parts are available. The main criterion for average size was the best fit with the head of the chosen average-sized femur (see below). The differences in morphology between male and female *Ovis* and *Capra* were considered valid also for *Candiacervus*: The male pelvis is bigger and more sturdily, its ilium wing is larger and the width of the ventro-medial border of the acetabulum is about twice as large as in a corresponding large female pelvis (Boesneck *et al.*, 1964). As partial pelvis were chosen Li-B 623 (dex) and Li-B 630 (sin).

LONG BONES OF THE LIMB

For the measurements of the selected limb bones, the reader is referred to Table 1.

The choice of two humeri was complicated by the fact that in this large bone a large variation in morphology is found. The muscular scars should be more or less the same for the right and the left humerus, but this was not an easy task. Also the height of the greater tubercle in respect to the height of the humeral head differed significantly between the many specimens. Another problem was the amount of damage, as especially the humeral head is subject to erosion and damage, whereas the trochlea is much stronger. One of our criteria was that the head should be intact, as it is supposed to fit to the glenoid cavity of the scapula. As average measurement we give priority to maximal length,

Fig. 8. The transversal processes of the lumbar vertebrae are more or less orientated horizontally in *Candiacervus* size II.

Fig. 8. *Els procesos transversals de les vèrtebres lumbars estan orientats més o menys horitzontalment a* Candiacervus *de la classe de mida II.*

as massivity is more dependent on gender than length. We were able to select humeri that are very close in the average length: Li-C 3 (dex) and Li-B 140 (sin).

The radius and ulna appear to be fused in the major part of the collection, which results in a 100% fitting of corresponding radius and ulna. For the establishment of an average-sized radius-ulna we took the radius as main reference, as the olecranon is broken off in many cases, which decreases the amount of judgeable specimens enormously. We were not able to find a fitting radius of the average size, whereas slightly smaller specimens appear to fit the selected humeri perfectly well. For the reason of fitting, we selected radius-ulna Li-B 269 (dex) and Li-B 265 (sin) (Fig. 6). In addition, our selected humeri have no distal DAP that deviates from the average.

The next step should consist of the selection of the carpal bones, but we decided to select the metacarpal bone first. The reason is that small deviations from the average measurements in the separate carpal bones are added, so that the fitting proximal metacarpal bone may deviate quite substantially from the average size. It's easier to fill in the carpal bones starting from an already selected distal humerus and proximal metacarpus. The selected metacarpal bones are Li-B 3 (dex) and Li-C 9 (sin), which are slightly but insignifantly smaller than the average, and proximally as well as distally slightly wider. Other specimens that were also close to the average in length were too gracile to be attributed to an adult male with a full-grown antler.

We continued our composition with the femur. Here, we encountered the same problems as with the femur. Most specimens were critically damaged, or lacking one or both epiphyses. Differences in robustness and place and shape of muscular scars are obvious to the spectator, and should therefore be taken as important criterion. The selected femurs are Li-Bc OD (dex) and Li-B 1325 (sin, including associated patella; Fig. 6). For the right femur we selected a right patella that is very similar to the associated left-sided specimen: Li-B 581. In all measurements the selected specimens deviate less than 0,5 mm from the average.

For the selection of the tibia the fitting with the distal femur is less helpful, due to the characteristics of the knee joint, in which there is no close-packing situation of the constructing elements. The only criterion is that the maximal width of the distal femur should be in accordance with the maximal width of the proximal tibia, as checked with the spotted deer and muntjac. The selected tibias, Li-B 212 (dex) and Li-C 197 (sin), are slightly smaller (2,5 mm), proximally slightly less wide (1,5 mm), but distally slightly wider (0,7 mm); overall they are close enough to the average size. The condyls of the selected femurs roll very well over the trochleas of the selected tibias, in the same way as those of a spotted deer. With the selected tibias at hand, the selection of the corresponding malleolar bone (remnant of distal fibula) is easy by fitting alone. Perfectly fitting are Li-B 1843 (dex) and Li-B 2206 (sin).

element	inventory no.	Length	DAPp	DTp	DAPd	DTd
Mc dex	Li-B 3	108,2	17,9	24,7	16,5	26,4
Mt dex	Li-B 61	136,1	23,2	23,2	15,9	26,3
Mt sin	Li-B 898	138,3	22,2	22,6	16,5	26,2
humerus sin	Li-B 140	146,5	48,4	42,3	17,4	37,9
tibia dex	Li-B 212	186,5	36,8	44,6	22,7	28,2
radius dex	Li-B 269	135,4	17,7	33,6	21,5	28,8
radius sin	Li-B 265	137,8	18,0	34,2	21,4	28,2
ulna dex	Li-B 269	169,3	29,4	-	-	-
ulna sin	Li-B 265	173,5	29,4	-	-	-
femur sin	Li-B 1325	161,0	22,7	28,6	56,2	23,2
patella dex	Li-B 581	25,6	13,2	23,7	-	-

Table 1. *Candiacervus* size II, measurements (in mm) of the limb bones of the composite skeleton.

Taula 1. Candiacervus *classe de mida II, mesures (en mm) dels ossos de les cames de l'esquelet compost.*

element	inventory no.	Length	DAPp	DTp	DAPd	DTd
scaphoid sin	Li-B 1820	-	19,1	8,8	-	-
scaphoid dex	Li-B 566	-	22,6	10,9	-	-
lunare sin	Li-B 574	-	21,6	11,6	-	-
lunare dex	Li-B 1831	-	20,8	11,8	-	-
ulnare sin	Li-B 2204	-	16,9	10,1	-	-
ulnare dex	Li-B 577	-	15,9	10,2	-	-
magnum sin	Li-B 559	-	16,4	15,1	-	-
magnum dex	Li-B 557	-	16,0	14,1	-	-
unciform sin	Li-B 2199	-	13,6	11,2	-	-
unciform dex	Li-B 563	-	14,4	11,1	-	-
cubo-nav. sin	Li-B 1789	-	25,0	26,6		
malleolare dex	Li-B 1843	14,0	8,5	10,9	-	-
malleolare sin	Li-B 2206	14,8	7,5	11,6	-	-
calcaneum dex	Li-B 403	63,0	25,8	19,1	-	-
calcaneum sin	Li-B 1397	63,5	26,3	19,4	-	-
astragalus dex	Li-B 1468	32,5	-	20,4	-	19,1
astragalus sin	Li-B 424	32,5	-	19,7	-	17,9

Table 2. *Candiacervus* size II, measurements (in mm) of the carpal and tarsal bones of the composite skeleton.

Taula 2. Candiacervus *classe de mida II, mesures (en mm) dels ossos carpians i tarsians de l'esquelet compost.*

More or less the same is valid for the tarsus as for the carpus, so that's why we proceed with the metatarsal cannon bone instead of with the tarsal bones. The selected cannon bones Li-B 61 (dex, including the cubonavicular bone), and Li-B 898 (sin; Fig. 6) are very close (less than 0,5 mm deviation) to the average sizes.

For the lateral metapodals (plesiometapodals) we selected five more or less equal-sized specimens (all unnumbered). As the corresponding size of a lateral metapodal is not known, nor whether there is size difference between front laterals and hind laterals, the selection is a mere guess. Of all bones, these bones are the most likely to be wrong. The variation in the lateral metapodals between the different living plesiocarpal/plesiotarsal deer is large, and we cannot reliably select one of the living deer to guide us.

THE CARPUS AND TARSUS

For measurements of the selected carpal and tarsal bones, see Table 2.

The selection of the carpal and tarsal bones is done almost entirely on fitting; this could be checked with available associated elements. For the left front limb, top row, the following carpals are selected: Li-B 1820 (scaphoid), Li-B 574 (lunare), Li-B 2204 (ulnare), and for the bottom row: Li-B 559 (magnum), Li-B 2199 (unciform), 2x unnumbered pisiform (both same side (sin?), one to be assigned to the other limb), and seven unnumbered sesamoids. For the right front limb, top row, the following carpals are selected: Li-B 566 (scaphoid), Li-B 1831 (lunare), Li-B 577 (ulnare), and for the bottom row: Li-B 557 (magnum), Li-B 563 (unciform), and seven unnumbered sesamoids. For the hindlimb, the following tarsals were selected: Li-B 1397 (calcaneum, sin), Li-B 403 (calcaneum, dex; Fig. 5), Li 1468 (astragalus, dex; Fig. 5), Li-B 424 (astragalus, sin) and four unnumbered sesamoids

The right cubonavicular was already associated with the metatarsal, so the selection of the left cubonavicular was more or less a question of finding the mirrored equivalent. The selected specimen, Li-B 1789 (sin), is not fused neither with the larger cuneiform nor with the lesser cuneiform. The right cubonavicular on metatarsus Li-B 61 is only very loosely fused to the metatarsal.

THE PHALANGES

For measurements of the selected phalanges, see Table 3.

The selection of fitting specimens was immensely eased by the presence of several associated feet in the collection, not only associated phalanges, but also in association with metapodals (Fig. 5). This made it possible to study the morphology of phalanges that for sure belong together. It appears for example that the posterior ph III are lower, slightly shorter, slightly more massive, slightly more pointed, and with a more straight anterior surface than the anterior hooves (Fig. 7). In the front hooves, the anterior surface is more convex. The overlap is, however, large, and only in combination with the corresponding opposite hooves this feature becomes obvious. The morphology of the first and second phalanges on the other hand can be attributed to front and hind limb with much more certainty.

To make things even more convenient, within the average size II selection, an articulated left front and left hind foot were available. The left front foot consists of Ph I (Li-B 435 + 436), Ph II (Li-B 480 + 481), Ph III (Li-B 538 + 537), and unnumbered sesamoids. The left hind foot consists of Ph I (Li-B 432 + 433), Ph II (Li-B 478 + 479), Ph III (Li-B 539 + 540), and unnumbered sesamoids. For the right front and hind foot, similar counterparts were chosen. Because of the huge quantity of phalanges in the collection, we could afford a very critical attitude. The following specimens were chosen for the front foot: Ph I (Li-B 458 and Li-B 1572), Ph II (Li-B 483 and Li-B 492), and Ph III (Li-B 515 and Li-B 514). For the hind foot were chosen Ph I (2x unnumbered Li OD), Ph II (2x unnumbered Li OD), and Ph III (Li-B 520 and Li-B 528). As spare for the right front limb, we included one phalanx I and two phalanges II that belonged to one individual (unnumbered, Li-Ba). The reason to select these spares was the nature and degree of damage to the selected specimens.

There are quite a lot of lateral third phalanges, so we assume for the moment that also size II had those lateral phalanges. The size is of course a delicate matter, due to the fact that the measured average size will tend to be larger

element	inventory no.	Length	DAPp	DTp	DAPd	DTd
ph I ant dex	Li-B 458	29,6	16,7	14,5	10,3	12,8
ph I ant dex	Li-B 1572	29,1	16,2	13,6	10,2	11,8
ph I ant sin	Li-B 435	28,6	14,1	12,9	11,5	11,9
ph I ant sin	Li-B 436	27,9	15,0	13,4	10,4	11,9
ph II ant dex	Li-B 483	22,6	17,4	12,4	15,9	11,3
ph II ant dex	Li-B 492	21,3	16,5	12,4	17,2	11,8
ph II ant sin	Li-B 480	21,2	15,7	12,4	17,4	11,8
ph II ant sin	Li-B 481	21,6	15,4	12,7	17,0	11,6
ph III ant dex	Li-B 514	31,7	21,0	15,3	-	-
ph III ant dex	Li-B 515	30,4	20,3	15,2	-	-
ph III ant sin	Li-B 537	31,0	19,3	12,2	-	-
ph III ant sin	Li-B 538	32,6	19,8	12,5	-	-
ph I post sin	Li-B 432	29,8	15,4	12,7	10,1	11,9
ph I post sin	Li-B 433	29,2	15,0	12,9	9,8	11,9
ph II post sin	Li-B 478	21,2	15,4	11,7	15,5	11,0
ph II post sin	Li-B 479	21,8	15,2	11,5	15,5	10,6
ph III post dex	Li-B 520	27,8	18,5	11,3	-	-
ph III post dex	Li-B 528	27,6	18,6	12,4	-	-
ph III post sin	Li-B 539	25,6	18,5	12,6	-	-
ph III post sin	Li-B 540	25,8	18,5	12,8	-	-

Table 3. *Candiacervus* size II, measurements (in mm) of the phalanges of the composite skeleton.

Taula 3. Candiacervus *classe de mida II, mesures (en mm) de les falanges de l'esquelet muntat.*

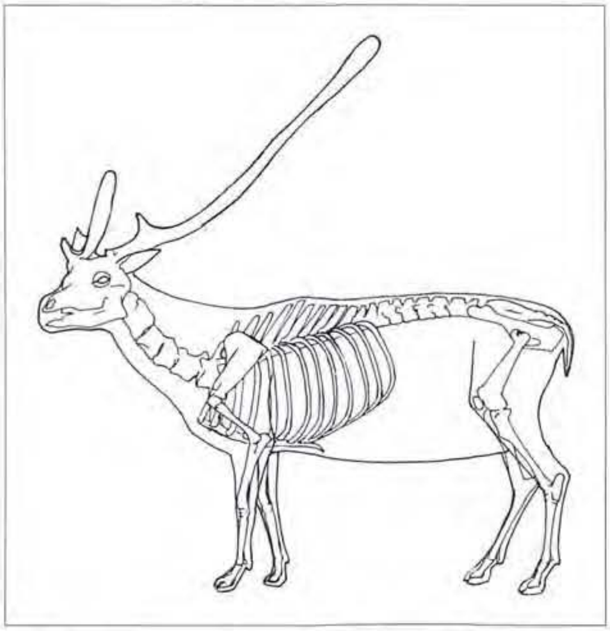


Fig. 9. *Candiacervus* size II from Liko Cave (Crete, Greece) appears to have had a heavy and massive trunk, a powerful neck and shoulder part, and stocky built and short but strong legs.

Fig. 9. Candiacervus *classe II de la cova de Liko (Creta, Gràcia) sembla haver tingut un tronc pesat i massís, un coll i unes espatlles poderosos, cames en forma de pilars, curtes, però fortes.*

than the real average size as the smallest specimens are more likely to have been lost. We select therefore four lateral third phalanges (all unnumbered) merely on common sense. The difference between adult, full-grown lateral phalanges and juvenile phalanges is easy to establish in this collection. All juvenile bones have a spongy and abrased appearance, are less firm, and have a lower weight.

DISCUSSION

The great additional value of a reconstructed skeleton above individual bones is that it informs us about the morphology of the complete animal. From the collection of metapodials it could already be inferred that the metatarsal is longer than the metacarpal, but now that we have a complete skeleton it is an undeniable fact. The average size of the metatarsal for size II is 137,2 mm, that for the metacarpal 108,2 mm, which results in a difference of 29 mm and a metacarpal/metatarsal index of 0,79, which is low compared to *Cervus elaphus* (0,89); this indicates that the metacarpal is relatively short in *Candiacervus* size II. Another striking feature of the complete animal is the curvature of the lumbar and lower thoracic region (Fig. 2). It appears that the back is only slightly curved (upward), more similar to a large deer like *Megaloceros verticornis* than to a small deer like *Axis axis*. The transversal processes are more or less orientated horizontally (Fig. 8) as in heavier bodied medium-sized artiodactyls like *Ovis*. In total, the animal has a heavy and massive trunk, a powerful neck and shoulder part, a stocky built and short but strong legs (Fig. 9).

An unexpected additional advantage of the composite skeleton is that we have now articulated bones, with the help of which functional morphologic interpretations can be made. Till now, such interpretations could only be done at the basis of individual bones, but not with articulations. The degree of flexion and other movements can now be checked with the joints themselves, not merely by extrapolating from articular surfaces.

The articulated, composite skeleton has illustrated once again the value of assembling a set of bones into a three dimensional animal. Features that are not otherwise obvious can be revealed when the bones are properly articulated and combined. The above mentioned difference in length between metatarsal and metacarpal, and the bending of the lumbar region are such cases. As a result, the animal gives a much different impression than expected.

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First of all, honour and gratitude are due to the late Paul Sondaar, who was the promotor behind all the Liko Cave excavations, and who never became tired of stressing the importance of the study of the evolution of island endemics, especially *Candiacervus*. From a more practical point of view, we'd like to thank Cor Strang for assisting us during all the stages of preparation and mounting and Chris Smeenk (both Nationaal Natuuhistorisch Museum, Leiden, The Netherlands) for enabling us to study the skeletons of the living deer. We also thank Aart Walen (Creatures Features, Doornenburg, The Netherlands) for the fruitful discussions we had with him on technical and anatomical subjects and Hans Brinkerink (Vista Natura, Baarn, The Netherlands) for making the cast of the skull and antlers.

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THE FOSSIL ENDEMIC GOAT *NESOGORAL CENISAE* N.SP. FROM CAMPIDANO, SARDINIA - CURSORIAL ADAPTATIONS IN INSULAR ENVIRONMENT

Jan VAN DER MADE

VAN DER MADE, J. 2005. The fossil endemic goat *Nesogoral cenisae* n.sp. from Campidano, Sardinia - cursorial adaptations in insular environment. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 347-368.

Resum

Es descriu el bòvid de Campidano i s'assigna a *Nesogoral cenisae* n.sp. Se suposa que alguns dels seus caràcters, com ara la possessió d'un metacarp llarg i gràcil, són una adaptació cursorial que ha modificat la seva morfologia caprina original.

Els ungulats insulars es coneixen per la seva "locomoció de marxes curtes" d'eficient energia. Una comparació dels artiodàctils fòssils insulars mostra com el seu tipus de locomoció depèn de la presència de carnívors a les illes, i se situa entre una locomoció de marxes curtes extrema als ambients lliures de carnívors i unes habilitats cursorials incrementades en presència de carnívors. Un nanisme moderat pot ocórrer quan hi ha carnívors.

Es discuteix l'evolució faunística de Sardenya. *Nesogoral* va arribar a l'illa durant la Crisi Messiniana. Rere l'aïllament de l'illa fa uns 5 Ma, va coexistir amb el hiènid *Chasmaporthetes*, i des de fa 0,9 Ma va conviure amb el cànid *Cynotherium*. O be l'ocupació d'un nínxol obert a les planes de l'illa va donar origen a una segona espècie, més cursorial, abans de l'arribada de *Cynotherium* (model de dos llinatges evolutius) o be l'arribada d'aquest cànid va fer que *Nesogoral* es tornés més corredor.

Paraules clau: Bovidae, Caprinae, nova espècie, endemisme, Sardenya, Pliocè, Pleistocè, locomoció, adaptacions cursorials, ambients insulars, paleoecologia.

Abstract

The bovid from Campidano (Sardinia) is described and assigned to *Nesogoral cenisae* n. sp. Some of its characters, such as a long and gracile metacarpal, are assumed to be a cursorial adaptation which modified its original caprine morphology.

Insular ungulates are known for their energy efficient "low gear locomotion". A comparison of endemic insular artiodactyls shows that the type of their locomotion depends on the carnivores on the island, and ranges between extreme low gear locomotion in carnivore free environment and an increase in cursorial abilities in the presence of carnivores. Moderate dwarfing may occur even when carnivores are present.

The faunal evolution of Sardinia is discussed. *Nesogoral* arrived to the island during the Messinian Crisis. After isolation of the island some 5 Ma ago, it coexisted with the hyaenid *Chasmaporthetes* and from some 0.9 Ma ago it coexisted with the canid *Cynotherium*. Either the occupation of an open niche on the plains of the island resulted in a second and more cursorial species already before the arrival of *Cynotherium* (two lineage model), or the arrival of this canid caused *Nesogoral* to become more cursorial (single lineage model).

Keywords: Bovidae, Caprinae, new species, endemic, Sardinia, Pliocene, Pleistocene, locomotion, cursorial adaptations, insular environment, paleoecology.

INTRODUCTION

A number of well fossilised bovid remains were collected by Paul Sondaar at Campidano in Sardinia from sediments that came from a well that was being dug. There were no remains of other animals. There were no means to know the age of the deposits or fossils. When I studied these fossils, they were in the Instituut voor Aardwetenschappen of the University of Utrecht (IVAU).

The known bovids of Sardinia are the Holocene/Recent *Capra* and *Ovis* and the Plio-Pleistocene *Nesogoral*. Sondaar (1987) and Sondaar *et al.* (1984, 1986) recognised two Plio-Pleistocene faunal associations in Sardinia, the earlier *Nesogoral* and the later *Tyrrhenicola* faunas. The earlier faunas are still not well known and *Nesogoral* is in fact known from only few localities. *Nesogoral melonii* was described by Dehaut on the basis of material he collected from Capo Figari. At present there are various fissure fillings known at Capo Figari, but it is not well known from which ones the older collections of Dehaut and Major come, which both contain this species. At the top of the hill there are two fissures, which are known as Capo Figari 1 and Capo Figari 2 and which have different faunas (Van der Made, 1988, 1999a). Gliozzi & Malatesta (1980) collected *Nesogoral* from Capo Figari 1 and stated that they believe that this is the place where the material described by Dehaut comes from. If this is correct, it is the type locality of the species. Capo Figari 2 has the arvicolid *Tyrrhenicola* and was believed to have no *Nesogoral*, but an astragalus from that locality was assigned to *Nesogoral* aff. *melonii* (Van der Made, 1999a). The material collected by Forsyth Major, either is homogeneous and comes from still another locality, or is a mixture of materials from Capo Figari 1 and 2. Thaler and a team of the IVAU also collected at Capo Figari. Pecorrini *et al.* (1973) mentioned, but did not describe, material from the earliest Pliocene of Capo Mannu as "Caprinae ?". Some fossils from that locality were described and figured as "*Nesogoral* sp." (Van der Made, 1999a). A second species of *Nesogoral* and an indeterminate caprine have been reported from Monte Tutavista near Orosei, but have not been described (Sondaar, 2000; Abazzi et al., 2004). In view of the still scarce record of the Plio-Pleistocene bovids from Sardinia, the material from Campidano is interesting.

Nesogoral is widely considered to be a caprine, and it is assumed to be particularly close to *Gallogoral*, *Nemorhaedus* and *Myotragus* (Gliozzi & Malatesta, 1980). *Nesogoral* and *Myotragus* were endemic to Sardinia (and Corsica) and the Eastern Balearics respectively. They are believed to have evolved from *Pachygazella*, an Asian bovid that reached these islands when they became connected to the continent during the Messinian Crisis (Gliozzi & Malatesta, 1980), when the Mediterranean became disconnected from the Atlantic Ocean and its sea level dropped several thousand meters (Hsü *et al.*, 1977). Gliozzi & Malatesta (1980) suggested that besides *Nesogoral* also *Myotragus*, *Gallogoral* and *Procamptoceras* form a branch that evolved from *Pachygazella*. DNA recovered from *Myotragus* fossils, situates this bovid within the Caprinae and suggests a closer relationship with *Budorcas*, *Ovis*, *Oreamnos* and *Rupicapra*, than with other caprines like *Capra*, *Hemitragus*, or *Ovibos*, *Capricornis* and *Nemorhaedus* (Lalueza-Fox *et al.*, 2000). After Lalueza-Fox *et al.* (this volume), *Myotragus* is closely related to the *Budorcas-Ovis* clade.

Whereas *Myotragus* is known by many fossils from many localities through studies that deal with a wide range of aspects of this animal and its ecology (Alcover *et al.*, 1981, 1999; Bover & Alcover, 1999; Köhler & Moyà-Solà, 2001, 2004; Lalueza-Fox *et al.*, 2000; Leinders & Sondaar, 1974; Spoor, 1988a, 1988b; etc.), *Nesogoral* is still not well known. Though all Sardinian bovids are considered to be Caprinae, we will see in the descriptions, that some morphological features do not fit normal caprines. For this, three relatively simple explanations will be discussed:

1) The bovid from Campidano is no caprine and does not belong to *Nesogoral*.

2) The bovid from Campidano belongs to *Nesogoral*, but this genus is not a caprine and became similar to caprines through convergent evolution.

3) The original caprine morphology of *Nesogoral* became modified due to the particular environment of Sardinia. This explanation implies the discussion of the ecology of insular environments.

MEASUREMENTS AND THEIR ABBREVIATIONS

Measurements are given in mm and are taken as indicated by Van der Made (1989, 1996).
DAP = Antero-posterior diameter, often length.
DAPd = DAP of the distal part of a bone.
DAPb = DAP at the base of the crown of the teeth.
DAPh = DAP of the "head" of a bone (eg. calcaneum, ulna).
DAPm = Minimal DAP of a bone.
DAPmax = maximal DAP pf a bone.
DAPn = DAP of the "neck" of a bone (eg. in calcaneum, ulna).
DAPo = Occlusal DAP in teeth.
DAPp = DAP of the proximal part of a bone.
DAPpf = DAP of the proximal articular facet of a bone.
DAPsf = DAP of the calcaneum, measured at the level of the sustentacular facet.
DAPIII, DAPIV, DAPl or DAPr = DAP of the distal articular surfaces of a metapodial, r /l indicates left or right of the axis of the bone, when it is not known whether the bone

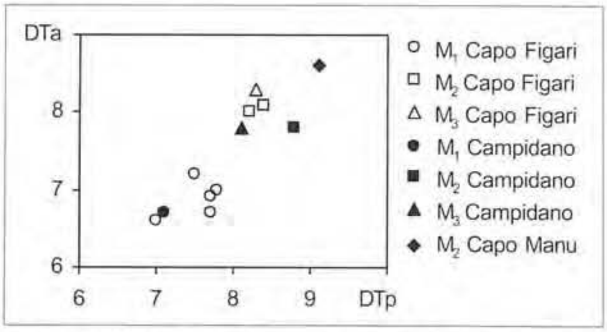


Fig. 1. Bivariate diagram of the lower cheek teeth of *Nesogoral* sp. from Capo Mannu (IVAU), *Nesogoral melonii* from Capo Figari 1 (IVAU; M_2, M_3), *Nesogoral* sp. from Capo Figari FM (NMB; M_1, M_2), and *Nesogoral cenisae* n. sp. from Campidano.

Fig. 1. Diagrama bivariat dels queixals de Nesogoral sp. De Capo Mannu (IVAU), Nesogoral melonii *de Capo Figari (IVAU; M_2, M_3),* Nesogoral *sp. from Capo Figari FM (NMB; M_1, M_2), and* Nesogoral cenisae *n. sp. from Campidano.*

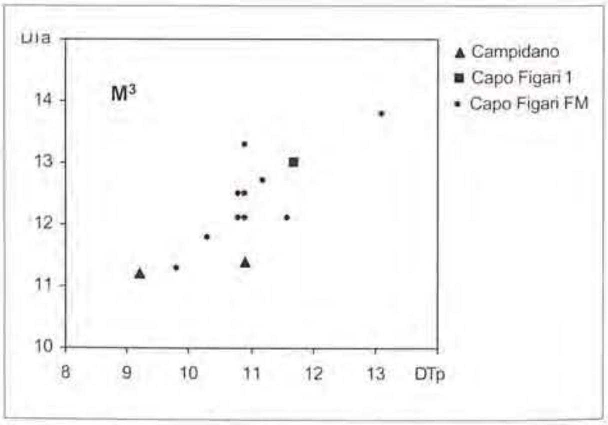


Fig. 2. Bivariate diagram of the M^3 of *Nesogoral* from Capo Figari 1 (IVAU) and Capo Figari FM (NMB) and from Campidano. (IVAU; M_2, M_3).

Fig. 2. Diagrama bivariat del M^3 de Nesogoral *de Capo Figari 1 (IVAU), Capo Figari FM (NMB) i de Campidano. (IVAU; M_2, M_3).*

itself is right or left.
DT = Transverse diameter.
DTa = DT of the anterior lobe of a tooth.
DTd = DT of the distal part of a bone.
DTfast = DT of the facet for the astragalus in the tibia or navicocuboid.
DTfu = DT of the upper part of the facet for the humerus of the ulna.
DTh = DT of the "head" of a bone (eg. in the calcaneum and ulna).
DTm = Minimal DT of a bone.
DTmax = Maximal DT of a bone.
DTn = DTof the "neck" of a bone.
DTp = DT of the proximal part of a bone, or DT of the posterior lobe of a tooth.
DTpf = DT of the proximal articular surface of a bone.
DTpp = DT of the third lobe of a M_3.
DTsf = DT of the calcaneum, measured at the level of the sustentacular facet.
H = Height.
h = Alternative height. In the magnum it is the minimal height of the elevated posterior structure at the posterior side of the bone.
Ha = H of the anterior lobe of a tooth.
L = length.
Lext = Length of the astragalus, measured at the lateral side. Length of the second phalanx, measured at the side that is not close to the axis of the foot.
Lint = Length of the astragalus, measured at the medial side. Length of the second phalanx, measured at the side that is close to the axis of the foot.
Lm = Length of the astragalus, measured in the middle of the bone.
Lu = Length of the upper part of a bone.
T1 = Thickness of the enamel measured at the first or anterior lobe of a tooth (also Ta).

COLLECTIONS AND THEIR ABBREVIATIONS

The material from Campidano is compared to recent and fossil material which I studied or which is kept in the following institutions:

AUT	Aristotle University of Thessaloniki.
CIAG	Centre d'Investigacions Arquelògics de Girona.
FASMN	Forschungsbereich Altsteinzeit Schloss Monrepos, Neuwied (Römisches-Germanisches Zentralmuseum, Forschungsinstitut für Vor- und Frühgeschichte).
FBFSU	Forschungstelle Bilzingsleben, Friedrich Schiller Universität Jena.
HMV	Historisches Museum, Verden.
HUJ	The Hebrew University of Jerusalem.
IGF	Istituto di Geologia, Firenze.
IPH	Institut de Paléontologie Humaine, Paris.
IPS	Institut de Paleontologia, Sabadell.
IPUW	Institut für Paläontologie der Universität, Wien.
IQW	Institut für Quartärpaláontologie, Weimar.
IVAU	Instituut Voor Aardwetenschappen, Utrecht.
LAUT	Laboratori d'Arqueologia, Universitat Rovira i Virgili de Tarragona.
LPTUP	Laboratoire de Prehistoire de Tautavel, Université de Perpignan.
LVH	Landesmuseum für Vorgeschichte, Halle.
MAC	Museo de Arqueología de Cartagena.
MB	Museo de Burgos, Burgos.
MCP	Musee Crozatier, Le Puy-en-Velay.
MNCN	Museo Nacional de Ciencias Naturales, Madrid.
MNHN	Muséum National d'Histoire Naturelle, Paris.
MRA	Musée Requien, Avignon.
NHCV	Natural History Collection of Vrisa.
NHM	Natural History Museum, London.
NMB	Naturhistorisches Museum, Basel.
NMM	Naturhistorisches Museum, Mainz.
NMMa	Naturhistorisch Museum, Maastricht.
NMW	Naturhistorisches Museum, Wien.
NNML	Nationaal Natuurhistorisch Museum, Leiden.
SMNK	Staatliches Museum für Naturkunde, Karlsruhe.
ZMA	Zoologisch Museum, Amsterdam.

DESCRIPTION AND COMPARISON

The **M_3** (Plate 1, fig. 5) is well worn, but what is left of the crown is still high. The enamel has a very fine crenelation. The lingual wall is relatively flat with a slight depression between the two anterior lobes and a third lobe that recedes a little, but with a well marked anterolingual stylid. The third lobe does not have a fossid. There is no interlobular column at the buccal side. A caprine fold is present, but it is not very strongly developed. The specimen is close in size to a specimen from Capo Figari (Fig. 1).

The **$M_{1/2}$** (Plate 1, fig. 1) have a morphology that is similar to that of the M_3, but of course, they lack the third lobe. These molars are close in size to their homologues in Capo Figari, while a specimen from Capo Mannu is a little bit larger (Fig. 1).

The **P_4** (Plate 1, fig. 3) has finely crenelated enamel and a high crown. The metaconid is well developed, placed far forward and the metaprecristid (terminology of Van der Made, 1996) extends forward to close the anterior fossid. The lingual wall is smoothly undulating, but the buccal wall has a deep grove separating the anterior and posterior lobe. In size the specimen is close to the P_4 from Capo Figari.

The **M^3** (Plate 1, figs. 2 & 4) has smooth enamel and a high crown. The buccal wall has three well marked styles with relatively flat areas between them (the exocristas are thus not well developed). The postero-buccal style extends also a little more distally than the rest of the tooth. There is no lingual interlobular column. The morphology is essentially similar to that of the specimens from Capo Figari (Pl. 1, fig. 6). The specimens are relatively small and one of them is even just outside the ranges of the Capo Figari sample (Fig. 2).

The **$M^{1/2}$** have morphologies that are largely similar to the M^3.

The **ulna** (Plate 2, fig. 5) has a facet for the humerus, which is rather wide in its upper part. In this it is like in Caprinae, but unlike other ruminants, where this facet tends to be narrower. The facet for the humerus meets the facets for the radius, forming little more or less horizontal crests. This is the widest part of the bone. The bone is not very wide here and there is no important lateral extension of the lateral facet for the radius. At this place, Caprinae tend to be wider and *Capra* has the ulna reaching even further medially than the radius. Besides, in *Capra*, the radius and ulna tend to be fused at this place, which evidently, is not the case here.

The **radius** (Plate 4, figs. 6-7) has a distal articular surface that has a relatively narrow appearance. The proximal facet sticks out medially over the shaft in a very pronounced way (Pl. 4, fig7a, 7c), which is typical in Caprinae, but not in most other Bovidae, including gazellas.

The **magnum** has a morphology that is common among ruminants. If seen from the back, the highest point of the bone is where the facets for the scaphoid and lunar meet; immediately laterally the surface slopes down. In Caprinae and *Nesogoral* from Capo Figari (Plate 4, fig. 5), this slope is steeper and there seems to be more difference in height between these two points than in other ruminants. In this respect, the magnum is not very caprine-like.

The **metacarpal** (Plate 2, fig. 1) is a surprisingly long and slender bone. The shaft widens gently towards the distal articulations, not abruptly as in most Caprinae.

The distal articular surface has some interesting features. When seen from distal, the outline is more or less trapezoidal, and in most bovids and cervids, the lateral sides of the "trapezium" are more or less straight and clearly convergent. In some bovids, including Caprinae, these sides are more or less parallel, or are parallel in their plantar half and convergent in their dorsal half. This is also the case in this metapodial and in a specimen from Capo Figari 1 (Plate 2, fig. 6), which might be a metacarpal. But in the metatarsal, the sides seem to be predominantly straight and convergent.

Each of the two distal articular surfaces is composed of two half cylinders, the smaller one having a much smaller diameter than the larger one in many Caprinae. In the specimen from Campidano, the difference is not so great and in this it is more like other bovids and like cervids. In Caprinae, the dorsal surface of the smaller cylinder tends to be horizontal, or even slightly dipping towards the larger cylinder, whereas in other bovids and cervids, this surface tends to slope away from the larger cylinder. In this, the Campidano metapodial is more like most bovids and cervids.

In most bovids and cervids, when seen from the side, the cylindrical distal articular surface is about half of a cylinder, but in Caprinae, it is a larger section, permitting thus a wider range of dorso-plantar movement of the first phalanx. In Campidano, the morphology is more like in cervidae and most bovidae that are no Caprinae.

Between the two cylinders of each of the two distal articular surfaces, there is a crest, which is often more marked on the plantar side than on the dorsal side. This crest is very well developed at any place in Caprinae, and in particular in *Capra*, but not in so much in other bovids, cervids and in the specimens from Campidano and Capo Figari. The two crests of the two articular surfaces converge usually dorsally, but tend to be parallel or converging plantarly in Caprinae. In this character, the specimen from Campidano is more like cervids and most bovids.

As said above, the metacarpal is surprisingly long and gracile. That is, compared to Caprinae and bearing in mind the common shortening of metapodials in insular environments. The specimen is more elongate than in other recent and fossil Caprinae (Fig. 3). There is a very clear difference with *Myotragus*, which is assumed to be closely related and which is also an insular endemic. While *Myotragus* has (together with *Budorcas*) the most robust metapodials of the Caprinae, *Nesogoral* has the most gracile or elongate ones (Fig. 4). Size and proportions of the metapodial are close to that of the continental Late Miocene *Gazella*.

The **tibia** is poorly preserved.

The **calcaneum** (Plate 4, fig. 4) has a head, that, when seen from the side, has a pointed shape that overhangs the tuber. This shape is unlike in *Capra*, but occurs in other Caprinae.

The **astragalus** (Plate 4, figs. 1-3, 8) has a short and wide appearance as in Caprinae, whereas in most other bovids and in cervids this bone has a more elongate appearance. The specimens from Campidano have the same size as those of *Nesogoral melonii* from Capo Figari (FM collection), but are larger than the one of *Nesogoral* sp. from Capo Figari 2. All these specimens are clearly larger than that of the smallest cervid from Sardinia, which is *M. cazioti* (Fig. 5).

The **metatarsal** (Plate 2, figs. 2 & 4) is represented by proximal and distal fragments. The proximal end is wide and has a short antero-posterior diameter. The posterior facet with the navico-cuboid is directed transversely and its end that is in the middle of the bone is clearly elevated above the proximal surface of the bone forming a point that can be seen very well in anterior view (Plate 2, fig. 2a). This is a typical bovid morphology, cervids do not have this facet on a point-like elevation. In cervids, the proximal end of the bone is as wide at the posterior side as in the middle. In bovids, this is often not the case. In many bovids, the antero-posterior diameter of the bone is large compared to the transverse diameter. This is noted in the shaft, but even better in the the proximal surface of the bone, where the posterior facet for the cubo-navicular and the smaller cuneiform are placed further backwards on a narrow posterior extension of the proximal surface. Such a morphology is seen in for instance *Gazella*. The metatarsals of the Caprinae, and the specimen form Campidano, have a relatively large transverse diameter and have the two posterior facets, mentioned above, placed more anteriorly.

The distal end of the metatarsal has an open gully in the middle as in bovids, whereas cervids have this gully covered by a bony bridge. The shaft widenes gently, and not abruptly, towards the distal end. The morphology of the distal articular surfaces is like in the metacarpal. There is one exception, and that is one of the two articulations of a distal metatarsal (Plate 2, figure 4b). There are no clear signs of deformation that could explain this otherwise a-typical morphology. Otherwise the morphology is unlike in Caprinae as is also seen in a particularly well preserved distal metapodial (Plate 2, fig. 3).

Some of the phalanges appear to articulate with each other and with a distal metatarsal. These specimens are marked with an asterisk in the tables.

Fig. 3. Bivariate diagram of the metacarpal in selected Caprinae. The taxa included and the provenance of the data is indicated under Figure 4.

Fig. 3. Diagrama bivariat del metacarpià de Caprinae seleccionats. Els taxa inclusos i la seva procedència, com a la figura 4.

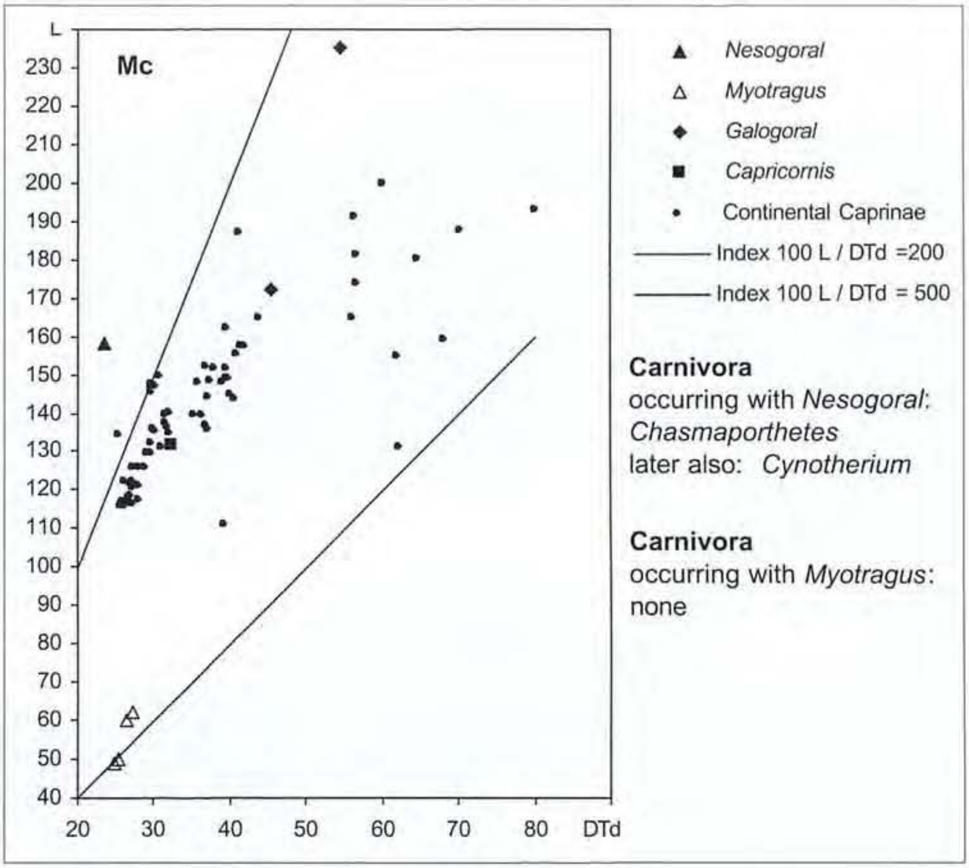


Fig. 4. Metacarpal index 100 L / DTd in selected Caprinae. *Myotragus* from Son Maiol (IVAU), recent *Budorcas taxicolor* (NHM), *Praeovibos priscus* from Bad Frankenhausen (IQW; estimated), recent *Ovibos moschatus* (NML), *Ovibos suessenbornensis* from Süssenborn (IQW), recent *Oreamnos americanus* (NMW), *Soergelia elisabethae* from Süssenborn (IQW) and Apollonia 1 (AUT), *Megalovis* from Senèze (NMB) and Nihowan (MNHN), *Galogoral* from Senèze (NMB) and (?) Olivola (IGF), *Hemitragus bonali* from Hundsheim (NMB), *Capra ibex* from Petralona (AUT), recent *Capra ibex* (LPTUP), *Capriconris sumatrensis* (NML), recent *Capra pyrenaica* (MNCN), *Ovis antiqua* from Cueva Victoria (MAC), *Capra alba* from Quibas (MNCN), recent *Pseudois nayaur* (NHM), recent *Rupicapra* (LPTUP), *Nesogoral* from Campidano (IVAU).

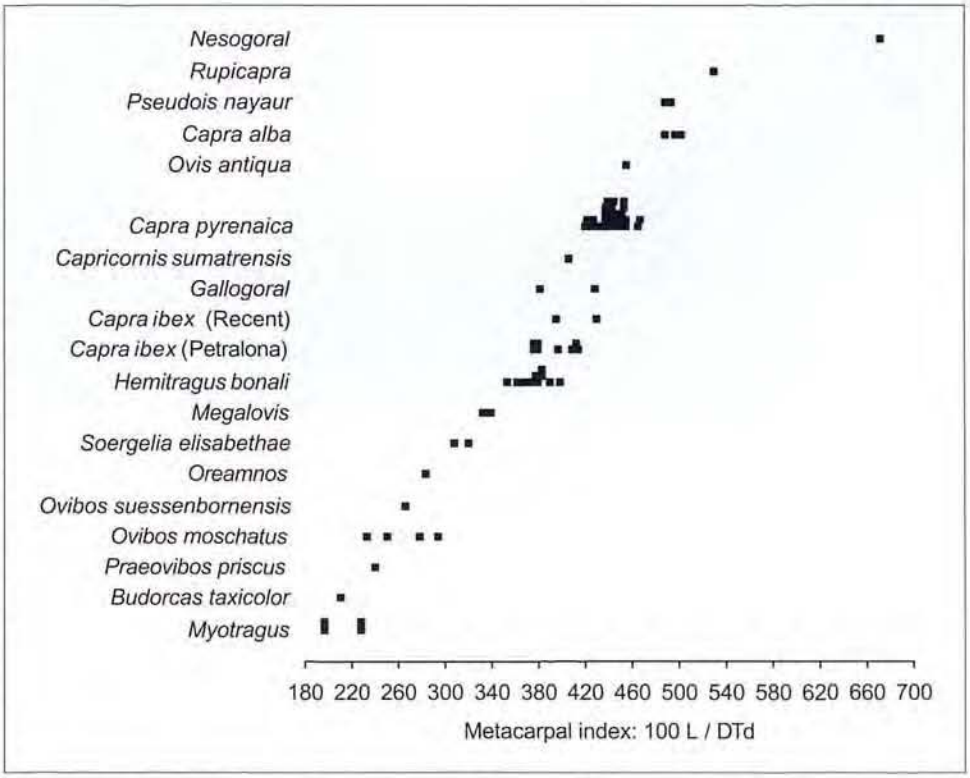


Fig. 4. Index metacarpià, 100 L / DTd, a Caprinae seleccionats. Myotragus *de Son Maiol (IVAU),* Budorcas taxicolor *recent (NHM),* Praeovibos priscus *de Bad Frankenhausen (IQW; estimat),* Ovibos moschatus *recent (NML),* Ovibos suessenbornensis *de Süssenborn (IQW),* Oreamnos americanus *recent (NMW),* Soergelia elisabethae *de Süssenborn (IQW) i Apollonia 1 (AUT),* Megalovis *de Senèze (NMB) i Nihowan (MNHN),* Gallogoral *de Senèze (NMB) i (?) Olivola (IGF),* Hemitragus bonali *de Hundsheim (NMB),* Capra ibex *de Petralona (AUT),* Capra ibex *recent (LPTUP),* Capriconris sumatrensis *(NML),* Capra pyrenaica *recent (MNCN),* Ovis antiqua *de Cueva Victoria (MAC),* Capra alba *de Quibas (MNCN),* Pseudois nayaur *recent (NHM),* Rupicapra *recent (LPTUP),* Nesogoral *de Campidano (IVAU).*

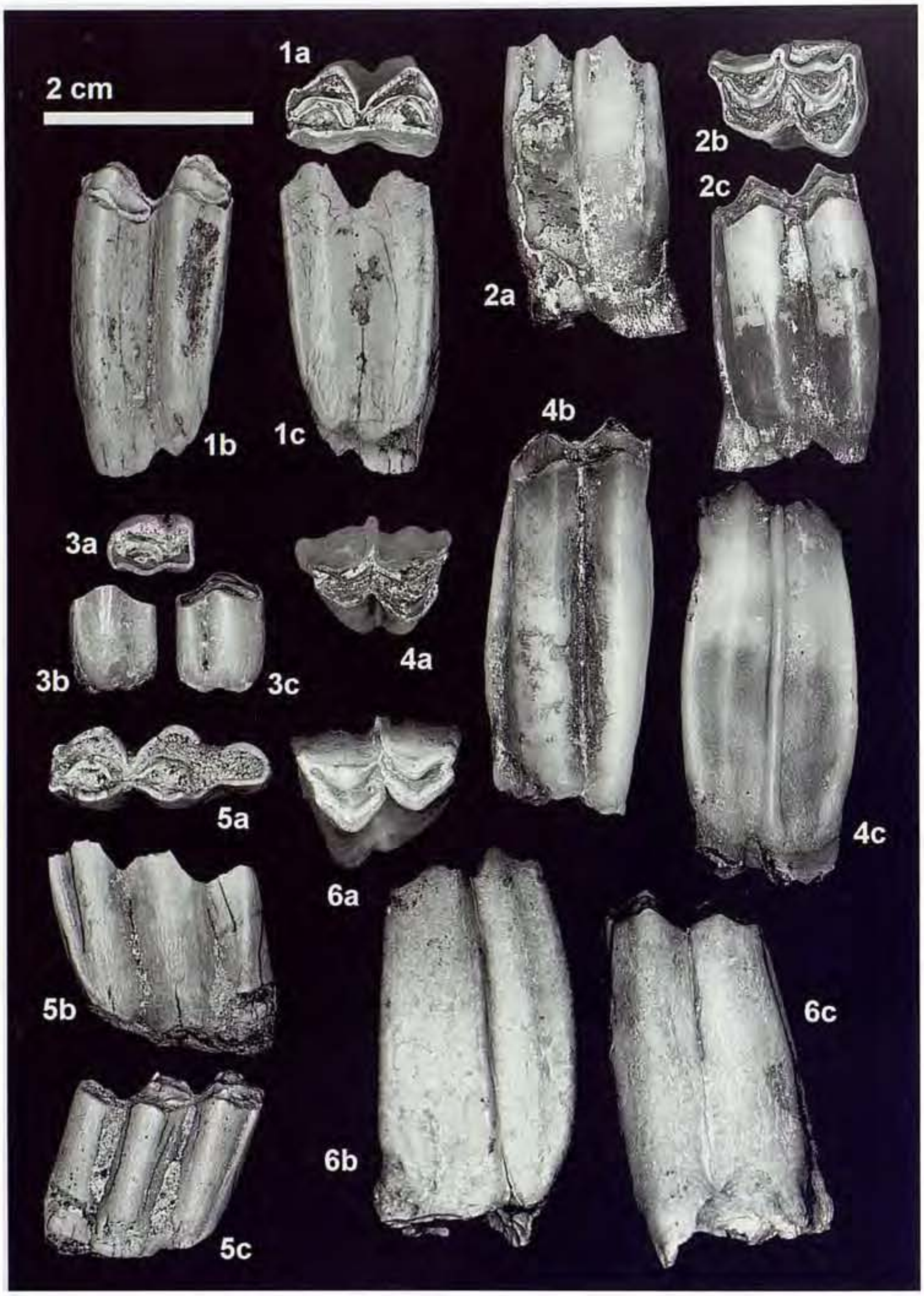


Plate 1. *Nesogoral cenisae* n.sp. from Campidano (figs. 1-5) and *Nesogoral* from Capo Figari FM (fig. 6; NMB).
Figure 1. Right M_2: a) occlusal view, b) buccal view, c) lingual view.
Figure 2. Right M^3:a) buccal view, b) occlusal view, c) lingual view.
Figure 3. Right P_4: a) occlusal view, b) lingual view, c) buccal view.
Figure 4. Right M_3: a) occlusal view, b) lingual view, c) buccal view.
Figure 5. Right M_3: a) occlusal view, b) lingual view, c) buccal view.
Figure 6. Ty 5439 - left M^3: a) occlusal view, b) buccal view, c) lingual view.

Làmina 1. Nesogoral cenisae *n.sp. de Campidano (figs. 1-5) i* Nesogoral *de Capo Figari FM (fig. 6; NMB).*
Figura 1. M_2 Dret: a) norma oclusal, b) norma bucal, c) norma lingual.
Figura 2. M^3 Dret:a) norma bucal, b) norma oclusal, c) norma lingual.
Figura 3. P_4 Dret: a) norma oclusal, b) norma lingual, c) norma bucal.
Figura 4. M_3 Dret: a) norma oclusal, b) norma lingual, c) norma bucal.
Figura 5. M_3 Dret: a) norma oclusal, b) norma lingual, c) norma bucal.
Figura 6. Ty 5439 - M^3 esquerre: a) norma oclusal, b) norma bucal, c) norma lingual.

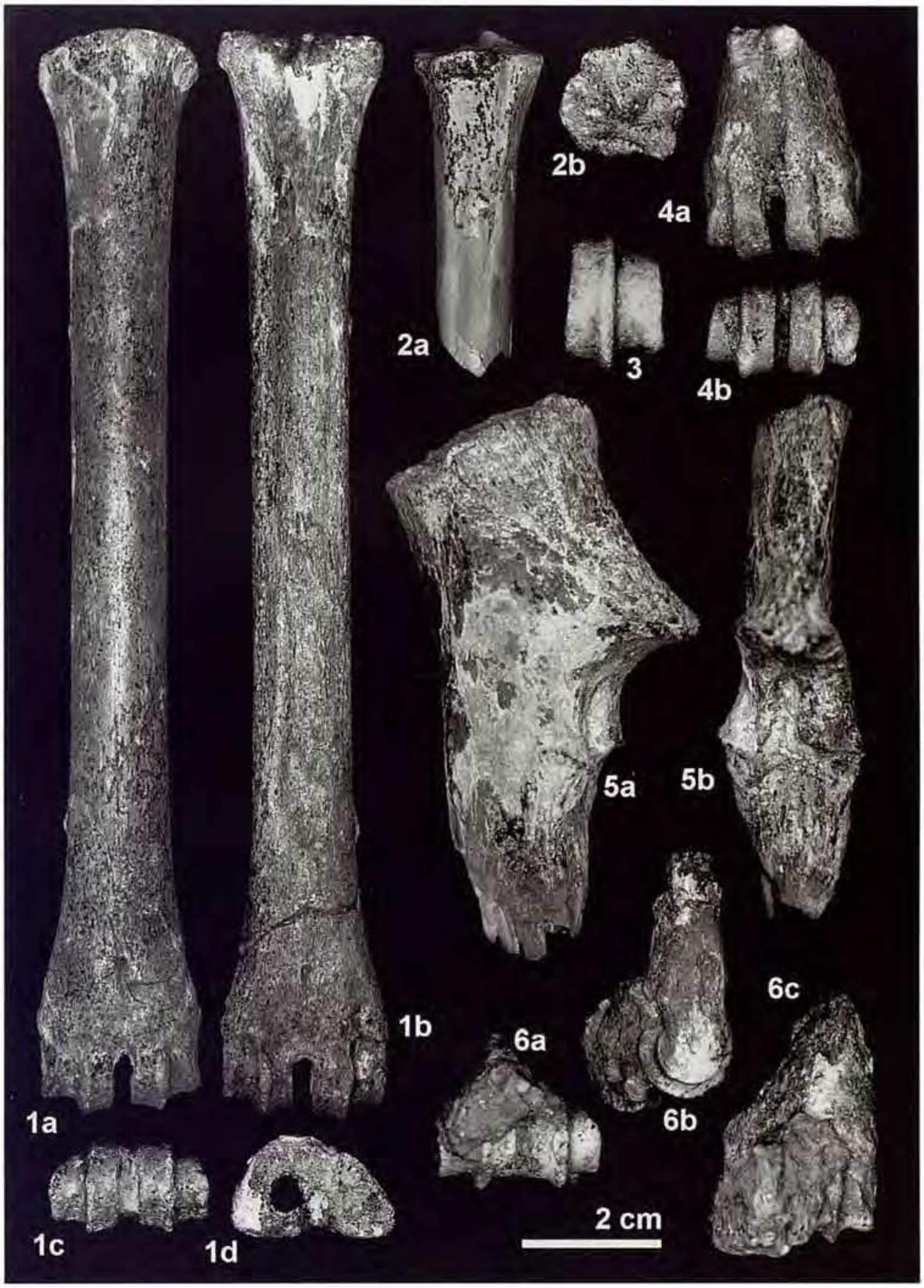
The **first phalanx** is represented by specimens from the fore limb (Plate 3, fig. 1) and hind limb (Plate 3, figs. 3 & 4). Whereas in most Bovidae and in Cervidae, the bone is laterally compressed, in Caprinae the phalanx is wide. The specimens from Campidano are not very wide. When seen from proximal, not much bone can be seen below (or plantar) of the facet, as in most Caprinae. The upper border of the proximal facet is not flat (as in Caprinae), but slopes away from the axis of the foot. In one of the specimens there is a little bump on the dorsal surface (Plate 2, fig. 2c) that is elevated above the facet, which is common in cervids, but usually absent in Caprinae. The proximal facet has a vertical furrow in the middle (that articulates with a crest on the metapodials). The part of the facet on the external side of the furrow is relatively wide in Caprinae, but not so in the specimens from Campidano. In Caprinae, the two little facets for the sesamoids, are lower and relatively wider than in other Bovidae, in Cervidae and in the phalanges from Campidano. All these characters contribute to the wide aspect in Caprinae and the more narrow appearance in other ruminants and Campidano.

In the specimens from Campidano, the distal end of the first phalanx is relatively high, but not as high as in cervids and most bovids. The plantar surface is rather flat, as is the case as in Caprinae.

The **second phalanx** (Plate 3, fig. 2) has a small "facet post-articulaire" (sensu Heintz, 1970) on the proximal surface. Not only does it extend only a little in plantar direction, but its surface slopes plantarly and is placed

Plate 2. *Nesogoral cenisae* n.sp. from Campidano (figs. 1-5) and *Nesogoral melonii* from Capo Figari 1 (fig. 6; IVAU).
Figure 1. Right metacarpal: a) anterior view, b) posterior view, c) distal view, d) proximal view.
Figure 2. Left metatarsal: a) anterior view, b) proximal view.
Figure 3. Distal metapodial: distal view (not to scale).
Figure 4. Distal metatarsal: a) anterior view, b) distal view.
Figure 5. Right ulna: a) lateral view, b) anterior view.
Figure 6. Distal metapodial: a) distal view, b) view from the side, c) dorsal view.

Làmina 2. Nesogoral cenisae *n.sp. de Campidano (figs. 1-5) i* Nesogoral melonii *de Capo Figari 1 (fig. 6; IVAU).*
Figura 1. Metacarpià dret: a) norma anterior, b) norma posterior, c) norma distal, d) norma proximal.
Figura 2. Metatarsià esquerre: a) norma anterior, b) norma proximal.
Figura 3. Detàpode distal: norma distal (no a escala).
Figura 4. Metatarsià distal: a) norma anterior, b) norma distal.
Figura 5. Ulna dreta: a) norma lateral, b) norma anterior.
Figura 6. Metàpode distal: a) norma distal, b) visió des del costat, c) norma dorsal.



more distally than the proximal articulation surface. This morphology is typical of Caprinae, and occurs also in Antilopinae like *Gazella* and *Madoqua*, but most other bovids and all cervids have this "facet post-articulaire" developed as a massive proximally and plantarly projecting bump.

The proximal facet is wide, as is common in Caprinae, but unlike in most other Bovidae and in Cervidae. When seen from the side with the plantar side horizontal, the plantar part of the facet is approximately vertical and the dorsal part overhangs and is the most proximal part of the bone. This is common in Caprinae, whereas in most other Bovidae and in Cervidae, the plantar part of the facet is dipping proximally and not even the dorsal part of the facet is vertical. As a result, the plantar part of the facet extends more in proximal direction. Seen from the side, the curvature of the facet is like a small section of a circle, as common in Caprinae, but a much smaller section than in cervids and most other bovids.

The distal facet is wide, as is typical in most Caprinae, whereas most other bovids and cervids have narrower facets. This is shown very well with an index 100 DAPd / DTd, which has low values in wide facets and high values in narrow facets. Most Caprinae tend to have values between 100 and 125, while Cervidae and many bovids, including *Gazella*, have values between 120 and 155 (Fig. 6). Some Caprinae, like *Capricornis* and *Gallogoral* may have relatively high values, while other bovids, like *Cephalophus* and *Gazellospira* may have relatively low values. The large Bovini are expected to have low

Teeth	DAP	DAPb	DTa	DTp	DTpp	Ha	DAPmax	T1
M3	dext	21.7	20.3	7.8	8.1	5.1		
M1/2	sin	10.6	>10.6	6.7	7.1			
M1/2	dext	13.9	10.0	—	—			
M1/2	dext	14.4	13.4	7.8	8.8		>>25.6	0.6
P4	dext	8.3	8.4	5.6	5.8			
M^3	dext	14.1	15.3	16.4	10.9		>33.5	16.8
M^3	sin	15.0	14.6	—	—			15.4
M^3	sin	16.7	15.8	—	—			
M^3	dext	14.3	14.6	11.2	9.2		>>22.9	15.5
M$^{1/2}$	dext	≥13.7	—	—	10.4			
M$^{1/2}$	sin	12.8	11.8					
M$^{1/2}$	dext	13.1	12.0	—	—		>28.4	
Ulna	DTh	DAPn	DTn	DTfu	DTmax	DAPmax	DAPf	Lu
dext	—	20.1	7.9	—	16.9	24.7	16.9	—
dext	—	20.7	8.8	11.2	15.5	26.8	17.9	—
dext	10.6	21.3	8.0	10.7	—	21.9	—	42.9
Radius	DAPp	DTp	L	DAPd	DTd	DAPdf	DTdf	
dext	>13.5	>26.8	—	—	—	—	—	
dext	14.9	—	—	—	—	—	—	
sin	—	—	—	20.1	29.8	15.8	26.1	
dext	—	—	—	20.5	29.3	15.9	25.7	
Magnum	DAP	DT	H	h				
sin	14.9	14.3	10.5	7.7				

Table 1

values, like Caprinae, but then they also tend to have robust metapodials, which is another similarity. In insular cervids, the phalanges may become shortened and more robust like the metapodials (eg. De Vos, 1979). Some specimens of *Cervus* aff. *cerigensis*, which has extremely shortened metapodials, do not show an increase in width of the distal facet of the second phalanx (Fig. 6), suggesting that the shortening of the phalanges, as an adaptation to insular environment, does not affect the relative width of the distal facets.

The distal facet of the second phalanx consists of two parts, separated by a furrow. The part that is closest to the axis of the foot is low, but not as low as in *Capra* and many other Caprinae. This part of the facet does not project much more forward beyond the other part of the distal facet. This is as in most ruminants, including *Gazella*, but unlike in most Caprinae, including *Capricornis*. *Nesogoral* from Capo Figari has the axial part of the facet low and a little more protruding than in Campidano, but not so much as in most Caprinae (Plate 3, fig. 6).

The **third phalanx** (Plate 3, fig. 5) is short and high. Caprinae like *Capricornis*, and many other Bovidae and Cervidae, have much more elongate phalanges, that end in a sharper distal "point", but *Ovis*, *Capra*, *Hemitragus* etc. have short and high phalanges.

Seen from lateral, the dorsal profile of the anterior part is relatively steep and convex. The extensory apophysis is large and, when seen from lateral, does not show up as a separate elevation, but forms part of this convex profile. However, behind the apophysis there is a relatively large depressed area. The proximal facet ends dorsally much below the apex of the extensory apophysis. A large elevated extensory apophysis is common in many Caprinae, but not in other Bovidae and in Cervidae.

When seen from the side, the proximal facet is vertical in its dorsal part and horizontal in its plantar part and forms more or less a quarter of a circle. This is common in many Caprinae, but some Caprinae (eg. *Capricornis*), Cervidae and other Bovidae have less curvature. The plantar part of the facet extends far proximally and forms a relatively large horizontal surface. *Myotragus* has this facet with a similar morphology (Spoor, 1988, Pl. 2, fig 12) or with less curvature and lacking an extensive horizontal part (Köhler & Moyà-Solà, 2001, Fig. 3).

DISCUSSION

The morphology of the Campidano bovid compared to the Caprinae

The first and second explanations mentioned in the introduction for some morphologies in the Campidano

Metapodial	Mc	Mc	Mc	Mt	Mt	Mt	Mt*	Mp
	dext	?	right	sin	dext	?	?	left
DAPp	15.0	—	—	18.6	>17.7	—	—	—
DTp	23.8	—	—	18.7	—	—	—	—
DAPpf	≥14.4	—	—	17.3	—	—	—	—
DTpf	22.9	—	—	17.6	—	—	—	—
DAPm	10.1	—	—	—	—	≤11.4	—	—
DTm	14.5	—	—	—	12.0	—	—	—
DTd	23.5	23.4	—	—	—	≥21.9	22.5	—
DAPIII/ DAPl	13.6	15.6	—	—	—	13.7	14.3	14.3
DTIII / DTl	10.3	10.3	—	—	—	9.8	10.5	9.9
DAPIV/ DAPr	13.8	14.8	—	15.4	—	13.9	14.3	—
DTIV /DTr	10.0	10.1	—	11.1	—	-10.3	9.7	—
L			158.0					
L3			153.7					
L4			154.5					
Phalanx	DAPp	DAPpf	DTp	L	DAPd	DTd	Lint	Lext
phalanx 1		right	14.2	12.6	9.6	36.8	8.2	9.7
phalanx 1		left	—	—	—	—	8.2	8.4
phalanx 1	manus?	right	15.6	14.2	12.1	34.2	>9.4	11.3
phalanx 1	pes?	left	14.2	13.3	11.2	34.2	8.6	9.7
phalanx 1	pes?	right	14.1	13.1	11.1	34.4	8.4	9.6
phalanx 1	manus	left	—	—	12.7	33.8	—	—
phalanx 2		right	—	—	—	>18.3	≥8.5	—
phalanx 1*	pes	left	14.9	14.4	11.6	32.2	8.5	9.8
phalanx 1*	pes	right	14.9	13.7	11.4	33.2	8.5	9.6
phalanx 2*	pes	left	12.6	10.5	19.2	9.2	8.2	21.7
phalanx 2*	pes	right	12.8	10.6	19.9	9.2	8.5	—
phalanx 3*	pes	left	13.8		8.5	23.3		
phalanx 3*	pes	right	13.4		8.6	22.6		
Tibia	DAPd	DTd	DTfast					
dext	17.6	22.2	15.9					
Calcaneum	DAPh	DTh	DAPn	DTn	DAPsf	DTsf	Lu	
dext		—	—	15.1	7.0	18.4	16.0	
dext		15.5	14.8	14.3	8.1	—	—	-37.4
Astragalus	Lext	Lm	Lint	DTp	DTd			
sin	29.5	24.2	27.5	18.8	18.0			
sin	—	22.9	26.2	16.2	—			
sin	≥25.1	21.8	25.2	16.1	16.1			
dext	30.6	24.8	>27.7	—	18.9			

Table 1. Measurements of the teeth and bones of the bovid from Campidano. All measurements are in mm. The metapodial and phalanges marked with * belong to the same foot. Where "sin" and "dext" are indicated, this refers to the side of the body. In phalanges and fragments of metapodials, it is often not known whether they belonged to a right or left limb, and where "right" and "left" is indicated, this refers to the position relative to the axis of the foot.

Taula 1. *Mesures de les dents i ossos del bòvid de Campidano. Totes, en mm. Els metàpodes i falanges marcats amb un asterisc (*) pertanyen al mateix peu. On s'indiquen « sin » i « dext », es refereix al costat del cos. Les falanges i fragments de metàpodes soviet no se sap si pertanyen a un membre dret o esquerre, i on s'indica «right» i «left» es refereix a la posició respecte l'eix del peu.*

material that do not seem to fit the Caprinae either imply that: the Campidano material is no *Nesogoral*, or *Nesogoral* is not a caprine, but became similar to caprines through convergent evolution. For this it is necessary to discuss the morphology of early Caprinae.

Caprinae appeared relatively late in the fossil record, but existed in Europe from the early Late Miocene onwards (Köhler *et al.*, 1995; Alcalá & Morales, 1997; Gentry *et al.*, 1999). The latter authors state that the Caprinae are a well defined group on the basis of DNA, but that there are few or no morphological characters that define the subfamily and proceed to discuss some cranial and dental characters. However, Caprinae have so many peculiar morphologies in the post cranial skeleton, that it should be possible to find characters that help to recognise most members of this subfamily. Though, as usual, the many typical morphologies may get fewer closer to the origin of the group.

Gliozzi & Malatesta (1980) indicated *Pachygazella* as the most likely ancestor of *Nesogoral*, but some Late Miocene Caprinae were described after their study. I have not had access to postcranial material of *Pachygazella* or to a publication describing it, but of at least some of the European Late Miocene caprines, phalanges and metapodials have been described and figured. *Norbertia* from the latest Miocene of Maramena is primitive in being still not very hypsodont and having a P4 that may have the anterior fossid open or more or less closed, but already very typically caprine in having a wide second phalanx with a proximal facet that overhangs a little and has relatively little curvature, a reduced "plateau post-articulaire" and a low axial half of the distal facet that protrudes much distally, and in having a third phalanx with a very extended horizontal part of the proximal articular facet and a well developed extensor apophysis (Köhler *et al.*, 1995). These morphologies form part of foot type C of Köhler (1993).

Köhler (1993) described a number of characters that are typical of three foot types and interpreted these in terms of ecology (A wooded and humid, B open flat and dry, C mountainous habitats) and believed that these types do not reflect phylogeny. This is certainly true for most characters, but type C seems to be mainly restricted to Caprinae and Neotragini, and a number of characters related to the C type adaptation have probably evolved only in Caprinae. Köhler (1993) used *Gazella* as an example of foot type B, but also indicated that this type is of the open landscapes. *Bison* was common in open landscapes and has a large "plateau postarticulaire" and therefore a locomotion that is different from that of *Gazella*. Antilopinae, like *Gazella* and *Madoqua* have second phalanges with a reduced "plateau postarticulaire" and an overhanging proximal facet and third phalanges with a proximal facet with a well developed horizontal part. These morphologies indicate a posture that is necessary for the "pogostick effect" described by Leinders (1979).

This pogostick effect is known from horses and ruminants. This is an adaptation which involves the modification of several muscles, tendons and ligaments. One of them is the *musculus interosseus*. Contraction of this muscle causes volar flexion of the foot. When this muscle is replaced through tendofication by a tendon, the Tendo interosseus or suspensory ligament, the elastic properties of the tendon cause volar flexion. Dorsal flexion of the phalanges causes this elastic tendon to become extended, and thus acts to absorb the shock of landing after jumping. If not constrained by the action of muscles, the extension of this tendon will automatically cause volar flection as a reaction. This is a mechanism which preserves or re-uses energy in running.

For the pogostick effect to function, a particular posture in rest is necessary. While normally the metapodial and phalanges are approximately alligned, in animals with pogostick locomotion, the first phalanx tends to have some dorsal flexion with respect to the metapodial, the second phalanx has volar flexion with respect to the first phalanx, and the third phalanx has again dorsal flexion. This posture is seen in many morphologies, some of the easiest recognisable are:

- Distal articulations of the metapodials that permit more movement in dorso-plantar direction.
- A distal facet in the first phalanx that extends much on the plantar side.
- An "overhangning" proximal facet in the second phalanx.
- A reduced (or receding) plateau post articulaire in the second phalanx.
- A well developed extensor apophysis in the third phalanx.
- A proximal facet in the third phalanx with a relatively large horizontal part.

This "pogostick locomotion" is probably a necessary pre-adaptation to arrive at a C type of locomotion and starting with this morphology, the Caprinae, developed existing morphologies further and acquired a set of morphologies which are possibly a further adaptation to mountainous or rocky environements, like:

- A wide second phalanx having the axial part of the distal facet protruding much distally.
- Shorter and more robust metapodials with: a shaft that widens abruptly towards the distal articulations, and distal articulations with a particular shape (see under "description and comparison").
- No elevated area of insertion of tendon of the lateral or medial digital extensor muscles on the proximal end of the dorsal surface of the first phalanx.
- Reduction of the "height" of the facets for the sesamoids on the first phalanx.
- Shorter third phalanges.

In addition, Caprinae have typical morphologies in the proximal metatarsal, ulna, and many carpal and tarsal bones. (Which possibly are also adaptations to a rocky or mountainous environment). The Antilopinae do not only share the pogostick locomotion (and corresponding morphologies) with the Caprinae, but also many dental characters, like: the loss of interlobular columns, flat lingual walls in the lower molars, the shape of the buccal wall of the upper molars, etc. Caprinae, have a dentition that is basically more hypsodont and usually with more reduced premolars. It is possible that Caprinae evolved from Antilopinae.

Bearing the foregoing in mind, the characters that suggest that the Campidano bovid may not be a caprine are:

- A long and gracile metacarpal.
- The gradual increase in width from the shaft of the metapodials to the distal end of the bone.

Fig. 5. Bivariate diagram of the astragalus: *Nesogoral* from Capo Figari FM (NMB), Campidano and Capo Figari 2 (IVAU) and *Megaloceros cazioti* from Corbeddu (IVAU).

Fig. 5. Diagrama bivariat de l'astràgal de: Nesogoral *de Capo Figari FM (NMB), Campidano i Capo Figari 2 (IVAU), i* Megaloceros cazioti *de Corbeddu (IVAU).*

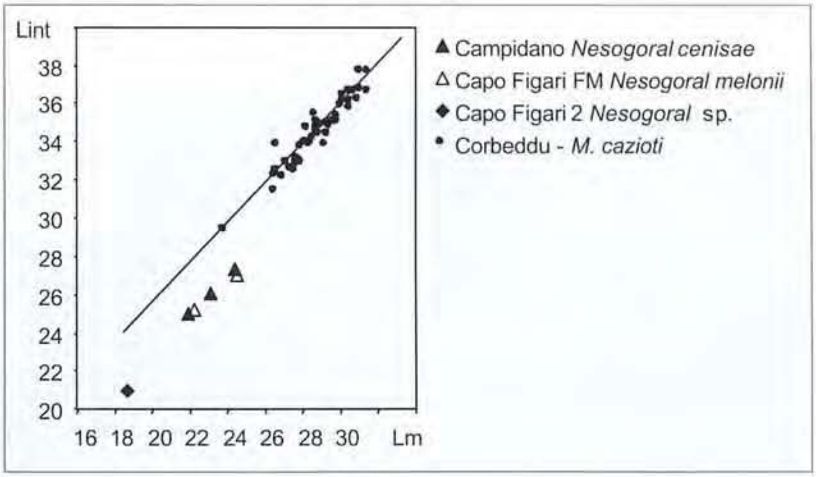


Fig. 6. The index 100 DAPd / DTd in the second phalanx in selected Bovidae and Cervidae.

A) Bovidae with a second phalanx with a reduced facet post articulaire: *Nesogoral* from Capo Figari FM (NMB) and Campidano, *Myotragus* from Son Mayol (IVAU), *Praeovibos* sp. from Quibas (MNCN), *Praeovibos / Ovibos* from the Olyorian (PIN), *Praeovibos priscus* from Atapuerca TD7 (MB) and Bad Frankenhausen, *Capra ibex* from Petralona (AUT), *Hemitragus bonali* from Hundsheim (IPUW), recent *Budorcas taxicolor* (NHM), *Gazellospira torticornis* from Pyrgos (IVAU), *Gallogoral* from Senèze (NMB), recent *Capricornis sumatrensis* (NNML), recent *Madoqua saltiana* (NMW), *Gazella* from Pikermi (NMW), Gerakarou (AUT), Vátera (NHV), Ubeidiya (HUJ) and recent (LAUT).

B) Bovidae and Cervidae with a second phalanx with large facet post articulaire: recent *Cephalophus niger* (NHM), recent *Anoa depressicornis* (ZMA, IVAU), *Bison schoetensacki* from Bilzingsleben (FBFSU), *Bison menneri* from Untermassfeld (IQW), *Bos primigenius* from Miesenheim (FASMN), Torralba (MNCN), Neumark Nord (LVH), Lehringen (HMV), *Leptobos* from Montopoli (IGF), Olivola (IGF), Láchar (MNCN) and Pyrgos (IVAU), *Megaloceros giganteus* Ireland (NHM), *Megaloceros* aff. *cazioti* from Santa Lucia 1 (IVAU), Cervidae from Liko and Liko 2D on Crete (IVAU), *Dama dama geiselana* from Neumark Nord (LVH), *Cervus elaphus spelaeus* from Neumark Nord (LVH), *Alces* from East Runton (NHM), Voigtstedt (IQW), Süssenborn (IQW) and Mauer (SMNK), and *Capreolus* from Can Rubau (CIAG).

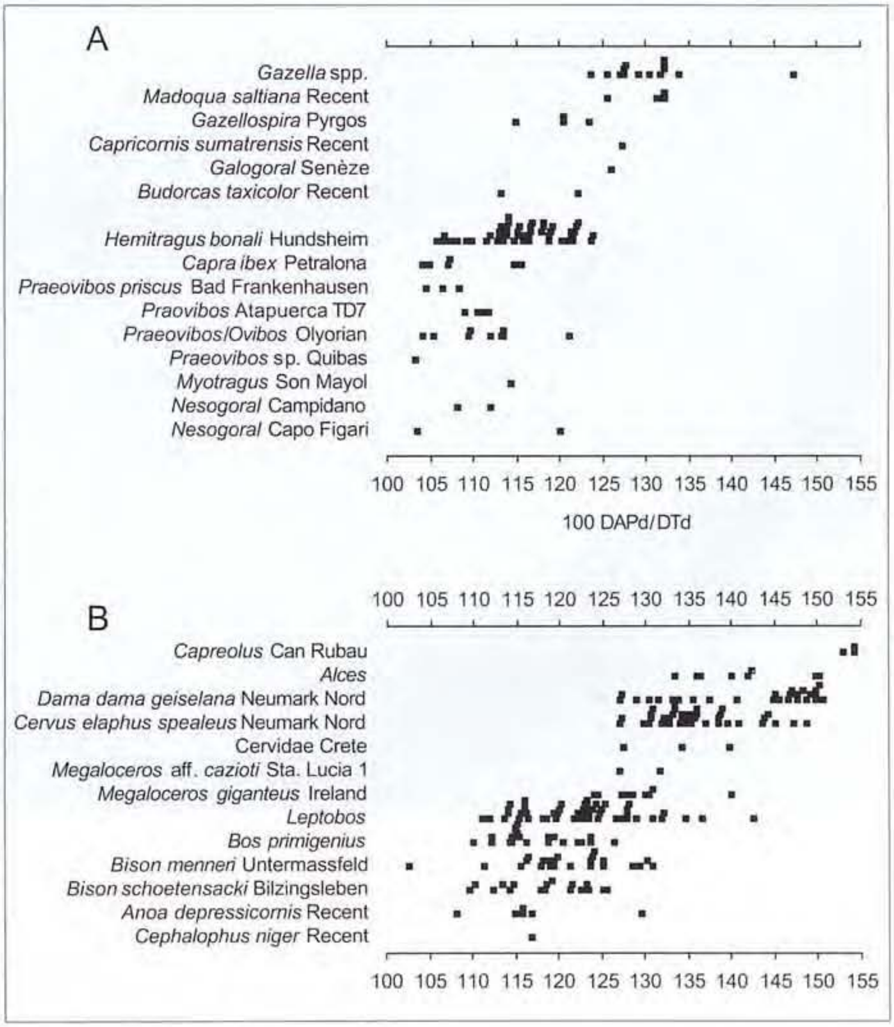


Fig. 6. L'index 100 DAPd / DTd a la segona falange de Bovidae i Cervidae seleccionats.

A) Bovidae amb una segoona falange amb una faceta post-articular reduïda: Nesogoral *de Capo Figari FM (NMB) i Campidano,* Myotragus *de Son Maiol (IVAU),* Praeovibos *sp. de Quibas (MNCN),* Praeovibos/Ovibos *de Olyorian (PIN),* Praeovibos priscus *d'Atapuerca TD7 (MB) i Bad Frankenhausen,* Capra ibex *de Petralona (AUT),* Hemitragus bonali *de Hundsheim (IPUW),* Budorcas taxicolor *recent (NHM),* Gazellospira torticornis *de Pyrgos (IVAU),*Gallogoral *de Senèze (NMB),* Capricornis sumatrensis *recent (NNML),* Madoqua saltiana *recent (NMW),* Gazella *de Pikermi (NMW), Gerakarou (AUT), Vàtera (NHV), Ubeidiya (HUJ) i recent (LAUT).*

B) Bovidae i Cervidae amb una segona falange amb una faceta post-articular grossa: Cephalophus niger *recent (NHM),* Anoa depressicornis *recent (ZMA, IVAU),* Bison schoetensacki *de Bilzingsleben (FBFSU),* Bison menneri *de Untermassfeld (IQW),* Bos primigenius *de Miesenheim (FASMN), Torralba (MNCN), Neumark Nord (LVH), Lehringen (HMV),* Leptobos *de Montopoli (IGF), Olivola (IGF), Láchar (MNCN) i Pyrgos (IVAU),* Megaloceros giganteus *Irlanda (NHM),* Megaloceros *aff.* cazioti *de Santa Lucia 1 (IVAU), Cervidae de Liko i Liko 2D a Creta (IVAU),* Dama dama geiselana *de Neumark Nord (LVH),* Cervus elaphus spelaeus *de Neumark Nord (LVH),* Alces *d'East Runton (NHM), Voigtstedt (IQW), Süssenborn (IQW) i Mauer (SMNK), i* Capreolus *de Can Rubau (CIAG).*

Plate 3. *Nesogoral cenisae* n.sp. from Campidano (figs. 1-5) and *Nesogoral* from Capo Figari FM (Fig. 6; NMB).

Figure 1. First phalanx right of the axis of the manus: a) volar view, b) axial view, c) palmar view, d) antiaxial view, e) proximal view.

Figure 2. First phalanx right of the axis of the pes: a) dorsal view, b) plantar view, c) proximal view, d) antiaxial view.

Figure 2. First phalanx left of the axis of the pes: a) dorsal view, b) axial view, c) plantar view, d) antiaxial view, e) proximal view, f) distal view.

Figure 4. Second phalanx left of the axis of the pes: a) dorsal view, b) axial view, c) plantar view, d) antiaxial view, e) proximal view, f) distal view.

Figure 5. Third phalanx left of the axis of the pes: a) proximal view, b) axial view, c) dorsal view, d) antiaxial view, e) plantar view.

Figure 6. Second phalanx right of the axis of the pes (?): a) axial view, b) dorsal view, c) antiaxial view.

Làmina 3. Nesogoral cenisae *n.sp. de Campidano (figs. 1-5) i* Nesogoral *de Capo Figari FM (Fig. 6; NMB).*

Figura 1. Primera falange dreta de l'eix del peu anterior: a) norma volar, b) norma axial, c) norma palmar, d) norma antiaxial, e) norma proximal.

Figura 2. Primera falange dreta de l'eix del peu posterior: a) norma dorsal, b) norma plantar, c) norma proximal, d) norma antiaxial.

Figura 3. Primera falange esquerra de l'eix del peu posterior: a) norma dorsal, b) norma axial, c) norma plantar, d) norma antiaxial, e) norma proximal, f) norma distal.

Figura 4. Segona falange esquerra de l'eix del peu posterior: a) norma dorsal, b) norma axial, c) norma plantar, d) norma antiaxial, e) norma proximal, f) norma distal.

Figura 5. Tercera falange esquerra de l'eix del peu posterior: a) norma proximal, b) norma axial, c) norma dorsal, d) norma antiaxial, e) norma plantar.

Figura 6. Segona falange dreta de l'eix del peu posterior (?): a) norma axial, b) norma dorsal, c) norma antiaxial.

- The shape of the distal articulations of the metapodials.
- The narrow first phalanges, occasionally having an elevated area for insertion of the tendon of the digital extensor muscle.
- The second phalanx with a distal articulation that does not project more distally on the axial side.
- The ulna having a lateral facet or area of contact with the radius, that is not much extended in lateral direction.

All these characters are present in the Antilopinae. Some of the characters mentioned in the descriptions are like in Caprinae, but do not exclude other affinities:

- Hypsodont teeth. Increase in hypsodonty is common in insular environment.
- Tooth morphology: no interlobular column, caprine fold, flat lingual walls of the lower molars, flat buccal walls of the paracone and metacone, three pronounced buccal styles in the upper molars, P_4 with metaprecristid closing the anterior fossid.
- First phalanx with facets for the sesamoids that have a very short dorso-plantar diameter.
- Second phalanx with a reduced "plateau post-articulaire" and a overhanging proximal facet.
- Third phalanx with a facet that has a proximal facet that has a long section that is parallel to the plantar surface of the bone.
- Third phalanx with a well developed extensor apophysis.

Again, all these characters are also found in some or

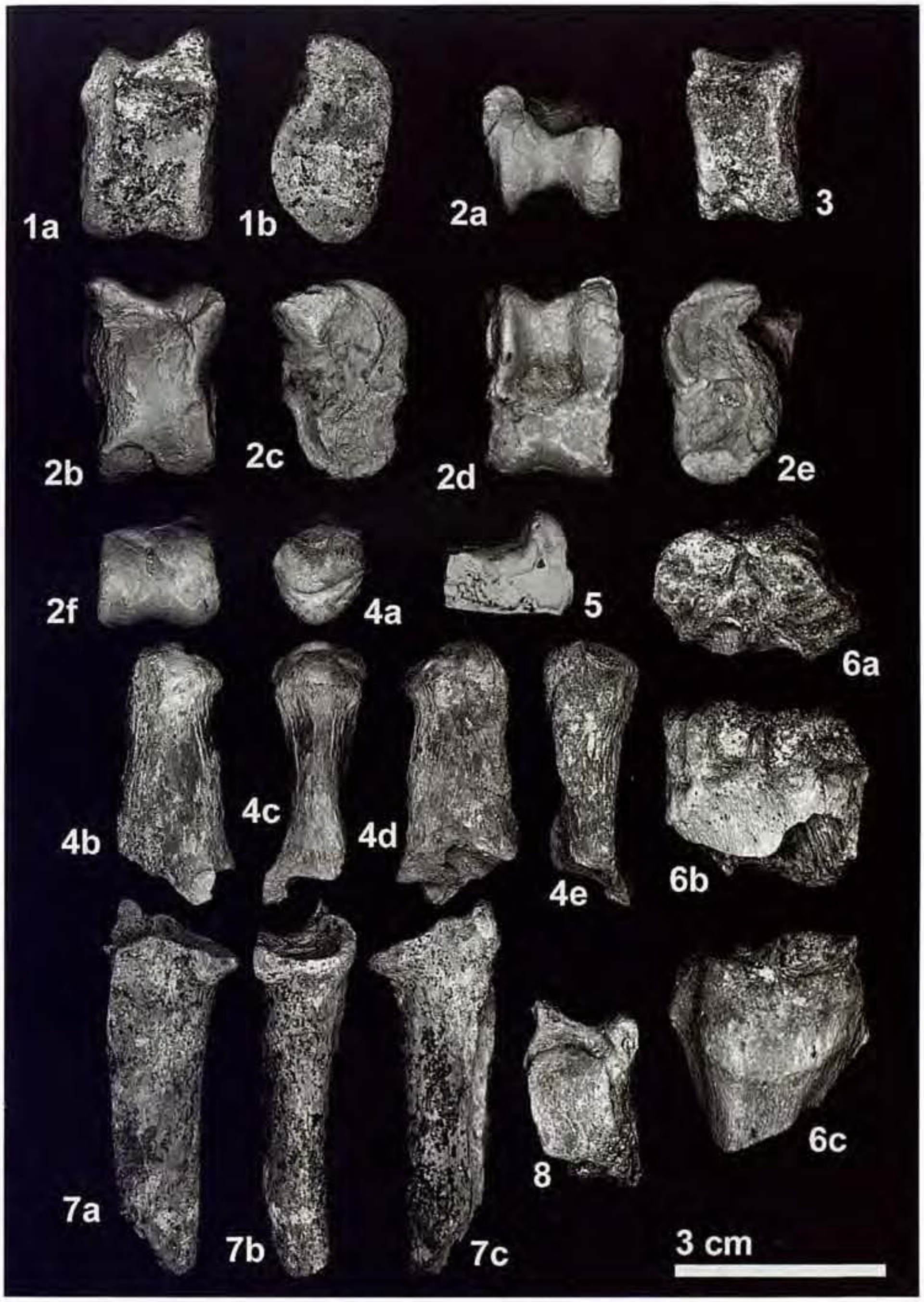


Plate 4. *Nesogoral cenisae* n.sp. from Campidano (figs. 1-4, 6-8) and *Nesogoral* from Capo Figari FM (Fig. 5; NMB).
Figure 1. Right astragalus: a) posterior view, b) lateral view.
Figure 2. Left astragalus: a) proximal view, b) posterior view, c) medial view, d) anterior view, e) lateral view, f) distal view.
Figure 3) Left astragalus: posterior view.
Figure 4) Right calcanaeum: a) upper view, b) lateral view, c) anterior view, d) medial view, e) posterior view.
Figure 5) Right magnum: posterior view (not to scale).
Figure 6) Left distal radius: a) distal view, b) posterior view, c) anterior view.
Figure 7) Right radius, proximo-medial part: a) anterior view, b) medial view, c) posterior view.
Figure 8) Left astragalus: posterior view.

Làmina 4. Nesogoral cenisae *n.sp. de Campidano (figs. 1-4, 6-8) i* Nesogoral *de Capo Figari FM (Fig. 5; NMB).*
Figura 1. Astràgal dret: a) norma posterior, b) norma latera.
Figura 2. Astràgal esquerre: a) norma proximal, b) norma posterior, c) norma medial, d) norma anterior, e) lateral, f) norma distal.
Figura 3) Astràgal esquerre: norma posterior.
Figura 4) Calcani dret: a) norma superior, b) norma lateral, c) norma anterior, d) norma medial, e) norma posterior.
Figura 5) Capitatotrapezoide dret: norma posterio (no a escala).
Figure 6) Left distal radius: a) distal view, b) posterior view, c) anterior view.
Figura 7) Radi dret fragment distal, part proximo-medial: a) norma anterior, b) norma medial, c) norma posterior.
Figura 8) Astràgal esquerre: norma posterior.

all of the Antilopinae. Some characters or combination of characters seems to be typical for all or at least most of the Caprinae:

- Second phalanx that is wide, and in particular in combination with the reduced or receding "plateau post-articulaire" and the overhanging proximal facet.
- Ulna with wide facet for the humerus.
- The morphology of the proximal surface of the metatarsal.
- Wide astragalus.

Most of the differences between *Nesogoral* and the majority of the Caprinae are in the metapodials and in the phalanges and may well be related. Similarly, the caprine *Myotragus* changed the original morphology of its phalanges in response to insular environment, acquiring a morphology and a locomotion type that are very different from those of all continental Caprinae (Köhler & Moyà-Solà, 2001). In the ulna from Campidano, a derived character of most Caprinae is absent (it is not very wide at its widest point); it is thus primitive. The maintenance of a primitive character in a caprine lineage that originated some 5 Ma ago is not surprising. The characters that are typical of the Caprinae, are from different parts of the skeleton (wide facet for the humerus in the ulna, metatarsal, second phalanx). It is difficult to see how these different characters, which are not directly related, may have evolved convergently. It is, however, possible to explain the differences from most Caprinae as a single adaptation, which is in favor of a placement of the bovid from Campidano within the Caprinae.

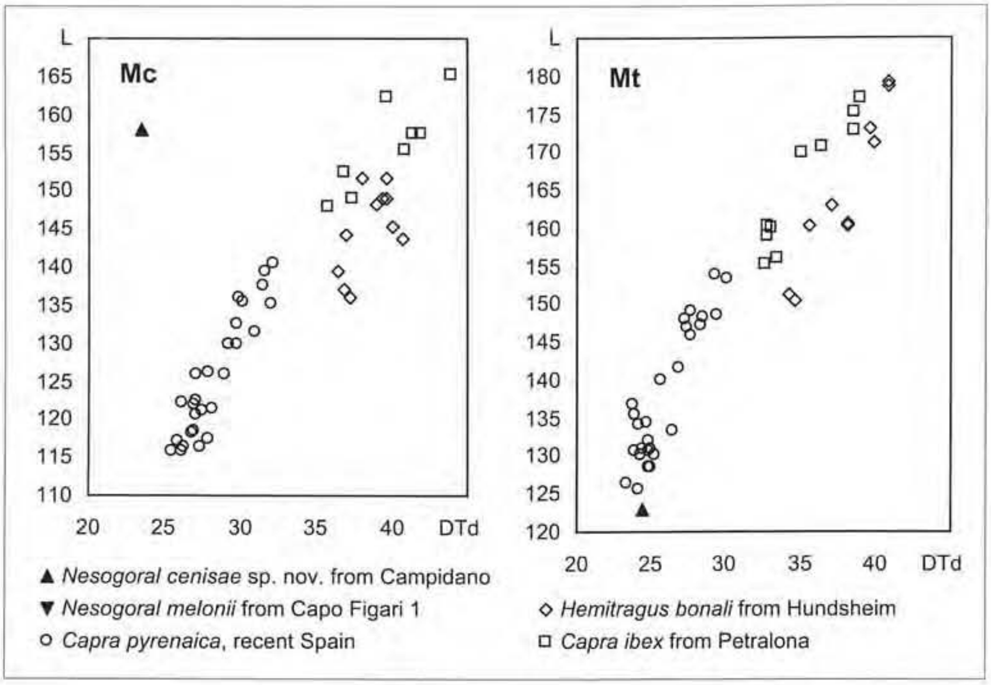
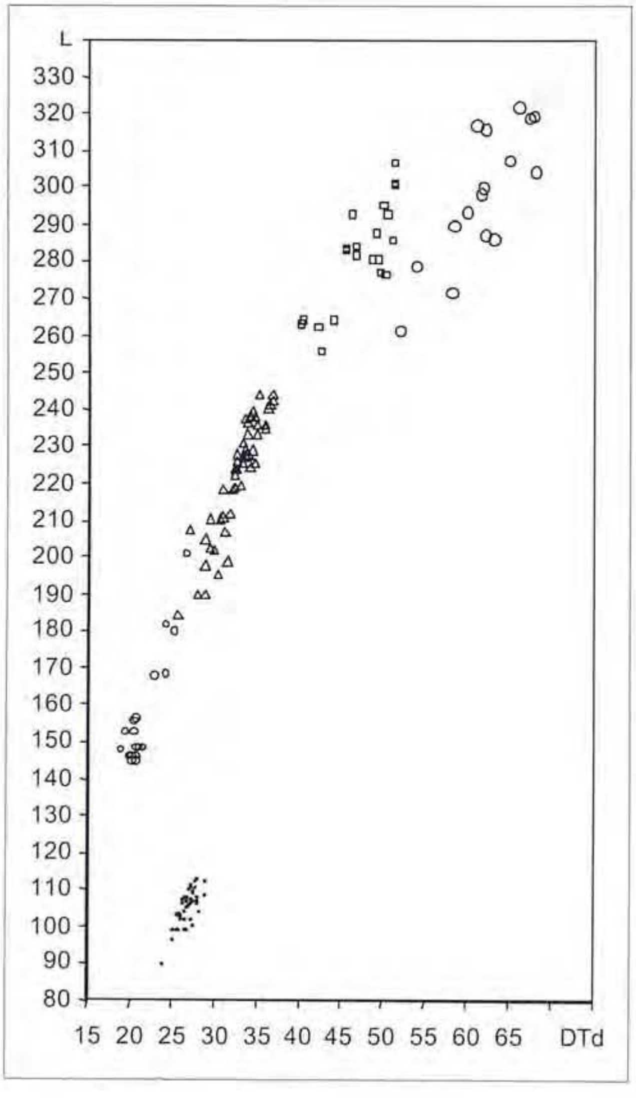


Fig. 7. Bivariate diagram of the metacarpals and metatarsals of selected caprines. Provenance of data as in Figure 4, and *Nesogoral melonii* from Capo Figari 1 (Gliozzi & Malatesta, 1980).

Fig. 7. *Diagrama bivariat dels metacarpians i metatarsians de caprins seleccionats. Dades de procedència, com a la figura 4, i* Nesogoral melonii *de Capo Figari 1 (Gliozzi & Malatesta, 1980).*



Carnivora
occurring with the deer from Karpathos:
none

- · Karpathos
- ▫ *Cervus elaphus*
- ◦ *Capreolus*
- ▵ *Dama*
- ○ *M. solilhacus*

Fig. 8. Bivariate diagram of the metacarpal of *Cervus cerigensis* from Kandilia Cave (Kuss, 1975) and *Cervus* aff. *cerigensis* from Karpathos I and II (IVAU) compared with *Cervus elaphus* from Voigtstedt (IQW), Petralona (AUT) and Neumark Nord (LVH). *Dama* from Montopoli (IGF), Ubeidiya (HUJ), Tegelen (NHMM), Casa Frata (IGF), Il Tasso (IGF), Valdarno (IGF), Petralona (AUT), Neumark Nord (LVH), Lehringen (HMV), Gimbsheim (NMM), and recent *Dama mesopotamica* (HUJ); *Capreolus* from Pirro Nord (?; cast IGF), Mosbach (NMM), Grotte des Cèdres (MRA), Ehringsdorf (IQW), Lehringen (HMV) and recent from Spain (MNCN) and the Netherlands (NML); *Megaloceros solilhacus* and related forms from Ubeidiya (HUJ), Voigtstedt (IQW), Süssenborn (IQW), Solilhac (MCPV), Trimmingham (NHM), Sidestrand (NHM), Mundesley (NHM), and Petralona (AUT).

Fig. 8. *Diagrama bivariat del metacarpià de* Cervus cerigensis *de la Cova Kandilia (Kuss, 1975) i* Cervus *aff.* cerigensis *de Karpathos I i II (IVAU) comparat amb* Cervus elaphus *de Voigtstedt (IQW), Petralona (AUT) i Neumark Nord (LVH).* Dama *de Montopoli (IGF), Ubeidiya (HUJ), Tegelen (NHMM), Casa Frata (IGF), Il Tasso (IGF), Valdarno (IGF), Petralona (AUT), Neumark Nord (LVH), Lehringen (HMV), Gimbsheim (NMM), i* Dama mesopotamica *recent (HUJ);* Capreolus *de Pirro Nord (?; motlle IGF), Mosbach (NMM), Grotte des Cèdres (MRA), Ehringsdorf (IQW), Lehringen (HMV) i recent de la Península Ibèrica (MNCN) i dels Països Baixos (NML);* Megaloceros solilhacus *i formes relacionades de Ubeidiya (HUJ), Voigtstedt (IQW), Süssenborn (IQW), Solilhac (MCPV), Trimmingham (NHM), Sidestrand (NHM), Mundesley (NHM), i Petralona (AUT).*

The morphology of the Campidano bovid compared to *Nesogoral melonii*

In most cases when the morphology could be compared with *Nesogoral melonii* from Capo Figari 1 and the Forsyth Major collection, there are no great differences. A possible exception is the width or robusticity of the first phalanx, which might be more caprine-like in Capo Figari. However, the typical wide second phalanx which lacks the distal projection of part of the distal articular facet is similar in both. It has to be assumed that both bovids are closely related and there does not seem to be a good reason for not classifying the bovid from Campidano as *Nesogoral*.

However, fragments of two metatarsals of *Nesogoral* from Capo Figari (Gliozzi & Malatesta, 1980, p. 328, Pl. 4, figs. 1 & 4) seem to be relatively long and gracile within the Caprinae, but with lengths of 119 and 123 and a distal width of 24.4 mm, these bones seem to be shorter and more robust than what could be expected in the Campidano bovid. In bovids, the metatarsal is usually clearly longer and less robust than the metacarpal. However, the metacarpal from Campidano is nearly one third longer than the metatarsal from Capo Figari 1 and has a comparable distal width. It is thus much more gracile. A comparison of the Nesogoral metapodials with the metacarpals and metatarsals in *Hemitragus bonali* from Hundsheim, *Capra ibex* from Petralona and recent *Capra pyrenaica* shows that, the bovids from Campidano and Capo Figari 1 represent different species (Fig. 7). The bovid from Campidano is *Nesogoral*, but is not *Nesogoral melonii*. A new species is named here:

Nesogoral cenisae nov. sp.

Holotype: the metacarpal figured in Plate 2, fig. 1.

Paratypes: the other specimens from Campidano described here.

Definition: *Nesogoral* close in size and morphology to *Nesogoral melonii*, but with longer and more gracile metapodials.

Derivatio nominis: the species is named in honour of Cenis Valdés.

Type locality: Campidano.

Age of the type locality: not exactly known, probably early Middle Pleistocene.

CARNIVORES AND LOCOMOTORY ADAPTATIONS OF INSULAR ARTIODACTYLS

In the classic model of insular environment and evolution, typical insular faunas are characterised by a particular taxonomical composition, with Carnivora tending to be absent, which leads to a series of adaptations: size reduction in large mammals and size increase in small mammals, low gear locomotion, and particular visual and dental adaptations (Sondaar, 1977, 1986). However, predators are not always absent and low gear locomotion is not always developed to the same extreme. Low gear locomotion is more energy efficient and would thus be an advantage in any environment, if it were not for the presence of predators. Low gear locomotion is seen in the morphology of the bones, fusions of bones, the proportions of the different segments of the limb, and the proportions of the individual bones (Leinders & Sondaar, 1974; Sondaar, 1977; Leinders, 1979; De Vos, 1979; Spoor, 1988a and b; Köhler & Moyà-Solà, 2001; and others). The metacarpal is probably the bone that most clearly reflects this adaptation.

The metacarpal of *Myotragus*, which lived in a carnivore-free environment, is very short and robust (Figs. 3 & 4).

The fossil endemic fauna from Karpathos included deer but no predators (Kuss, 1975; Dermitzakis & Sondaar 1979). Two species of deer have been described *Cervus cerigensis* and *C. pygadiensis*, which probably form a lineage. Antlers of the more primitive species have a crown as in *Cervus elaphus*, which is its probable ancestor. The metacarpals in Fig. 8 are from a form which is probably intermediate between the type material of the two species. *Cervus elaphus* changed much in size at various moments in the Pleistocene, and we do not know the size of the founder population on Karpathos. Nevertheless, the distal width (DTd), which is probably related to body weight, reflects an important decrease in size in comparison to any continental *Cervus*. But the length decreased relatively more and as a consequence the metapodials are more robust than in any continental deer. Such short and robust metapodials indicate low gear locomotion.

The fossil deer from Crete have been described by De Vos (1979, 1984). No Carnivora have been reported from the faunas that occurred with these deer. The ancestors of the deer are debated, but to me it seems likely that *Cervus elaphus* and *Dama* gave rise to at least some of these endemic deer. There were various contemporaneous species of deer which had different locomotory adaptations. Some of the deer may have had a giraffe-like appearance. Most deer however, were dwarfed and had robust metapodials that reflect low gear locomotion (Fig. 9).

The Pleistocene deer of Sardinia are usually assigned to *M. cazioti*, though there are of very different sizes. These deer are usually assumed to be descendants of *Megaloceros solilhacus* (or similar forms, referred to under a variety of names, including *Megaceroides*, *Praemegaceros* and *"verticornis"*). The metapodials of the Sardinian deer are much more gracile than those of *M. solilhacus* and it was noted that either we have to assume this deer became more cursorial, or we have to consider a possible descendance from species with more gracile metapodials such as: *Dama*-like deer, a form close to *Eucladoceros tetraceros*, *Eucladoceros giulii* and *Arvernoceros* (Van der Made, 1999a). Palombo *et al.* (2003) suggested that Van der Made (1999a) believed that *Eucladoceros giulii* is ancestral to *M. cazioti*, derived *M. cazioti* from "slender-limbed megalocerines" (which includes material assigned by Van der Made, 1999b to *E. giulii*) and suggested a size decrease in a *M. cazioti* lineage and increase in robusticity of the metapodials. In addition to large material from Capo Figari FM (NMB) and Sadali, a particularly large metapodial from Santa Lucia 1 (the isolated dot in Fig. 10) is much larger than *M. cazioti* from Corbeddu and is wider and more robust than any continental *Dama*, suggesting that these authors may have

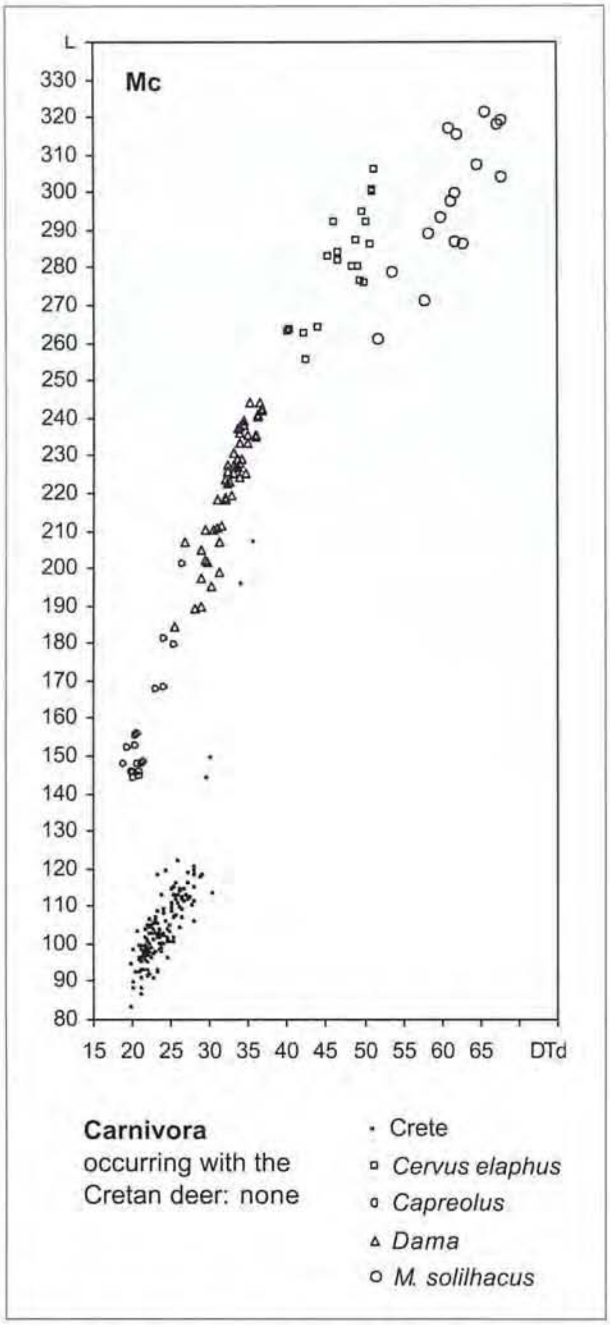


Fig. 9. Bivariate diagram of the metacarpal of the Pleistocene Cervidae from Crete (IVAU, SMNK) compared with *Cervus elaphus*, *Dama*, *Capreolus* and *Megaloceros solilhacus* and related forms (provenance of data as in Figure 10).

Fig. 9. *Diagrama bivariat del metacarpià de Cervidae del Pleistocè de Crete (IVAU, SMNK) comparat amb* Cervus elaphus, Dama, Capreolus *and* Megaloceros solilhacus *i formes relacionades (procedència de les dades com a la Figura 10).*

been correct in assuming a large species to be ancestral, and a size decrease in the Sardinian lineage. However, we have to note that the "slender-limbed megalocerines"of these authors also include include the deer from Ubeidiya, which is related to *M. solilhacus* and which has a metacarpal with an index of 517, which is more robust than any of the *M. cazioti* from Corbeddu. If the Sardinian deer descended from *Dama*, this would imply an increase in size, which is not very likely in insular environment. It is of importance here to note that *M. cazioti* became either: 1) much smaller with more gracile metapodials (if a descendant of a member of the *M. solilhacus* lineage) or 2) much smaller with very slightly more robust metapodials (if a descendant of *E. giulii* or "slender-limbed megalocerines"), but that in any case it did not greatly increase the robusticity of its metapodials. The Sardinian deer have always lived together with *Cynotherium*.

Dama carburangelensis and *Cervus elaphus siciliae* are endemic forms from the Pleistocene of Sicily (Gliozzi & Malatesta, 1982; Gliozzi *et al.*, 1983) have metacarpals which show dwarfing and which, in the case of *Dama* show only a minor increase in robusticity, and in the case of *Cervus* even a decrease in robusticity (Figs. 11-12). These forms lived together with large carnivores like *Panthera leo, Crocuta crocuta* and *Ursus arctos* (Di Maggio *et al.*, 1999; Marra, 2003).

From the same faunas of Sicily, also endemic *Bos* and *Bison* have been reported (Brugal, 1987; Di Maggio *et al.*, 1999). The metacarpals of *Bos* show clearly dwarfing and a moderate increase in robusticity (Fig. 13).

The Pleistocene fauna from Pianosa was discussed by Stehlin and includes *Ursus, Vulpes, Equus*, "short-legged deer", deer of the size of *Cervus elaphus, Capreolus* and *Bos* (Stehlin, 1929; Brugal, 1987). The *Bos* shows dwarfing and a moderate increase in robusticity (Fig. 13). The short-legged deer has metapodials with indices 490 and 500 (calculated from the figures by Stehlin), while the larger deer is represented by a skull fragment that was reported to be similar in morphology to *C. elaphus*. If the "short-legged deer" is a descendant of *Cervus elaphus* or *Dama* it became smaller and more robust, but if it is a descendant of some *Megaloceros* species, it became smaller, but not more robust.

From Sardinia a dwarfed pig is known, *Sus sondaari*, which may have been more cursorial than its ancestor (Van der Made, 1999a). This suid was reported, along with *Chasmaporthetes* from Cava 6 near Orosei (Sondaar, 2000; Abazzi *et al.*, 2004).

From the foregoing it appears that Artiodactyla dwarfed and evolved "low gear locomotion" in predator free islands, but when predators were present they may have dwarfed but evolved little or nothing in the direction of "low gear locomotion" and may have even become more cursorial. It is proposed here that *Nesogoral* in the presence of predators became more cursorial (explanation 3 of the introduction). This resulted in longer and more gracile metapodials and first phalanges and different distal articulations in the metapodials and second phalanges. In terms of the classification of Köhler (1993) the animal changed towards locomotion type B, which is typical of open, flat and dry habitats.

Nesogoral may have lived during some 4 Ma together with *Chasmaporthetes* on Sardinia. The only other large mammals were *Sus* and *Macaca*. Sardinia may have had plains with an open niche for a large herbivore, which may have been occupied by *Nesogoral*. The more elongate metapodial in *Nesogoral cenisae* explained by various models, including the following:

1) *Nesogoral* moving into these plains and splitting up into two lineages, *N. melonii* in the mountains and the cursorial *N. cenisae* in the plains.

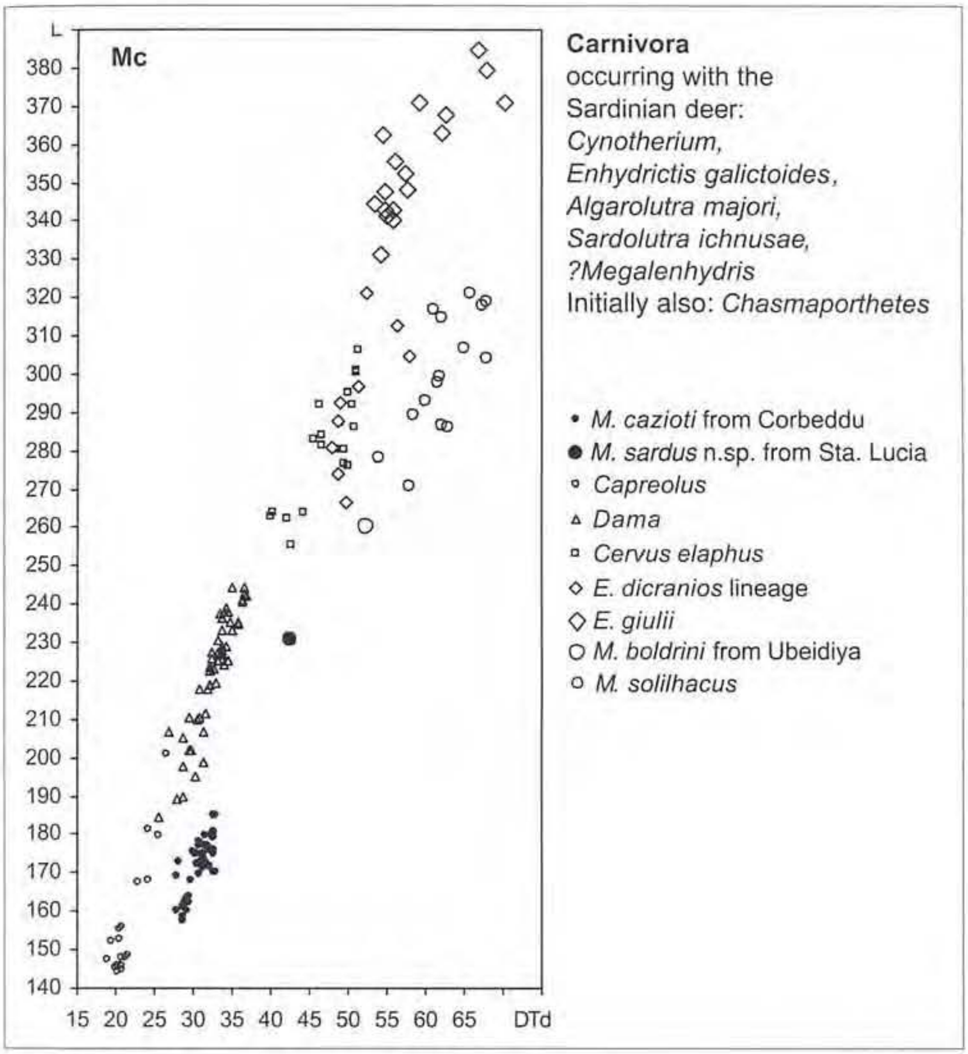


Fig. 10. Bivariate diagram of the metacarpal of *Megaloceros cazioti* and *M.* aff. *cazioti* from Corbeddu (Klein Hofmeijer, 1996) and Santa Lucia I (IVAU) in Sardinia, compared with *Cervus elaphus, Dama, Capreolus, Eucladoceros dicranios* lineage from Valdarno (IGF), *Eucladoceros giulii* from Untermassfeld (IQW), Venta Micena (Menéndez, 1987), Atapuerca TD4 (MB) and Apollonia (AUT), and *Megaloceros solilhacus* and related forms (provenance of data as in Figure 10), including *Megaloceros boldrini* from Ubeidiya (HUJ).

Fig. 10. Diagrama bivariat del metacarpià de Megaloceros cazioti *i* M. *aff.* cazioti *de Grotta Su Corbeddu (Klein Hofmeijer, 1996) i Santa Lucia I (IVAU) a Sardinia, comparat amb* Cervus elaphus, Dama, Capreolus, *línia d'*Eucladoceros dicranios *de Valdarno (IGF),* Eucladoceros giulii *d'Untermassfeld (IQW), Venta Micena (Menéndez, 1987), Atapuerca TD4 (MB) i Apollonia (AUT), anid* Megaloceros solilhacus *i formes relacionades (procedència de les dades com a la Figura 10), incloent-hi* Megaloceros boldrini *d'Ubeidiya (HUJ).*

2) The arrival of *Cynotherium* around the Early-Middle Pleistocene transition, which caused *N. melonii* to become more cursorial and thus evolve into *N. cenisae*.

The citation of two different species of *Nesogoral* in Orosei 6 (Sondaar, 2000; Abazzi *et al.*, 2004), seems to be in favour of the two lineage model, however, the indeterminate caprine in Orosei 10 hints of more important changes following the arrival of *Cynotherium* as in the single lineage model. We will have to await the description of this material.

NESOGORAL AND THE FAUNAL HISTORY OF PLIO-PLEISTOCENE SARDINIA

Sondaar (1987) and Sondaar *et al.* (1984, 1986) recognised an earlier "*Nesogoral* fauna" and a later "*Tyrrhenicola* fauna" for the Plio-Pleistocene of Sardinia. This became more complex, when it was recognised that *Nesogoral* and *Tyrrhenicola* had overlapping ranges (Van der Made, 1999a; Sondaar, 2000). Abazzi *et al.* (2004) recognized up to 4 faunal units in the Monte Tuttavista faunas, but this does not even include all possible faunal units.

A selection of localities and their faunal associations are given in Fig. 14, which is based mainly on Fig. 1 of Van der Made (1999a), Fig. 5 of Sondaar (2000), information by Abazzi *et al.* (2004) and the literature cited by these authors. Six to eight tentative faunal units are indicated. The Capo Figari collection of Forsyth Major is placed here close to Capo Figari 2, and though this seems to fit unexpectedly well for most of the taxa, some taxa do not quite fit. The exact provenance of this material is not known, nor whether it is a mixture or whether it reflects a true faunal association that once lived on Sardinia. Its suid is more advanced than the one from Monte Tuttavista in the reduction of the premolars and diastemata. Only one of the possible *Nesogoral* evolutionary models is shown. Some localities are included because they are the only or one of the few localities with this taxon, but their position relative to the other localities is a problem. There might be a problem with the assignation of the *Prolagus* material. In spite of these and other problems, the figure gives an impression of the faunal evolution of the island that basically seems coherent and shows a pattern similar to that in other islands. Some localities have been dated. The ESR dates by Dr. M. Ikeya (Osaka Univ.) are: 1,807,500 ± 20 % BP for Capo Figari 1, 450,000 ± 20 % for Santa Lucia 1, 366,950 ± 20 % BP for Capo Figari 2, and 15,375 BP for Cor-

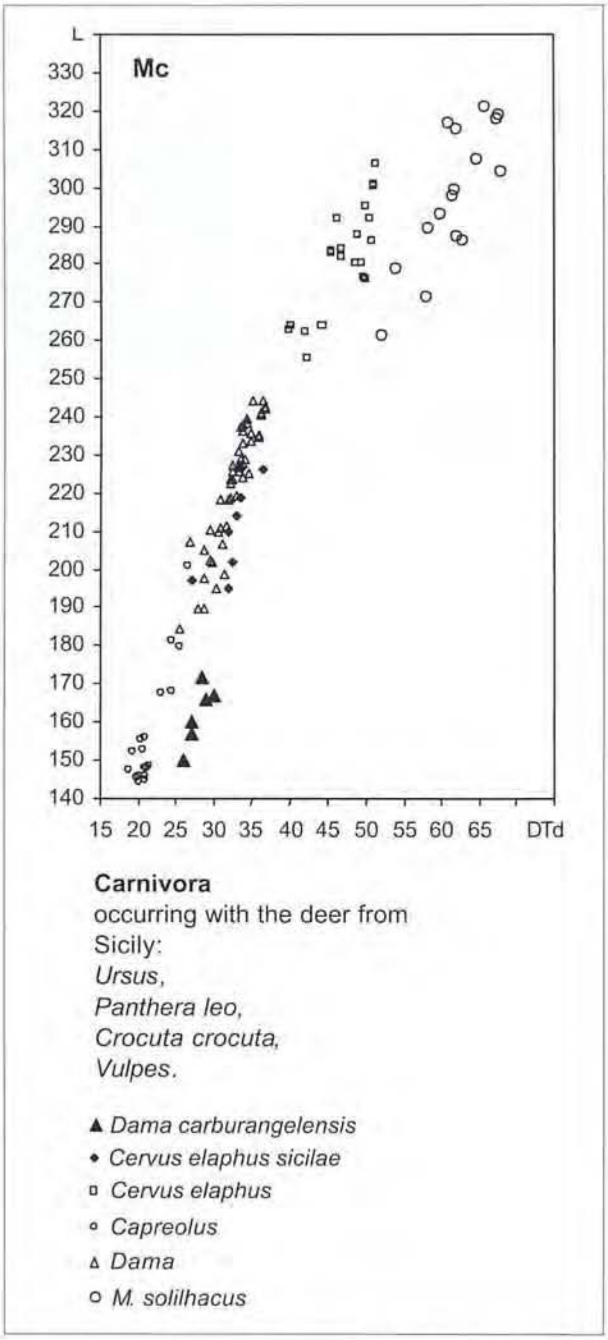


Fig. 11. Bivariate diagram of the metacarpal of *Dama carburangelensis* from Capo Tindari (Gliozzi & Malatesta, 1982) and *Cervus elaphus siciliae* from Puntali (Gliozzi, Malatesta & Scalone, 1983) in Sicily compared with *Cervus elaphus, Dama, Capreolus* and *Megaloceros solilhacus* and related forms (provenance of data as in Figure 10).

Fig. 11. Diagrama bivariat del metacarpià de Dama carburangelensis *de Capo Tindari (Gliozzi & Malatesta, 1982) i* Cervus elaphus siciliae *de Puntali (Gliozzi, Malatesta & Scalone, 1983) a Sicilia comparat amb* Cervus elaphus, Dama, Capreolus *i* Megaloceros solilhacus *i formes relacionades (procedència de les dades com a la Figura 10).*

beddu (pers. comm. D. Reese to Van der Made, 1999a). These dates serve to situate the faunal associations approximately. One of the main faunal events in the sequence is the arrival of *Tyrrhenicola*, the dog and the deer on the island. This is usually assumed to have ocurred during the sea level lowstand caused by the first severe glaciation. That is OIS22, around 900 ka. This is an adittional tentaive date. It is not quite clear whether the arrival of *Oryctolagus* and the mustelids is a different and earlier event.

Sardinia is believed to have been populated by a continental fauna during the Messinian Crisis. This model is supported by the fact that the earliest faunas include forms that are not known from oceanic or very isolated islands, probably because they are not good in dispersing over sea. Bovids tend to be rare on islands, and when present these islands are usually known to have been connected to the mainland. *Nesogoral* is very probably among the animals that reached Sardinia during the Messinian Crisis. For the same reason, it seems unlikely that during the Middle Pleistocene Caprinae that are not related to *Nesogoral* appeared in Sardinia.

This continental fauna became isolated after the Pliocene flooding and subsequently became empoverished and altered by the insular environment which differs from the continental environment. Today Sardinia is rather far away from the mainland and the fact that that in Capo Figari 1 only lineages are recorded which were already present in the earlier faunas suggest that it remained isolated during all the Pliocene. Even though it is recorded only from one of the Monte Tuttavista sites, *Chasmaporthetes* must have entered Sardinia during the Messinian Crisis because: 1) there are no documented cases of hyaenids which have crossed wide sea barriers, 2) it was extinct on the mainland of Europe, when from 0.9 Ma onward, more severe glaciations caused very low sea levels, which might have permitted it to cross from the shelf near Elba to Corsica. The presence of this hyaenid is probably the reason why *Nesogoral* did not adapt in the same way as *Myotragus*; it did not develop low gear locomotion. *Nesogoral* may even have even given rise at this time to a more cursorial species (*N. cenisae*) inhabiting the plains (two lineage model). The presence of a predator probably limited herbivore population size and herbivore pressure on the environment. This again is probably the reason why *Nesogoral* did not evolve extreme dental adaptations as in *Myotragus*.

Close to the Early-Middle Plestocene transition, the Sardinian fauna became enriched in one or several steps with the arrivals of *Oryctolagus*, mustelids, *Mammuthus*, *Tyrrheniclola*, canids and cervids. *Mammuthus lamormorae* is known from several isolated finds and from San Giovanni in Sinis. Its morphology suggests that it is a descendant of *Mammuthus meridionalis*, which occurred in Europe from some 2.6 to 0.7 Ma. Judging from the isotope record, OIS 22 was a particularly cold stage, while 18 and 20 were much milder. OIS 16 is another cold stage, but by that time *M. meridionalis* was already replaced on the main land by another species. OIS 22 is thus the best candidate for several new arrivals as indicated in Fig. 14.

This enriched fauna had a very peculiar composition: a group of lineages which arrived to the island walking and which had become reduced selection for survival in insular environment (*Nesogoral, Chasmaporthetes, Sus, Talpa*) and a group of new arrivals, which were selected primarily on their ability to colonize islands (cervids, *Mammuthus*). There were two large predators, *Chasmaporthetes* and *Cynotherium*. On the long run, this may have been too much for the island, and *Casmaporthetes* went extinct, though it is not clear when. *Chasmaporthetes* was a true carnivore and *Cynotherium*, being a canid,

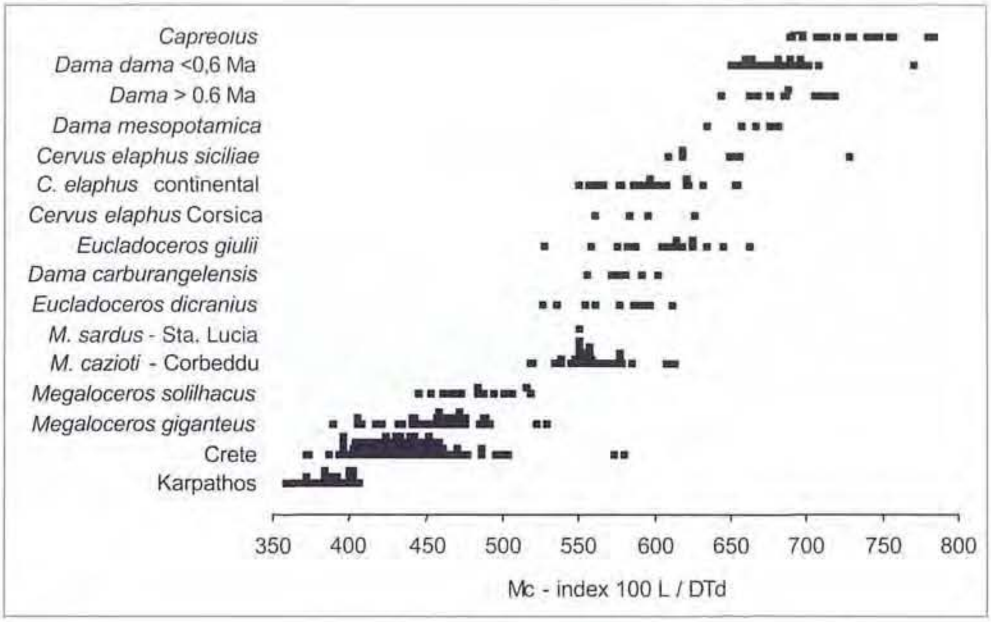


Fig. 12. The metacarpal index 100 L / DTd in selected Cervidae. Provenance of data as in Figures 8-11; in addition: recent *Cervus elaphus* from Corsica (IPH) and *Megaloceros giganteus* (Lister, 1994).

Fig. 12. L'index metacarpià 100 L / DTd a Cervidae seleccionats. Procedència de les dades com a les Figures 8-11; a més: Cervus elaphus *recent de Còrsega (IPH) i* Megaloceros giganteus *(Lister, 1994).*

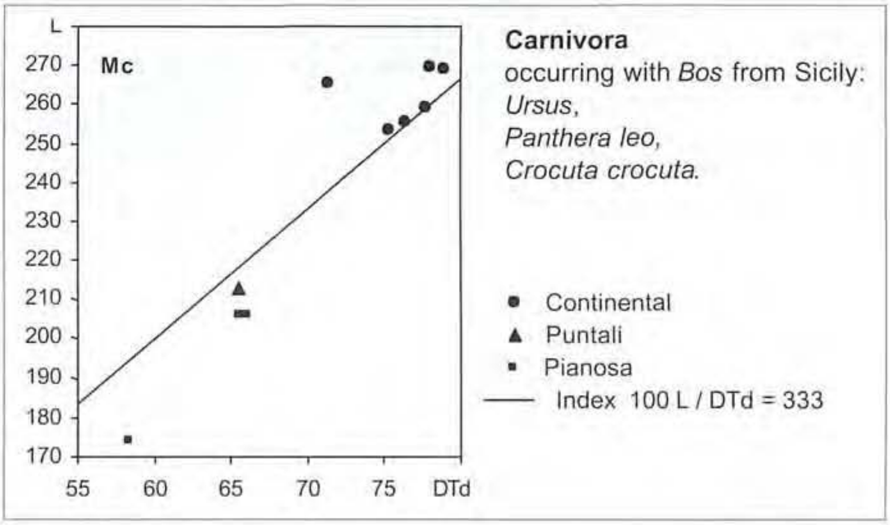


Fig. 13. Bivariate diagram of the metacarpal of *Bos*: continental *Bos primigenius* from Miesenheim (FASMN) and Neumark Nord (LVH), insular *Bos* from Puntali in Sardinia (Brugal, 1987) and Pianosa (Brugal, 1987).

Fig. 13. Diagrama bivariat del metacarpià de Bos: Bos primigenius *continental de Miesenheim (FASMN) i Neumark Nord (LVH),* Bos *insular de Puntali a Sardenya (Brugal, 1987) i Pianosa (Brugal, 1987).*

had a more diverse diet. This may have allowed for greater population densities for this genus, which thus may have gradually replaced the hyaenid. The arrival of a new carnivore, may have caused *Nesogoral* to have become more cursorial (single lineage model). Also the deer may have become more cursorial or at least did not become less cursorial and initially remained relatively large. From this time on, the fauna of Sardinia gradually empoverished again and several lineages went extinct.

At some time or period in the middle of the Middle Pleistocene *Cynotherium* became smaller as well as the deer and bovid, *Prolagus* and *Rhagamys* increased in size. It is not known whether this occurred during a short or long period. However, these changes may well be related to the size decrease in *Cynotherium*, or to the extinction of *Chasmaporthetes*, or to both, and in that case, may have occurred in a short period. If these changes occurred in a short period, this may have been between some 450 ka (age of Santa Lucia, where still a large deer is found) and 367 ka (age of Capo Figari 2, where a very small *Nesogoral* was found).

The disappearance of *Eliomys*, *Nesogoral* and possibly *Macaca*, may have occurred shortly after this event, if this had not happened earlier. Maybe these disappearances are still consequences of the same cause that also provoked the size changes in the different lineages.

Later changes in the fauna of Sardinia concern mainly evolutionary changes in *Tyrrhenicola*, the arrival of *Homo sapiens* and the replacement of the Pleistocene fauna by the species from the mainland. Noteworthy is the apparent early extinction of *Talpa*.

CONCLUSIONS

- The bovid from Campidano belongs to *Nesogoral*.
- *Nesogoral* from Campidano differs from *N. melonii* and is a new species: *N. cenisae*.
- *Nesogoral* belongs to the Caprinae, but *N. cenisae* lost some of the characters typical of this subfamily.

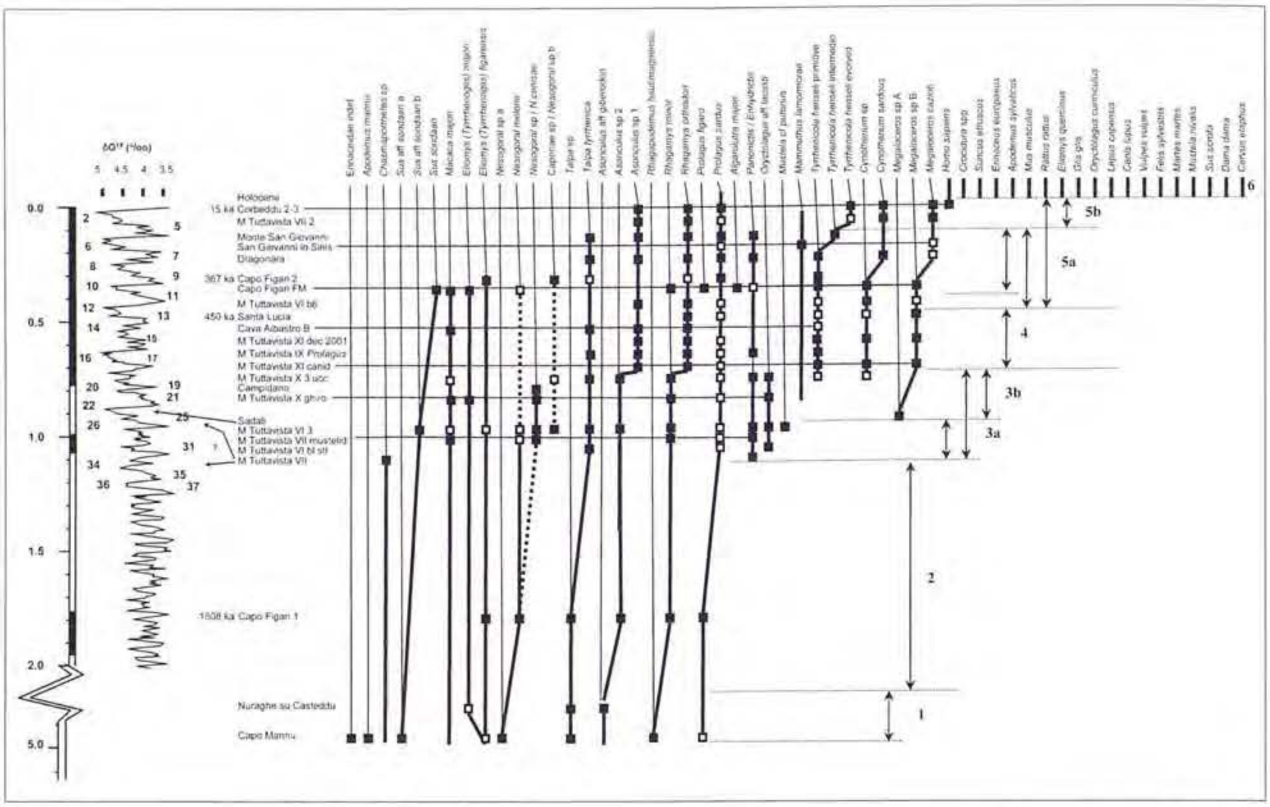


Fig. 14. The faunal evolution of Sardinia. On the left the palaeomagnetic and time scale in Ma and the oxygen isotope record (Shackleton, 1995). The localities are in approximate position, dates are ESR dates on tooth enamel by Dr. Ikeya (Osaka Univ.). Solid squares indicate presence of taxa in localities, open squares indicate doubts (sp., cf., aff. or ?), usually on the species, not on the presence of the genus. Thick lines indicate assumed temporal distribution, oblique lines indicate assumed ancestor-descendant relationships of species and the time range in which the transition occurred. Faunal events are indicated with arrows, and faunal complexes are indicated on the right. For *Nesogoral* only one of several possibilities is indicated (multi and single lineage models). Data and interpretations from Van der Made, 1999a, using data from Kotsakis (1980, 1986), Kotsakis & Palombo (1979), Gliozzi *et al.* (1984), and others, Abazzi *et al.* (2004), in addition Sondaar (2000).

***Fig. 14.** L'evolució faunística de Sardenya. A l'esquerra, l'escala paleomagnètica i temporal, en Ma, i el register d'isòtops d'oxigen (Shackleton, 1995). Les localitats es presenten en una posició aproximada, i les dates són dates ESR sobre esmalt dentari subministrades pel Dr Ikeya (Universitat d'Osaka). Els quadrats solids indiquen la presència de taxa a les localitats, els quadrats oberts indiquen dubtes (sp., cf., aff. o ?), normalment sobre l'espècie, no sobre la presència del gènere. Les línies gruixades indiquen la distribució temporal suposada, les línies obliques indiquen una relació ancestre-descendent de l'espècie i l'espectre temporal en el qual la transició hauria esdevingut. Els esdeveniments faunístics s'indiquen amb fletxes, i els complexes faunístics s'indiquen a la dreta. Per a* Nesogoral *només s'indica una de les diferents possibilitats (models d'una o múltiples línies evolutives). Dades i interpretacions de Van der Made (1999a), emprant dades de Kotsakis (1980, 1986), Kotsakis & Palombo (1979), Gliozzi* et al. *(1984); Abazzi* et al. *(2004); Sondaar (2000) i altres.*

- *Nesogoral cenisae* lost characters by adapting to a different and more rapid locomotion.
- The cursorial adaptation in *Nesogoral* may have been the result of either the entry of *Cynotherium* in Sardinia (single lineage model), or the occupation of an empty niche on the plains before the arrival of this canid (two lineage model).
- The absence of predators, or the types of predators present on an island, determine in large part the environment and thus the evolution of the prey species.
- Ungulates may evolve energy efficient "low gear locomotion" on predator free islands, may evolve a little in this way, not at all, or even may become more cursorial, depending on predator pressure.
- Size decrease in large mammals may occur in insular environment, even in the presence of carnivores, but becomes more pronounced when predator pressure is less.

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HUMANS AND *MYOTRAGUS*:
THE ISSUE OF SAMPLE INTEGRITY IN RADIOCARBON DATING

Mark VAN STRYDONCK, Mathieu BOUDIN & Anton ERVYNCK

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Resum

Una fita clau en la prehistòria de les Illes Balears és la data de l'arribada dels humans i la suposadament conseqüent extinció de *Myotragus balearicus*, degut a les interferències humanes. Al llarg dels anys s'han proposat diferents models cronològics. Els treballs que tracten aquest assumpte discuteixen tots en gran extensió la integritat arqueològica de les mostres emprades per a la datació radiocarbònica d'aquest esdeveniment. Emperò, cap dels treballs discuteix la integritat de les mostres d'ossos (tant d'humans com de *Myotragus*) emprats a les anàlisis radiocarbòniques. La nostra recerca mostra que la majoria dels ossos d'una localitat clau, la cova de Moleta, estan molt mal conservats. En conseqüència, els resultats no són fiables i en molts de casos la pregunta que caldria respondre és si hi ha alguna relació entre l'edat radiocarbònica de la mostra i l'edat real de l'os. En aquest treball discutim mètodes relativament senzills per contrastar la qualitat dels ossos i la fiabilitat de la data radiocarbònica.

Paraules clau: Illes Balears, *Myotragus balearicus*, extincions quaternàries, datació radiocarbònica, integritat de les mostres.

Summary

A crucial datum in the prehistory of the Balearic Islands is the arrival of humans and the supposed, consequent extinction of *Myotragus balearicus* due to human interference. Over the years several chronological models have been proposed. The papers dealing with this topic all discuss in great extent the archaeological integrity of the samples used for radiocarbon dating this event. None of the papers, however, discuss the sample integrity of the bones (of both humans and *Myotragus*) used in the radiocarbon analyses. Our investigation shows that most of the bones from the crucial site of Cova de Moleta are very badly preserved. Consequently, the results are unreliable and in many cases the question should be asked if there is any relationship between the radiocarbon age of the sample and the real age of the bone. In this paper, we discuss relatively simple methods to check the quality of the bone and the reliability of the radiocarbon date.

Keywords: Balearic Islands, *Myotragus balearicus*, Quaternary extinctions, radiocarbon dating, sample integrity.

INTRODUCTION: THE INTERACTION BETWEEN HUMANS AND *MYOTRAGUS*

Myotragus balearicus Bate, 1909 was a small goat-like artiodactyl, of which the fossil remains are only found on the Balearic Islands, more precisely on Mallorca, Menorca, Cabrera and Sa Dragonera. The species was present on these islands long before the arrival of humans, but now it is extinct. A recent review of the data available about this extinction concluded that a climatic change cannot be held responsible but that humans caused the disappearance of *Myotragus*. It is further hypothesised that this happened through a rapid 'overkill' process (Bover & Alcover, 2003). In contrast, however, it has also been argued that humans and *Myotragus* have co-existed for considerable time, and that the anthropogenic extinction of the later species was a very slow event (Patton, 2000). Some have even suggested a domestication attempt that finally failed (Waldren, 1974; 1982), although this idea is now heavily contested (Ramis & Bover, 2001).

One of the crucial approaches to the different theories concerning the possible interaction between humans and *Myotragus* is the absolute dating, by radiocarbon analysis, of fossils preferably from the earliest humans on the islands, and from the last surviving *Myotragus*. However, the data set obtained until now is not yet sufficient to solve all questions asked. Concerning the first arrival of humans on the Balearic Islands, different chronological models still exist (summarised by Ramis & Alcover, 2001, and Ramis *et al.*, 2002), *i.e.*, the 'Early Arrival Model' (prior to 7000 cal BC), the 'Classical Model' (prior to 5600 cal BC) and the 'Late Arrival Model' (in some indeterminate time inside the interval 3000 – 2000 cal BC). The uncertainties concerning the last dates for *Myotragus* have been reviewed by Bover & Alcover (2003). In general, the main reason why different models and uncertain dates still exist lies in the sometimes problematic reliability of the dated samples.

Species	Material	Sample reference	Lab. reference	^{14}C-age (BP)
Myotragus	Limb bones (collagen)	Balma de Son Matge ABSM-350 cm	BM-1408	4090±390
Goat	Mandibles with teeth removed (collagen)	Cova de Moleta SMLC- 25-50 cm	BM-1507	2360±90

Table 1. Early radiocarbon measurements on material from Cova de Moleta and Balma de Son Matge.

Taula 1. *Mesures radiocarbòniques primerenques sobre materials de la cova de Moleta i la balma de Son Matge.*

THE RELIABILITY OF THE RADIOCARBON DATES

Reviews dealing with the topics mentioned above often discuss the archaeological integrity of the samples used for radiocarbon dating (Alcover *et al.*, 2001; Guerrero, 2001; Waldren *et al.*, 2002; Ramis *et al.*, 2002; Bover & Alcover, 2003). Some include a statistical evaluation of the data and also stable isotope analyses are brought into the discussion (Davis, 2002). None of the papers, however, focuses on the sample integrity or radiocarbon integrity of the bones (of both humans and *Myotragus*) used in the analyses.

This neglect of the issue of sample integrity can be understood when dealing with the earlier papers since in those days the radiocarbon community was more concerned with the laboratory equipment, technical facilities and subsequent accuracy of the measurements, than with the samples themselves. As a consequence, it is difficult to find out whether or not these earlier samples would have been suitable for dating by our present-day standards. In some occasions, however, one gets indirect information about this. In a paper by Burleigh & Clutton-Brock (1980) a *Myotragus* bone from the rock shelter of Son Matge, and a goat bone (*Capra aegagrus* f. *hircus*) from the Moleta cave were dated in order to demonstrate the late survival of *Myotragus*. The results are summarised in table 1.

First of all, it has come to our attention that the text speaks of "bones" (plural). There could thus have been more than one animal involved in the tests and, consequently, the dates obtained could represent the mean of the ages of different animals. This was a standard procedure during the time before the Accelerated Mass Spectrometer (AMS) was introduced, but the problem for later evaluation is that the possible effects of the combining of bones are not discussed in the paper. Secondly, a large difference in standard deviation is observed between the *Myotragus* date and the goat date. This probably indicates that, after the necessary chemical manipulations of the *Myotragus* bone, there was not enough sample to fill the counter and the sample had to be diluted by ^{14}C-free carbon. So why was there not enough sample: because the laboratory did not get access to sufficient material or because the collagen recuperation rate was low? If the collagen recuperation rate was low this indicates that the bone was badly preserved and that the date might be wrong (as will be discussed below). That none of this is discussed in the paper looks an important negligence, but as said before, the radiocarbon laboratories in those days were focusing more on the quality of their measurements than on the quality of the samples, and when the laboratories did not discuss this topic, it is evident that we do not find this discussion in the archaeological papers.

A second example of the problem of sample integrity is provided by an early attempt to date the presumed earliest human bones found at Mallorca (Rosselló-Bordoy *et al.*, 1967; Waldren and Kopper, 1969) (Table 2).

In the first case, it is obvious that there was not enough sample material. In the second case there was enough material but the quality of the bone was not examined. Fortunately, the article mentioned the sample sizes because otherwise the evaluation of the reliability of the dates would have been more difficult. From the examples of Burleigh & Clutton-Brock (1980), and Rosselló-Bordoy *et al.* (1967), it can be concluded that only detailed information about the physico-chemical characteristics of the dated samples can allow to (re-) evaluate their integrity when including them into present interpretations.

Since the development of the AMS-technique mg-size samples can be dated and this has changed radiocarbon dating dramatically. Mixing bones in order to obtain a large enough sample is no longer necessary and single very small samples became datable. The new technique made it possible to date routinely many materials which were previously inaccessible to ^{14}C dating. At the same time, the use of AMS has the additional advantage that the laboratories can be much more selective in dealing with contaminants. Unfortunately, the laboratories' efforts to handle the problems of sample size and contamination are often still not discussed in the recent archaeological papers. Hardly any of the recently published papers pay a lot of attention to the bone quality problem. At most one gets a descriptive appreciation like: "The sample provided plenty of carbon for accurate AMS analysis and all analytical steps went normally" (Ramis and Alcover, 2001) or "Successful collagen extraction was achieved from 40 humans ..." (Davis, 2002). The first paper, relating to this topic, that gave information about the quality of the dated bones deals with the (until now) earliest humans on Menorca (van Strydonck & Maes, 2001).

Lab. reference	Amount of material used (g)	^{14}C-age (BP)
Unknown	39.6	10,686±3517
KBN-640d	500	5935±110

Table 2. Results of the first attempt to date early humans on Mallorca.

Taula 2. *Resultats del primer intent de datar humans primerencs a Mallorca.*

The most disadvantageous result of the neglect of the issue of sample integrity is that it maintains the endless discussions in literature. For example, Mestres (2000) commented upon an early date from Moleta but did, in fact, not dispose of all the necessary information to give a profound criticism on this result (Mestres, *pers. comm.*). In many other examples, dates are still used or criticised that should in effect be rejected on the basis of their physico-chemical characteristics. In this paper, we will discuss the contamination problems of bones, and how to deal with them. This discussion, however, will not lead to a critical review of all human and *Myotragus* dates obtained before, because the lack of published information mentioned before makes this impossible. Instead, we will focus on a new case study with the results from the important site of the Moleta cave at Sóller, Mallorca, in order to demonstrate how important sample integrity is. Moreover, it will first be explained that this factor is more significant than other possibly biasing factors.

THE RADIOCARBON EVENT OF BONES

The crucial question within archaeological radiocarbon dating asks what the relationship is between the radiocarbon event of bones and the human event of interest (van Strydonck *et al.*, 1999). In other words: does the radiocarbon age reflect the true calendar age of the bone (*i.e.*, the moment in time the individual died)? In 'living' bones, due to different rates of re-modelling through life, the apparent age of a bone is estimated between 0 and 30 years depending on the age of the person (Geyh, 2001). This means that the radiocarbon content of the bone of a deceased person will reflect a date 0 to 30 years before death. Although this residence time of carbon in bone collagen thus causes small discrepancies between the radiocarbon age and the actual year of death, a correction factor can be applied (Geyh, 2001). Moreover, when dating prehistoric material, a slight additional error of a few years is not that important compared to the dating of, for example, late medieval material, where a shift of a decade often implies a completely different historical meaning (see, *e.g.*, Callebaut *et al.*, 2002).

On the other hand, dietary effects can provoke a more important artificial ageing of the sample. The radiocarbon content of the sea is in most places significantly lower than that of the terrestrial biosphere. As a consequence, in terms of radiocarbon contents, the oceans' biosphere appears several hundred years earlier than the terrestrial biosphere. Consequently, it is obvious that the radiocarbon content of the bones from terrestrial animals (polar bears) or humans (Inuit) whose food derives mainly from the ocean will reflect the ocean and not the terrestrial ^{14}C reservoir (Tauber, 1979; Lanting & van der Plicht, 1996). However, investigations made on material from the Balearic Islands have shown that this is not really a problem for prehistoric samples because, apparently, marine food sources were never very important (van Strydonck *et al.*, 2002). There are only a few cases were a minor freshwater fish effect could be demonstrated. The stable isotope measurements from those samples could not lead to a quantitative interpretation of this effect (Wouters *et al.* 2002)

In conclusion, in the case of prehistoric terrestrial animals and humans from the Balearic Islands, the radiocarbon content of a well-preserved bone will closely reflect its true age. In the case of bad preservation, however, the situation can become problematic.

THE CONSERVATION OF BONE COLLAGEN

The most obvious way of dating bones is by analysing the radiocarbon content of the collagen fraction. However, collagen from demineralised bones decomposes rapidly. Bone dating will thus only be possible when the bone survived its stay within an archaeological context rather well. This preservation depends mostly on the characteristics of the soil (humidity, acidity, temperature, presence of oxygen, etc.) and the stability of these conditions. The compact structure of the bone makes infiltration of external molecules containing carbon difficult, although humification and the formation of soil-humic/collagen complexes can change the structure of the bone. Humic substances are formed during the decomposition of plant and animal matter. Their molecular weight can range from a few hundred to several thousand (Schnitzer and Khan, 1978).

Humic substances in an archaeological or buried bone may derive from the soil, from the *in situ* humification of the bone organic matter, or from both. Despite the visible changes of the collagen (the pure white colour of collagen becoming brownish), the *in situ* humification does not provoke erroneous ^{14}C dates (because no material with different ^{14}C content has been added to the sample). In other words: the radiocarbon event is still the same as before. van Klinken and Hedges (1995) concluded that because most archaeological bones give reasonably good radiocarbon dates in spite of colour variations, most humified matter in buried bones is *in situ* produced. Soil derived humic substances, however, are non-contemporary with the bone collagen and the collagen/humic interaction will form complexes that will give wrong ^{14}C dates. In that case, the sample's age will be the mean age of all components in the sample, *i.e.*, the bone's collagen and the humic acids. Moreover, due to the mobility of the humic acid molecules, they can come from soil layers with a different age. In the case of the Balearic Islands, bone preservation and the subsequent risk of contamination is the main issue within the context of sample integrity.

BONE PREPARATION AND QUALITY ASSESSMENT

Bone preparation

A summary of the studies on bone preparation and quality assessment can be found in Hedges and van Klinken (1992), van Klinken (1999) and van Strydonck and Wouters (2001). In this paper, we will only discuss the methods relevant to the study theme.

a) The Longin method

The first step in most of the preparation techniques is the Longin method (Longin, 1971). This method was developed before AMS dating techniques became available and was therefore originally designed for large bone samples. Downscaling for AMS considerably improved the degree of collagen recuperation (*e.g.*, using centrifugation instead of decantation). Fig. 1 depicts the Longin method in the case of AMS preparation. Although it is technically a relatively easy method, it does not allow separating the bone organic matter from the humic contamination.

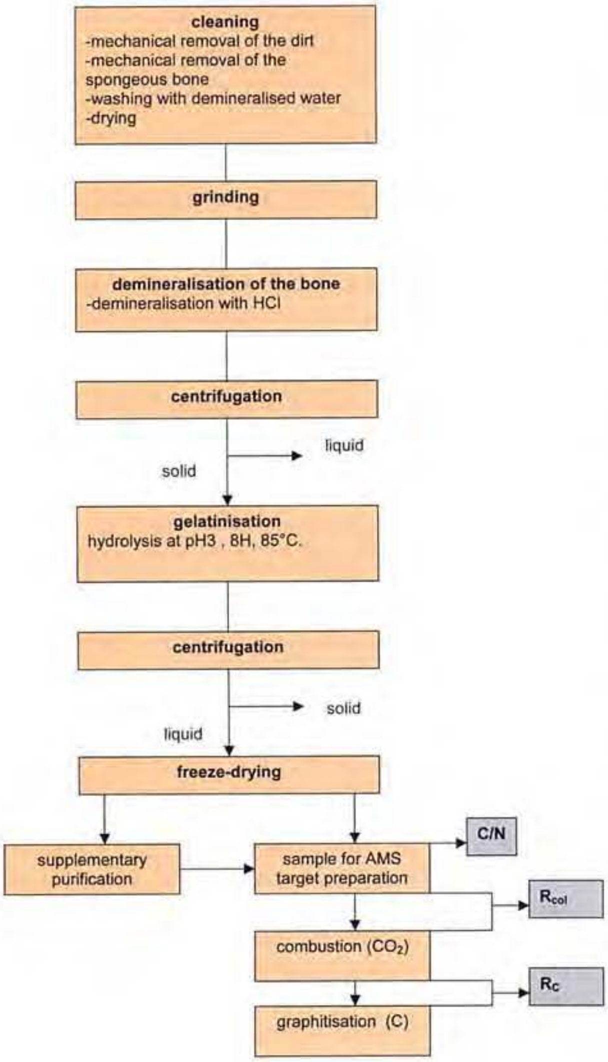


Fig. 1. Flowchart of the bone preparation technique used in this study.

Fig. 1. Esquema de la tècnica de preparació d'ossos emprada a aquest treball.

b) Ultra-filtration

An additional treatment of the sample with diluted NaOH during the Longin preparation helps to remove humic acids (Arslanov and Svezehentsev, 1993), but sometimes provokes a substantial loss of material and was therefore not used in this study. We did not use an ion exchange column either, another method that could have removed contamination (Law and Hedges, 1989). Instead, as an additional cleaning step, on some of the samples ultra-filtration was used. This technique separates the lower and the higher molecule fragments in the gelatine using a centrifuge. In this study Amicon-centripep 10kD cut-off filters were used. We tested the Longin method with and without ultra-filtration on a qualitatively good bone and found no aberrant results between both (Table 3).

Quality assessment

Next to the attempts to eliminate contamination out of a bone that will be subjected to radiocarbon dating, more attention is recently paid to the evaluation of the preservation condition of the bone. In the case of a bad evaluation, this can lead to the rejection of the sample prior to any treatment or dating. In fact, there are different techniques to test the quality of an archaeological bone. A very good analytical technique consists of breaking up the gelatine chain into its amino acids and analyse them with the HPLC technique (High Performance Liquid Chromatography). However, the disadvantage of this technique is that it is not only complex but also expensive.

a) C/N ratio

An excellent and less time consuming tool for measuring the quality (preservation condition) of a bone is the evaluation of the carbon nitrogen ratio (C/N). Within the amino acids that make up bone collagen carbon and nitrogen atoms are present in a specific ratio but in the case of humic acid intrusion this ratio will become higher due to a relative depletion in nitrogen in the bone. For archaeological bones this ratio should be below 3.6 (De Niro, 1985), while higher values of this ratio indicate humic intrusion.

b) Collagen recuperation rate (R_{col})

Another way of evaluating bone preservation is the calculation of the factor R_{col} (= weight bone x 100 / weight collagen). Fresh bone contains more than 20% collagen. Well-preserved archaeological bones contain about 10% of collagen. A very low collagen content is a strong indication of deterioration and possible contamination. Amino acid analyses on archaeological material have indeed shown that, in the case of low R_{col} values, the sample contains a lot of humic acid (Wouters *et al.*, 2002).

Lab. reference	preparation method	measurement technique	^{14}C-age (BP)
IRPA-1176/1186	Longin	liquid scintillation counting	2790±30
UtC-5532	Longin + ultra-filtration	AMS	2810±35

Table 3. Comparison of the dates obtained from a human bone from Binipatí using the Longin method, with and without ultra-filtration (C/N = 2.8, see further).

Taula 3. Comparació de les dates obtingudes a partir d'un os humà de Binipatí emprant el mètode Longin, amb i sense ultra-filtració (C/N = 2.8, veure més a sota).

c) Carbon recuperation rate (RC)

Yet another technique of evaluating bone preservation is the calculation of R_C (= weight of C after graphitisation / expected weight of C after graphitisation). When the collagen is contaminated by complexes containing inorganic molecules, the amount of carbon after graphitisation will be less than theoretically expected. This parameter is not very precise because most parameters concerning the reactor in which the graphitisation takes place (exact volume, pressure, temperature, etc.) are only estimated. Nevertheless, extreme values can be related to contamination. Table 4 gives the example of Puig den Pau, with a set of chronologically homogeneous dates with good preservation parameters and one aberrant date (KIA-12700). The quality assessment parameters of the later sample indicate contamination by humic acid.

As a last example of the impact of bone preservation, table 5 represents the results of two *Myotragus* bones. The bone from Cova de ses Tapareres was slightly burnt. In terms of possible bias of the dating results, burning is thus as important as contamination with humic acids but the effect can be evaluated in the same ways.

CASE STUDY: THE CAVE OF MOLETA

a) Description

The Moleta cave is located in the northern mountain range, the Serra Tramuntana of Mallorca (39° 35'N, 6° 25'E). The cave is located in an outcrop of Jurassic limestone overlooking the sea. There is a keyhole shaped mouth at the entrance of the cave and an inner mouth consisting in a small vertical chimney leading to the lower cave system. A detailed description of the cave is given by Waldren (1982) and Alcover *et al.* (2001).

b) Series 1

In a first radiocarbon dating campaign 5 samples, from both humans and *Myotragus*, were analysed (Table 6, Fig. 2).

From one *Myotragus* sample (SM-X-9), no material was left after hydrolysis. Although, with the naked eye, the bone appeared in good condition all organic matter had dissolved from the bone, leaving only the mineral fraction. This signifies that during the diagenetic alteration of the bone there was no supply of humic substances (from other layers or from contemporary material) and that the humified bone collagen was washed out completely without substitution. The preservation of the *Myotragus* bone from stratum 4 (SM-X-4) was almost as bad as that of the previous sample. The quality assessment parameters indicate the presence of a non-combustible fraction (a low R_C), possibly clay minerals, and the presence of humic acids (a high C/N). The preparation did not yield enough sample for the preparation of an AMS target.

Two out of three human samples (SM-Pocket cave, SM-Mu 145-H) also failed the quality assessment tests. One (SM-Mu 145-H) was dated later than the sample

sample reference	Lab. reference	^{14}C-age (BP)	C/N	R_{col}	R_C
434	KIA-12700	1260±40	8.3	1.40	0.10
207	KIA-14820	2590±30	2.8	8.50	0.63
200	KIA-14821	2770±30	2.8	8.18	0.48
554	KIA-14822	2545±30	2.9	19.36	0.76
186	KIA-14823	2735±40	2.8	10.86	0.92

Table 4. Example of an outlier due to contamination, within a chronologically homogeneous series of domesticated animals bones from Puig den Pau.

Taula 4. *Exemple d'una datació sortida de mare degut a contaminació, dintre d'una sèrie homogènia d'ossos d'animals domèstics del puig den Pau.*

Sample reference	Lab. reference	^{14}C-age (BP)	C/N	R_{col}	R_C
Cova de ses Tapareres	KIA-20202	1330±30	4.72	0.78	0.09
Cova des Tancats	UtC-3740	10020±50	2.93	N.A.	0.36

Table 5. Example of a well preserved and a contaminated bone from *Myotragus balearicus* (N.A. = not available).

Taula 5. *Exemple d'un os ben preservat i d'un os contaminat de* Myotragus balearicus *(N.A. = no disponible).*

Sample reference	Lab. reference	^{14}C-age (BP)	C/N	R_{col}	R_C
SM-E 008H human metapodial	KIA-20213	3850 ±25	2.73	10.8	0.98
SM-X-sector stratum 9: *Myotragus*	N.A	N.A.	N.A.	0	N.A.
SM-X-sector stratum 4: *Myotragus*	N.A	N.A.	6.63	0.44	0.02
SM-Pocket Cave: human tibia	KIA-20462	4135 ±25	7.29	1.20	0.24
SM-Mu 145-H: human long bone	KIA-20463	2670 ±25	5.36	1.82	0.30

Table 6. First series of radiocarbon dates from Moleta cave and "Pocket cave".

Taula 6. *Primera sèrie de datacions radiocarbòniques de la cova de Moleta i de la "Pocket cave".*

(SM-E 008H) that succeeded in the quality assessment while the other (SM-Pocket Cave) was dated earlier. Since the absorption of humic acids from earlier and deeper layers is very unlikely in the dry calcareous outcrop of Moleta, humic infiltration can only come from younger material that is deposited above the level of the bone sample. We have, in our laboratory, so far no record from any bone sample that was contaminated by older humic acids.

c) Series 2

In a second radiocarbon dating campaign 6 more samples from humans were analysed (Table 7, Fig. 2).

The yield of the collagen extraction of these samples was very low, so we tried another approach. An extra ultra-filtration step (10 kD) was added to the pre-treatment. During the ultra-filtration a deposit appeared at the high-molecular side of the filter. This is very unusual

sample reference	Lab. reference	^{14}C-age (BP)	C/N	R_{col}	R_C
SM-E-200-300; human femur	KIA-13997	3615 ±55	N.A.	1.54	N.A.
SM-X-200-300; human tibia	KIA-13998	4005 ±50	N.A.	1.20	N.A.
SM-CD-150; human tibia	KIA-14003	4165 ±30	N.A.	1.08	N.A.
SM-O-100-150; human bone	KIA-14004	3880 ±30	N.A.	1.44	N.A.
SM-O-100-150; human tibia shaft	KIA-14008	3990 ±50	N.A.	1.60	N.A.
SM-CD-100-150; human femur shaft	KIA-14026	4055 ±30	N.A.	1.26	N.A.

Table 7. Second series of radiocarbon dates from Moleta cave.

Taula 7. Segona sèrie de datacions radiocarbòniques de la cova de Moleta.

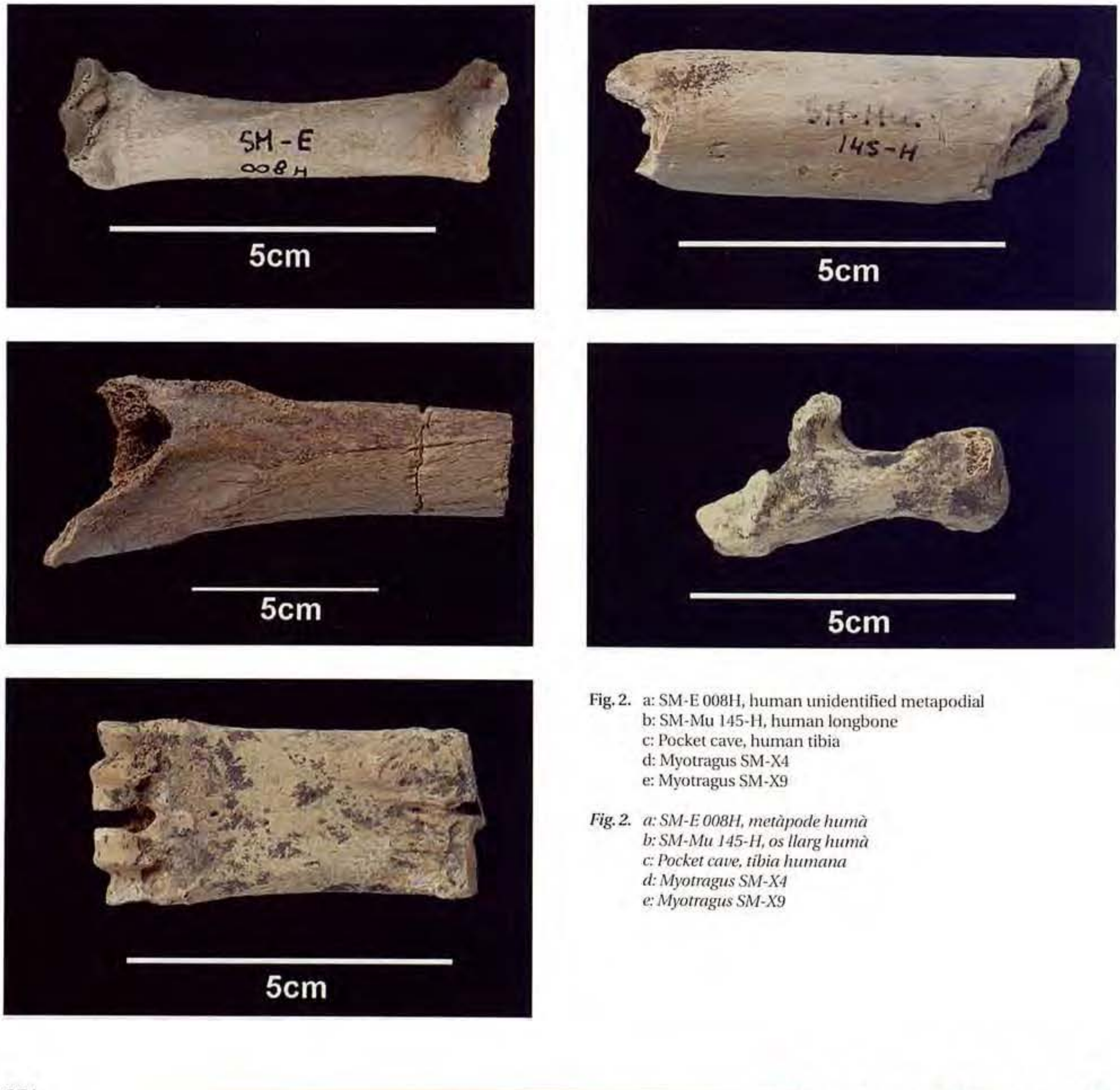
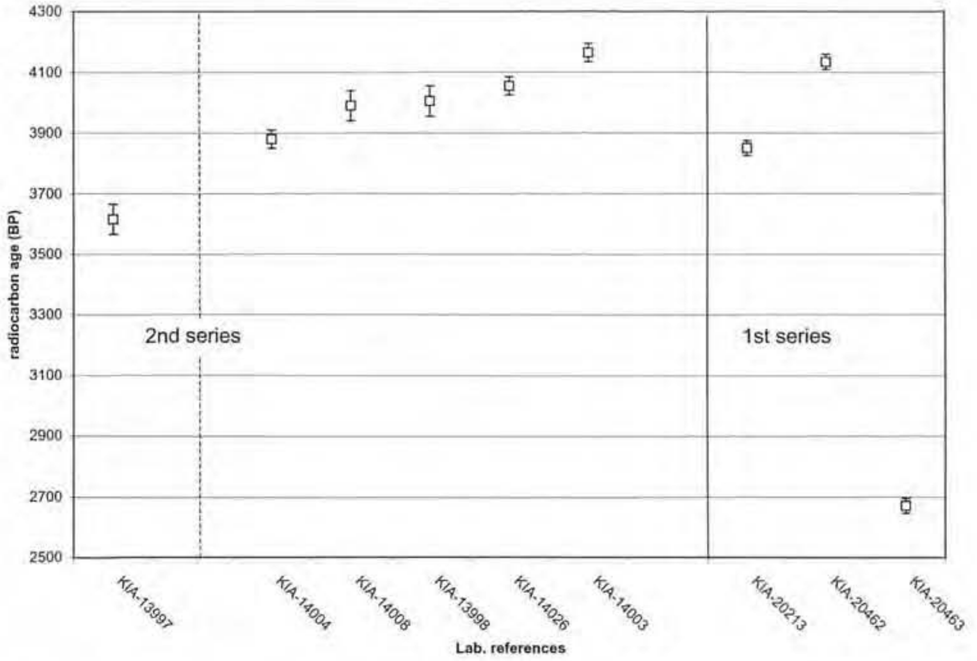


Fig. 2. a: SM-E 008H, human unidentified metapodial
b: SM-Mu 145-H, human longbone
c: Pocket cave, human tibia
d: Myotragus SM-X4
e: Myotragus SM-X9

Fig. 2. a: SM-E 008H, metàpode humà
b: SM-Mu 145-H, os llarg humà
c: Pocket cave, tíbia humana
d: Myotragus SM-X4
e: Myotragus SM-X9

Fig. 3. Radiocarbon ages (bp) of the cova de Moleta samples dated in this study.

Fig. 3. *Edats radiocarbòniques (bp) de les mostres de la cova de Moleta datades al present estudi.*



since collagen dissolves completely during the hydrolysis. It is probably humin [an organic fraction not extractable by weak acid or alkali] that was still in suspension before the ultra-filtration step, and precipitated during the centrifugation. This precipitation was removed by an extra filtration (Alltech Frits filter, 20 µm pores) except for sample KIA-13997. This sample was dated without the extra filtering. The results show that the residue contained carbon of a younger age than the dissolved -supposed- collagen. Because of the special nature of the ultra-filtration the R_c and the C/N factor were not measured, but the R_{col} shows very clearly the poor condition of the bones.

d) Discussion

Figure 3 summarises all radiocarbon data from this exercise. From the 11 Moleta samples analysed in this exercise, 10 failed the quality assurance tests. On this basis, the dates obtained cannot be considered as reliable. Assuming that the bones were contaminated with younger material, this implies that the obtained radiocarbon age most probably only gives a *terminus ante quem* date for the real age of the bone, with the real age remaining unknown. We cannot give any statement on the absolute difference between the radiocarbon age and the real age. It can be minor or important, it is impossible to deduct this from the data.

The fact that 10 bones out of 11 samples were heavily deteriorated, 9 of them contained humic acid, 1 bone did not contain any organic material anymore (SM-X-9), and only 1 bone (SM-E 008H/ KIA-20213) did very well in the tests indicates a complex sedimentation history of the cave. At some moments in time there must have been a still stand in the sedimentation of the cave or at least in some parts of it. This has provoked the complete degradation of the collagen, without the input of soil humic acids (SM-X-9). In other periods or places in the cave the degradation occurred with the input of soil humic acids, and in still other circumstances the bones must have been very rapidly covered by a protective layer causing the good preservation of (KIA-20213). This is a possible explanation for the differences in occurrence of the bones.

The bad preservation of the bones in the Moleta cave and the absence of any quality assurance tests on previously dated samples consolidate the enigma of the real age of the humans from cova de Moleta. To solve this problem, and given the importance of the site, only bones that withstand the severest tests should be allowed in a dating program and no (precious) bones should be wasted on dating projects that do not include the necessary quality assurance tests.

CONCLUSION

Can it be assumed that the situation of the sample quality at Moleta Cave is the same as for most other sites of similar age at the Balearic Islands, or does the situation of the cave in a high pluviosity locality create a special situation? It should therefore be concluded that the dating of the extinction of *Myotragus balearicus* and the arrival of humans on the islands will only become successful when new bone samples are tested on their integrity prior to dating. It has been demonstrated that the techniques to do so are available.

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DINORNIS –
AN INSULAR ODDITY, A TAXONOMIC CONUNDRUM REVIEWED.

Trevor H. WORTHY, Michael BUNCE, Alan COOPER & Paul SCOFIELD

WORTHY, T.H., BUNCE, M., COOPER, A. & SCOFIELD, P. 2005. *Dinornis* – an insular oddity, a taxonomic conundrum reviewed. *In* ALCOVER, J.A. & BOVER, P. (eds.): *Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach". Monografies de la Societat d'Història Natural de les Balears*, 12: 377-390.

Resum

Es revisa la història taxonòmica del gènere extingit de moa *Dinornis* (Aves: Dinornithiformes). Fins fa poc, les dimensions dels ossos i l'illa d'origen (Nord o Sud) eren els factors primordials per a la determinació específica dintre del gènere *Dinornis*, ja que es podia esperar que ocells avoladors evolucionats sobre diferents territoris aïllats podrien no pertànyer a la mateixa espècie. Anàlisis recents de DNA mitocondrial i nuclear han comportat una nova explicació de la variació de talla a *Dinornis*. En aquest treball establim una nova hipòtesi, derivada de la genètica, d'una espècie per illa, en la qual la variació de mida registrada a partir de les dades morfomètriques es deu a dimorfisme sexual revertit. Les dades de llargària dels principals ossos llargs s'analitzen per regió o per localitat i es demostra una bimodalitat clara en la qual les mitjanes per a les formes masculines i femenines varien entre regions/localitats, però pugen o baixen en paral·lel. Les bases de dades regionals demostren que a l'Holocè mitjà – superior els ocells més petits es trobaven a les zones subalpines i als boscos de muntanya i els més grans a les baixes altituds i a les regions pluvials baixes, tals com Canterbury (a l'est de l'Illa del Sud) i a la costa d'Horowhenua, al nord de Wellington, al sud de l'illa del Nord.
Paraules clau: *Dinornis*, Nova Zelanda, DNA fòssil

Abstract

The taxonomic history of the extinct moa genus *Dinornis* (Aves: Dinornithiformes) is reviewed. Until recently limb bone dimensions and island of origin (North or South) were the pre-eminent factors in species determination within the genus *Dinornis* due to the expectation that flightless birds on distinct landmasses could not be the same species. Recent morphological analyses applying modern concepts of biological variation reduced the number of acceptable taxa, but size remained of paramount importance in defining species boundaries. Recent analyses of mitochondrial and nuclear DNA have resulted in a radical new explanation of the size variation in *Dinornis*. Here we assess the new genetics-derived hypothesis of one species per island where the size variation seen in the morphometric data is due to reversed sexual dimorphism. Length data from main limb bones is analysed by region or site and demonstrates clear bimodality where averages for the male and female forms vary between regions/sites but move up or down in parallel. The regional datasets demonstrate that in the mid-late Holocene, birds were smallest in subalpine zones and montane forests and largest in low altitude and low rainfall regions such as Canterbury (in eastern South Island) and the Horowhenua coast north of Wellington in southern North Island.
Keywords: *Dinornis*, New Zealand, Ancient DNA

INTRODUCTION

The moas (Aves: Dinornithiformes) of New Zealand have excited palaeontologists and evolutionary biologists ever since their discovery by the scientific world in 1839 (Owen, 1840; 1842). Following the initial announcement that there had existed in New Zealand a struthious bird about the size of an ostrich, a wealth of bones were sent to England resulting in many species being described over the next few decades notably by Richard Owen, Julius von Haast, Richard Lydekker, and Frederick Hutton , as fully reviewed in Worthy & Holdaway (2002).

From the outset with Owen's early papers, size as measured by length and widths (proximal, shaft, and distal) of the leg bones (femora, tibiotarsi, tarsometatarsi) were the main criteria for separating and diagnosing species of moa. Shape characters such as might be used in modern cladistic studies were not identified until Hutton's work in the 1890s. However, even for Hutton, size was of paramount significance, and he "allowed" only a certain amount of size variation within a species. For example, after not accepting the distinctiveness of *Palapteryx plenus* Hutton, 1891 and *Dinornis altus* Owen, 1879, Hutton (1892) distinguished the true dinornithids with length ranges for tibiotarsi as shown in Table 1.

After just a few years Hutton abandoned the method of separating moa species by absolute length and started to use a 'method of averages' where he plotted length and width onto cluster diagrams. Using such diagrams, he identified three 'clusters' in the data from the large South Island assemblages from Kapua and Enfield, causing him to accept just *D. maximus*, *D. robustus* and *D. torosus* from these sites (Hutton, 1896a,b) and also from Glenmark (Hutton, 1897a). These analyses have influenced the subsequent taxonomic treatment of *Dinornis* and for first half of the twentieth century, three species in each of the North and South islands were generally accepted, e.g., Archey (1941). Oliver (1949) also basically accepted this arrangement but erected two new taxa for outliers in the size ranges in the North Island: *D. gazella* for a very small form and *D. hercules* for a very stout large form.

Authors supporting the distinctiveness of the North and South Island forms presented no data or only compared a very few bones. They did state, however, that the South Island forms attained greater size and had leg bones tending more robust than those in the North Island (e.g., Owen, 1846; Lydekker, 1891; Hutton, 1897b; Archey, 1941).

Like most palaeontological taxonomy in the 19th century the taxonomic decisions were influenced by the principles of Uniformitarianism formulated by Hutton and Lyell, which dictated that moas were giant flightless birds and were on separate island landmasses and thus had always been so. Until the acceptance of plate tectonics in the 1960s, the fixity of the present geography was generally assumed and certainly the rapidity with which tectonic activity can result in significant modifications to the geography was not appreciated. However, Archey (1941) noted that Cook Strait cannot have been a consistent barrier as he perceived one taxon with a New Zealand wide distribution, and that the several North-South taxon pairs varied in the amount of difference exhibited between the members of a pair, and that the Strait was geologically young – 'Late Pliocene'. He placed more significance on mountain barriers, but we now know that the axial ranges about Wellington for example are less than 2Ma old and the Southern Alps, less than 5-10Ma (Suggate, 1978). However, many of the terrestrial birds found in the North and the South islands constitute North-South pairs of various antiquity. In the first catalogue of the birds of New Zealand (Hutton, 1871), only one flightless species was recorded as found on both islands: all others were restricted to one island. Among volant taxa, well distinguished North-South species pairs were recognised then, and continue to be now e.g., within the genera *Turnagra*, *Philesturnus*, *Callaeas*, *Petroica*, and *Mohoua* (Holdaway *et al.*, 2001, Worthy & Holdaway, 2002). Observations of the modern fauna undoubtedly swayed the interpretation of the osseous fragments.

North Island:	Length	Metric conversion
D. excelsus	37.5-38 inches	952-965 mm
D. giganteus	34.2-36.0 inches	869-914 mm
D. firmus	30.0-33.0 inches	762-838 mm
D. ingens	27.0-29.5 inches	686-749 mm
D. gracilis	25.0-26.5 inches	635-673 mm
D. struthoides	22.0-23.5 inches	559-597 mm
South Island:		
D. maximus	39.0-39.2 inches	991-996 mm
D. validus	34.0-35.5 inches	864-902 mm
D. robustus	30.0-32.7 inches	762-831 mm
D. potens	27.0-29.5 inches	686-749 mm
D. torosus	24.0-25.3 inches	610-643 mm

Table 1. The length ranges in inches advocated by Hutton (1892) for tibiotarsi of *Dinornis* species.

Taula 1. Intervals de llargària, en polçades, esmentats per Hutton (1892) per als tibiotarsos de les espècies de Dinornis.

MODERN MORPHOLOGICAL STUDIES

A modern biological approach to moa classification was introduced by Cracraft (1976a, b, c) when he applied acceptable ranges of size variation as ascertained from extant taxa to intrageneric populations of moa bones. Size variation was assessed by coefficients of variation (CV) and CVs of 10-12 were considered acceptable values in sexually dimorphic species, in contrast to species that lacked sexual size dimorphism where values of 3-5 were considered usual. This philosophy combined with a multivariate analysis of length and width measurements led Cracraft to accept just three species in *Dinornis*: *D. struthoides*, *D. novaezealandiae*, and *D. giganteus* ranging over both North and South islands, and provisionally *D. torosus* in the South Island.

One of the problems with assessing size variation in *Dinornis* is that members of this genus are generally uncommon in fossil sites and usually only a few individuals are represented in contrast to relatively much more abundant emeids. Therefore the data from the very large sites such as Kapua, Enfield and Glenmark that was available to Hutton was very significant. Due to judicious exchanges by Hutton and others a majority of these assemblages is now spread through many institutions around the world, making measurements of the original large samples impractical. Lumping data from individuals from many sites is less desirable as this introduces temporal and geographic variation which is known to be significant in other moa (Worthy & Holdaway, 2002). The remarkable assemblage from Makirikiri near Wanganui is the largest from a single site still accessible in a single collection. Worthy (1989) presented a simple length frequency analysis of the *Dinornis* femora, tibiotarsi and tarsometatarsi overlaid with joined lines for bones from individual skeletons. For each element there was a distinct group of small individuals that were referred to *Dinornis struthoides*. As the size range of larger bones spanned the range for *D. novaezealandiae* and *D. giganteus*, as given by Archey (1941) and Oliver (1949), Worthy (1989) considered that both taxa must be represented. Detecting a break in the distribution of tibiotarsi near 750 mm and using the linked lines of known individuals, *D. giganteus* was defined as having femora longer than 320 mm, tibiotarsi longer than 750 mm, and tarsometatarsi longer than 440 mm. These values are near the boundaries given by Archey (1941) and Oliver (1949) and so the three species arrangement seemed to be confirmed.

Having been able to distinguish other moa taxa on sets of characters for most leg bones and other major elements (Worthy, 1988), the inability to do likewise for *Dinornis* species was problematic. In an attempt to redress this situation, Worthy (1994) reassessed the taxonomy of *Dinornis* using cranial characters and multivariate analysis of leg bone measurements and accepted just three species with *D. torosus* in the synonymy of *D. novaezealandiae* following Worthy (1989). Taxa were separated on cranial features and then measurements of the associated leg bones from individual skeletons analysed. Crania were separated into three forms with the large and small size classes essentially identical, and the median size class separated from them by less well developed postorbital processes, not so prominent occipital tuberosities, and poorly developed mamillar tuberosities.

The analysis was hampered by small sample sizes and that as the groups of leg bones were predefined by crania that primarily differed in size, then they too necessarily were separated primarily by length. Multivariate analysis indicated that the middle sized class had slightly stouter bones. The three forms were accepted as species, and this taxonomic arrangement seemed to corroborate the trimodal structure Hutton (1896a,b; 1897b) had detected and which also seemed to be present in the large sample from Makirikiri in the North Island (Worthy, 1989). Moreover, as an earlier analysis of the distribution of moas had shown that while *D. struthoides* appeared to have a widespread distribution, *D. novaezealandiae* and *D. giganteus* had largely non-overlapping distributions (Worthy, 1990), the acceptance of three taxa made sense.

However, a recent reanalysis of the large Pyramid Valley *Dinornis* assemblage revealed that lengths for all individuals except one contributed to an essentially normal and unimodal size distribution. For example, excluding the smallest individual, tibiotarsi had a mean of 838 mm, ranged from 681-992 mm, and had a CV of 9.65. As a result all were referred to *D. giganteus*, except the small one, which was referred to *D. struthoides*. Elsewhere in New Zealand there are few faunas with sufficient numbers of *Dinornis* to analyze for the presence of distinct size clusters among individuals that may be presumed to represent natural groups, but the surviving bones in New Zealand collections from Te Aute constitute one. The 107 leg bones of *Dinornis* had a bimodal size distribution with the grouping of larger individuals having a size distribution near double the absolute range of that of the smaller individuals. As a result, two species *D. struthoides* and *D. giganteus* were accepted (Worthy, 2000).

Thus throughout the taxonomic history of the genus *Dinornis*, size has been of paramount importance in defining the taxa and no fewer than 17 species have been erected for dinornithids. There has been in essence an unwritten paradigm that only a certain amount of size variation is acceptable within a species. The degree of acceptable variation has increased through time so that recently Worthy & Holdaway (2002) indicated that lengths of tibiotarsi of *D. struthoides* ranged 27% less than the maximum length of 620 mm, *D. novaezealandiae* 23% less than 740 mm, and *D. giganteus* 31% less than of 992 mm.

This summary of the history of dinornithids essentially mirrors that for the moa group as a whole. Some 64 species have been erected (Worthy & Holdaway, 2002), but the most recent morphological analysis only accepted 11 species, two families, and six genera (Worthy & Holdaway 2002, Fig. 4.34 p. 130). In that study, based on 82 morphological characters, a consensus parsimony analysis provided strong support for the distinction of *Dinornis* from other moa, but was unable to resolve the branching order of *Anomalopteryx*, *Pachyornis*, *Emeus*+ *Euryapteryx*, and *Dinornis*.

ANCIENT DNA INVESTIGATIONS OF DINORNITHIDS

DNA degrades rapidly post-mortem; however given the right preservation conditions (cold and constant temperatures) DNA can persist in the environment for thousands of years. The extraction and amplification of "old" DNA, primarily from bones, is referred to as ancient DNA (aDNA). New Zealand is fortunate to have a suitable climate and an extensive Quaternary fossil record, a combination which makes it an ideal locality for aDNA studies.

The first aDNA investigations of moa were based on 12S mitochondrial DNA (mtDNA) and were designed to test the relationship between moas and other ratites (Cooper *et al.*, 1992). These early analyses were expanded and resulted in the complete mitochondrial genome for two moas being sequenced, revealing much about ratite phylogeny as well as plate tectonics following the break-up of Gondwana (Cooper *et al.*, 2001; Haddrath & Baker, 2001). MtDNA genes that mutate rapidly also provided valuable insights into the internal phylogenetic structure of Dinornithiformes (Cooper, 1997).

Initial analysis of sequence results from *Dinornis* somewhat surprisingly showed that phylogenetic trees bore no relationship to accepted morphological based taxonomy. Continued investigations into the *Dinornis* phylogeny using an enlarged data set and both mitochondrial and nuclear DNA have supported initial findings and reveal that all *Dinornis* individuals analysed, irrespective of referred taxon, form two genetically distinct allopatric populations dependant on the island of origin (Bunce *et al.*, 2003; Huynen *et al.*, 2003). Furthermore, there was no support for the association of individuals into taxa such as *D. struthoides* or *D. giganteus* within each island clade (Fig. 1). Even in the largest analysis that included several mitochondrial genes (in total about 2000 base pairs) and 32 individuals, no associations were evident that made sense relative to the current morphological taxonomy (Bunce *et al.*, 2003).

Good DNA preservation in some specimens has also allowed extraction and analyses of nuclear DNA, and so the sex-specific KW1 gene, first identified for ratites by Huynen *et al.* (2002), became the key to sexing moa. Many of the individuals could be sexed and the conclusion that *D. struthoides* were male birds and all larger individuals of *Dinornis* were female was reached more or less simultaneously by two research teams using an overlapping but not identical set of specimens (Bunce *et al.*, 2003; Huynen *et al.*, 2003). As a result, Bunce *et al.* (2003) advocated that *Dinornis* fossils can henceforth be referred to *D. novaezealandiae* in the North Island and *D. robustus* in the South Island. Morphologically there is little to separate these two allopatric populations, but the deep genetic split may reflect a mid-Pleistocene divergence of the clades (Bunce *et al.*, 2003).

The data show that *Dinornis* had unprecedented (amongst birds) reversed sexual size dimorphism (RSD) with the largest females some 280% the weight and 150% the height of the largest sympatric males. Individual mass ranged 76-242 kg for females and 34-85 kg for males. Support for a single species of *Dinornis* is provided by data from sites and regional faunal assemblages that indicate average sex ratios, assuming *D. struthoides* were males and others female, of 1 male to 1.44 females, which is within the normal range for extant ratites (Bunce *et al.*, 2003).

This taxonomic arrangement serves to resolve several problems. For instance, Worthy (1994) noted that the type of *Dinornis giganteus* was not very representative of bones usually referred to that species, being rather small and therefore not overly good to distinguish the larger taxon from *D. novaezealandiae*. In addition, recent collections of *Dinornis* specimens have included several skulls in the size range of *D. novaezealandiae* yet with well-developed post-orbital processes, and prominent occipital and mamillar tuberosities (e.g., MNZ S32677), so it now appears that the development of these features has no taxonomic significance. As each feature is associated with the attachment site for ligaments, it is more probable that the prominence or otherwise of these features is individually variable and may be related to age of

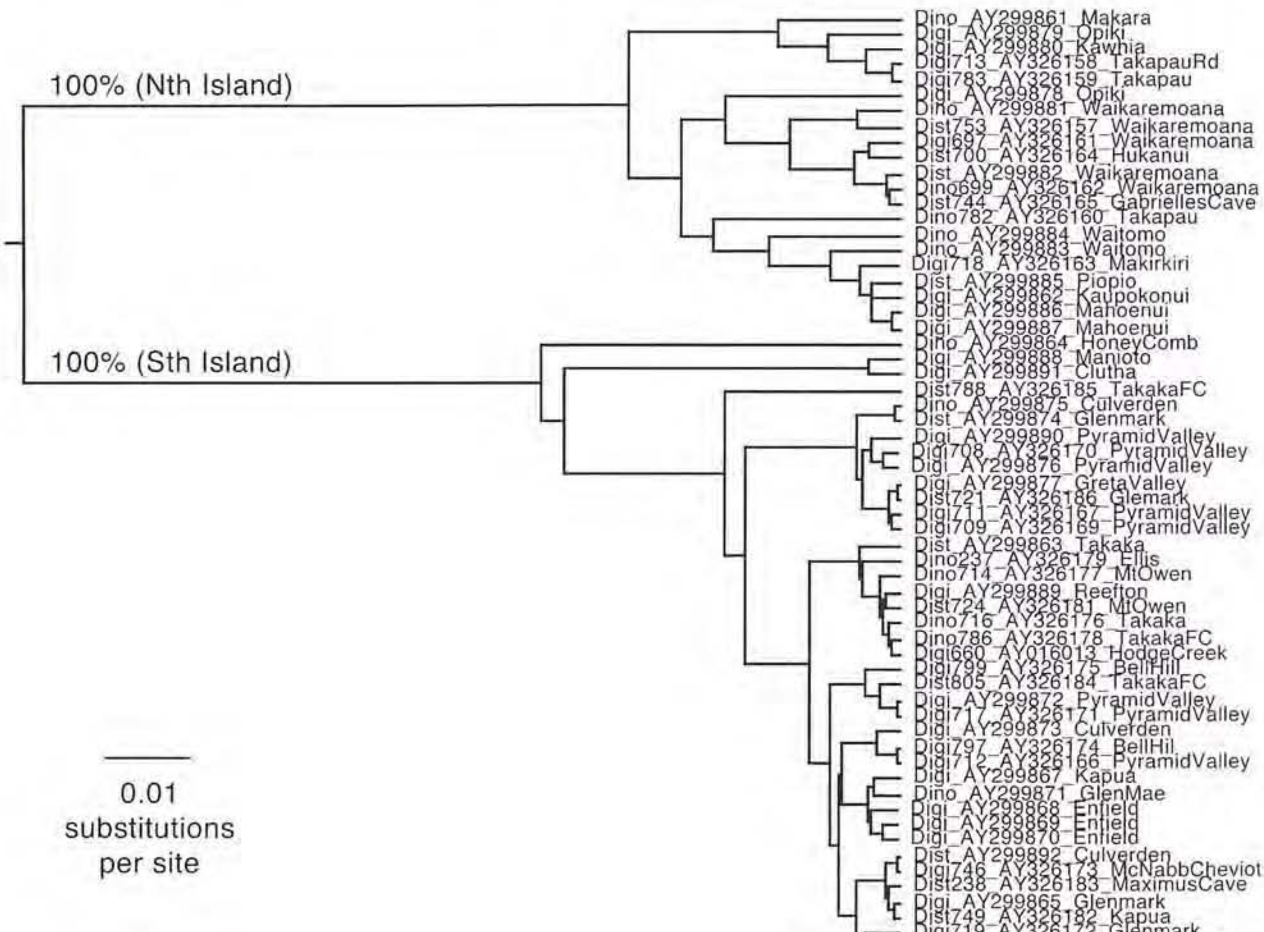

Fig. 1. The maximum *a posteriori* tree of *Dinornis* mitochondrial control region DNA sequences generated from the posterior distribution using Metropolis–Hastings MCMC (Drummond *et al.*, 2002). The sequences of between 243 and 375 base pairs in length are a combined dataset of Bunce *et al.* (2003) and Huynen *et al.* (2003). The associated tags indicate original species designation, GenBank accession number and sample location respectively (*D. giganteus* = Digi, *D. novaezealandiae* = Dino and *D. struthoides* = Dist). The split between the islands has a posterior probability of 100%, and based on other avian molecular rates, is estimated to be mid-Pleistocene in origin. Support for other nodes on the tree are not shown. Bayesian analysis was performed using BEAST (http://evolve.zoo.ox.ac.uk/beast/) using an HKY + G + I substitution model for 5000000 generations (Drummond *et al.*, 2002; Drummond & Rambaut, 2003).

***Fig. 1.** L'arbre a* posteriori *màxim de les seqüències de DNA de la regió control mitocondrial generada a partir de la distribució posterior fent servir MCMC Metropolis-Hastings (Drummond* et al., *2002). Les seqüències d'entre 243 i 375 parells de bases són una base de dadas combinada de Bunce* et al. *(2003) i Huynen* et al. *(2003). Les etiquetes associades indiquen respectivament les designacions específiques originals, els nombres d'accés al GenBank i la localització de la mostra (*D. giganteus *= Digi,* D. novaezealandiae *= Dino i* D. struthoides *= Dist). La separació entre les illes té una probabilitat posterior del 100%, es basa en altres taxes moleculars ornítiques i s'estima que es va originar al Pleistocè mitjà. No es mostra el suport per a altres nodes de l'arbre. Es va dissenyar un anàlisi Bayesià emprant BEAST (http://evolve.zoo.ox.ac.uk/beast/) fent servir un model de substitució HKY + G + I per a 5000000 generacions (Drummond* et al., *2002; Drummond & Rambaut, 2003).*

the bird at death. The post-orbital processes do not consist of a specific bone identifiable in the juvenile bird such as the lacrymal, which contributes to the prefrontal process. Rather, post-orbital processes are just outgrowths of the frontals and expand through ontogeny (Worthy & Holdaway; 2002: 79-83) so mature birds might be expected to have better developed ones than younger yet also adult birds, as assessed by nasal fusion (last element in skull to fuse to rest of skull).

REGIONAL AND TEMPORAL VARIATION COMPLICATES MATTERS

How is this new hypothesis of small males and larger females to be resolved with the apparently disjunct distributions of *D. novaezealandiae* and *D. giganteus* described by Worthy (1990)? Hutton was the first to document regional and or temporal variation in a moa when he noted that specimens of *Meionornis* [now *Emeus*] were on average bigger in the presumed younger deposit of Enfield compared to those in Glenmark (Hutton, 1897a). And more recently Worthy (1987) and Worthy & Holdaway (1995; 2002) have demonstrated that there is significant regional size variation in some taxa, and equivalent or greater variation in mean individual size over time. That some moa exhibit geographical size variation does not seem to explain why females might change in size yet apparently the males did not across a landscape, which is what the differential distribution of *D. novaezealandiae* and *D. giganteus* necessitates.

This issue was resolved by Bunce *et al.* (2003) who presented some data to show that mean individual size in different populations of *Dinornis* assumed to be of similar Holocene age did vary significantly with habitat. They suggested that both sexes varied in size across a geographic gradient, but that as the size increase was small in absolute terms in the smaller sex (*D. struthoides*), it was not so obvious and the total size variation for the small sex was able to be encompassed in the one taxon. In contrast, for the larger sex, a 20% increase in size, essentially moved some individuals out of the acceptable range for one species (*D. novaezealandiae*), so that they were necessarily referred to *D. giganteus.*

Our aim here is to enlarge the datasets used by Bunce *et al.* (2003) and assuming *D. struthoides* to be male and larger *Dinornis* to be female, assemble comparative data for various fossil localities or regions to assess geographic variation in limb bone sizes and whether it is in fact consistent for each sex.

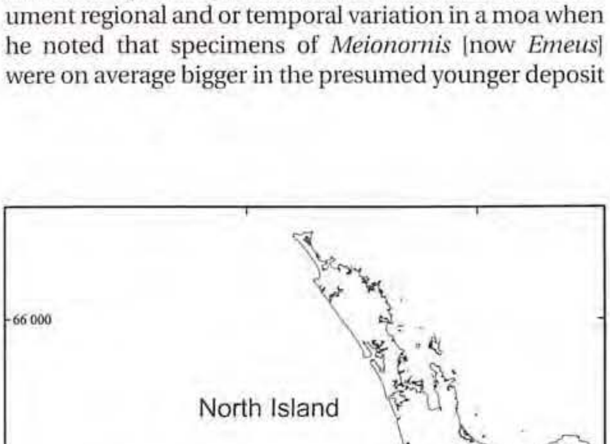

Fig. 2. Map of New Zealand showing study regions and sites from which samples of *Dinornis* bones were analysed. The 1000 m contour lines are shown and the margins show the New Zealand map series 260, 1:50000 metric grid.

Fig. 2. *Mapa de Nova Zelanda que mostra les regions d'estudi i les localitats a partir de les quals s'han analitzat les mostres d'ossos de* Dinornis. *Es mostren les línies de contorn de 1000 m i els marges, mapa de Nova Zelanda sèrie 260, xarxa mètrica 1:50000.*

METHODS

The database provided by Bunce *et al.* (2003) was taken as a starting point and expanded by THW. Data was collected for *Dinornis* from selected study regions and sites as follows (Fig. 2). Total lengths of adult *Dinornis* bones were measured for specimens as per the methods of Worthy (1987). For the North Island, the data from disassociated bones used in the Makirikiri analysis (Worthy, 1989) and Te Aute (Worthy, 2000) were augmented by measurements of individuals from the Takapau Road site, whose fauna was described by Worthy (1989), and a combination of individual skeletons from numerous cave sites located within lowland closed forest habitat in the Waitomo and Waikaremoana areas in the central North Island. The Makirikiri fauna is of late Holocene in age (Huynen *et al.*, 2003), Te Aute dates to the Late Glacial (Worthy, 2000), and Takapau is of late Holocene age (authors unpublished data). The individuals from the Waitomo and Waikaremoana areas are assumed to be mainly of Holocene age as all were surface collected specimens and all Waikaremoana specimens are from sites within the rockfall that formed the lake 2200 yrs BP (Newnham *et al.*, 1998).

For the South Island, only Pyramid Valley provides a large assemblage that is now easily accessed, the material from others like Kapua, Enfield and Glenmark is now either destroyed or dispersed to dozens of museums around the world where often its locality data is now lost. The Pyramid Valley site has a unique taphonomy

(Holdaway & Worthy, 1997) and females dominate the *Dinornis* assemblage. Therefore, variation in the Canterbury region was assessed by making regional compilations of data from disassociated material from late Holocene sites. Data were taken from bones from Pyramid Valley, Glenmark, Bell Hill Vineyard, Cheviot Swamp, Kapua, and Enfield (Worthy & Holdaway, 1996; Worthy 1997; 1998).

Data from the north-western South Island region for sites under 600 m altitude were compiled from individuals from the Punakaiki karst region (Worthy & Holdaway, 1993), Honeycomb Hill Cave System in the Oparara River (Worthy, 1993), and from karst in the Buller River. All these individuals were found on cave floors and most are assumed to be of Holocene age. An upland assemblage of fossils from this same region but from sites above 600 m was compiled from individual skeletons from caves on Mt Owen, Mt Arthur and Takaka Hill. Those on Mt Owen and Mt Arthur are assumed to be of Holocene age as these regions were ice-covered during the late Pleistocene. Those from Takaka Hill are assumed or known to be mostly of Holocene age (Worthy & Holdaway, 1994; Worthy & Roscoe, 2003).

Sex was assessed by plotting the lengths of all bones from the site or assemblage as histograms which revealed clear bimodal size distributions. Boundaries between the two size distributions were determined as described in Appendix 1. Thus femora shorter than 290 mm in the Waitomo-Waikaremoana area were classed as males, those longer as female. For assemblages based on individuals, the summary statistics of the lengths of the associated tibiotarsi and tarsometatarsi were then calculated for each femur-determined sex. For the assemblages based on disassociated individuals the intermediate point

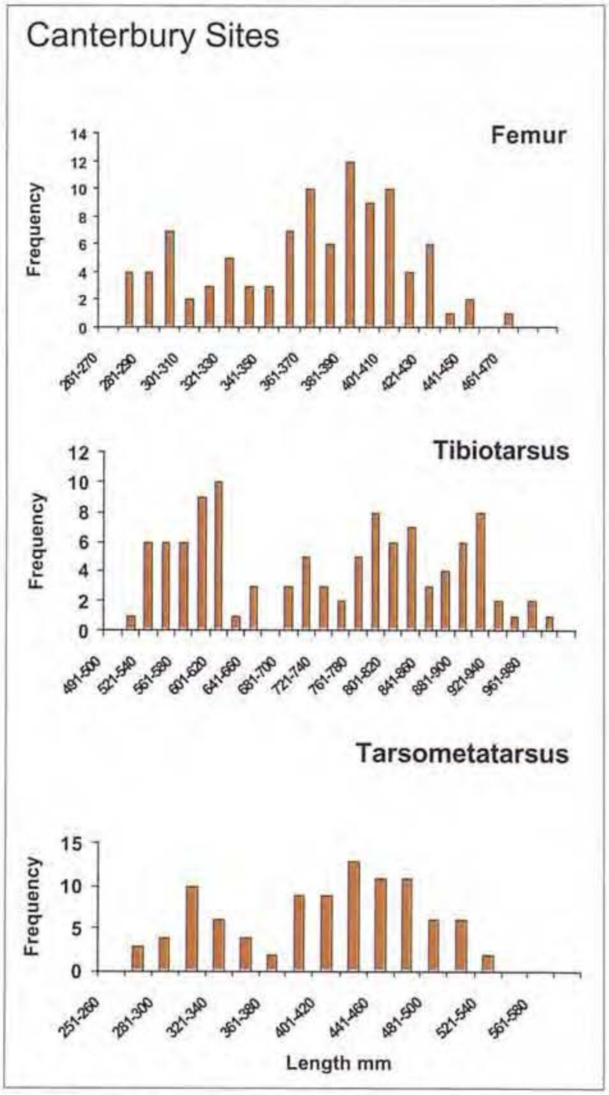

Fig. 3a. Length frequency histograms for named elements of *Dinornis* from Canterbury sites, specimens listed in Appendix 2.

Fig. 3a. Histogrames de freqüència de llargàries per als elements indicats de Dinornis *de les localitats de Canterbury, exemplars llistats a l'apèndix 2.*

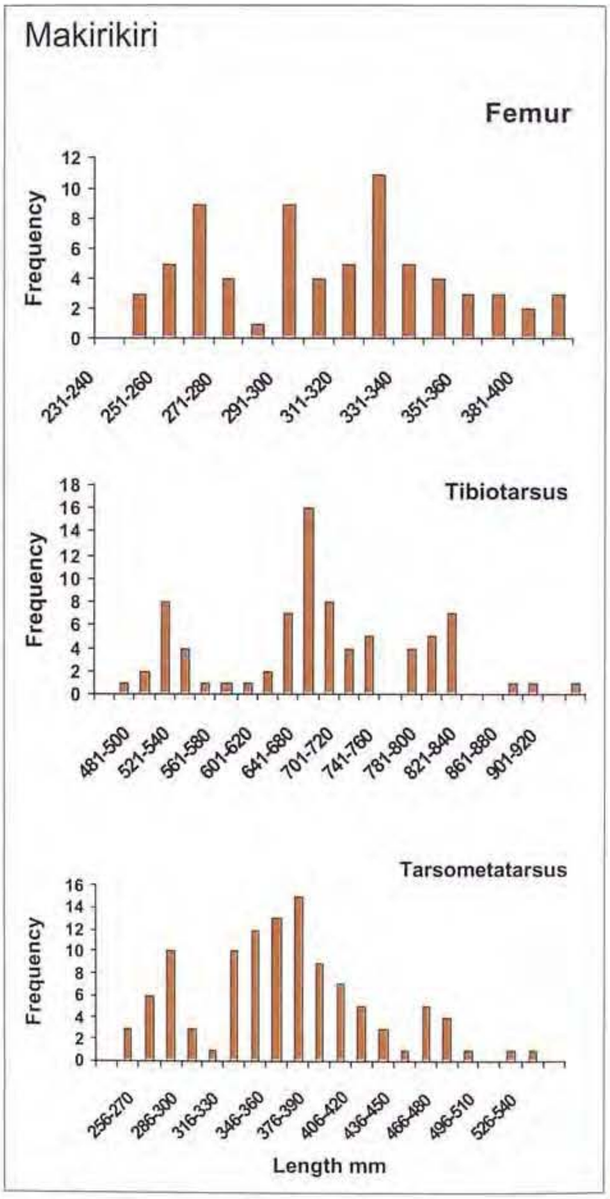

Fig. 3b. Length frequency histograms for named elements of *Dinornis* from Makirikiri, North Island, data from Worthy (1989).

Fig. 3b. Histogrames de freqüència de llargàries per als elements indicats de Dinornis *de Makirikiri, Illa del Nord, dades de Worthy (1989).*

between each mode for each element was used to delimit putative sex boundaries. Femur lengths of each sex only overlapped in the Northwest Nelson >600 m assemblage, but here the males were noticeably more slender than females. Eight of the 15 individuals were sexed genetically including all in the overlap zone (Appendix 2).

Height of the birds was assessed as the sum of the lengths of the femur, tibiotarsus and tarsometatarsus. It is acknowledged that the femur is usually held at about 30-45 degrees below horizontal (Worthy & Holdaway, 2002) and so only about half of its length contributes to the bird's height, but the tibiotarsus and tarsometatarsus are usually oriented near enough to vertical in life. However, the height above the femur in the pelvis and overlying tissues roughly equates to half a femur length so the sum of lengths of the three bones roughly approximates the height of the bird at its back. While this may be inexact, the method gives a consistent comparative height for the back among individuals. Comparative estimates of mass were generated with an algorithm based on femur length (Prang *et al.*, 1979).

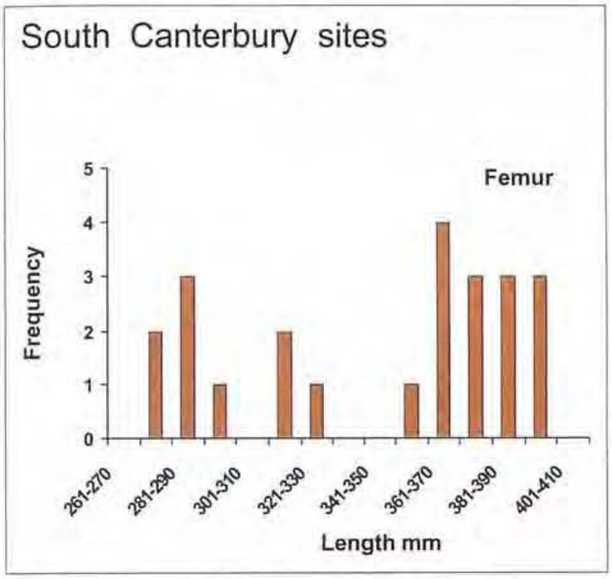

Fig. 3c. Length frequency histograms for femora of *Dinornis* from combined South Canterbury sites, specimens listed in Appendix 2.

Fig. 3c. Histogrames de freqüència de llargàries per a fèmurs de Dinornis *de les localitats combinades de Canterbury, exemplars llistats a l'apèndix 2.*

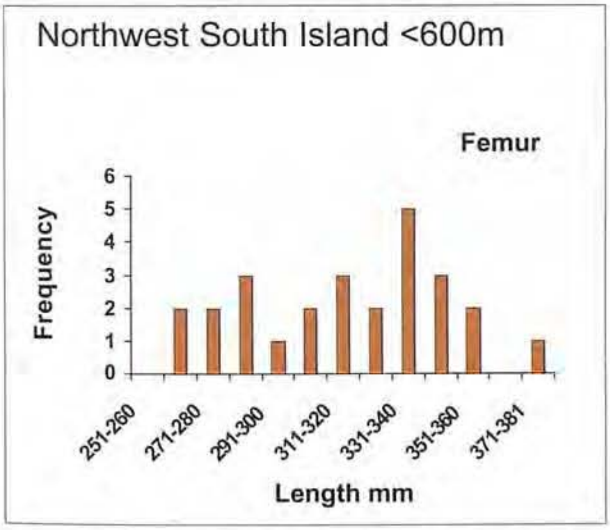

Fig. 3d. Length frequency histograms for femora of *Dinornis* from sites less than 600 m altitude in northwest South Island, specimens listed in Appendix 2.

Fig. 3d. Histogrames de freqüència de llargàries per a fèmurs de Dinornis *de localitats de menys de 600 m d'altitud al nord-oest de l'Illa del Sud, exemplars llistats a l'apèndix 2.*

RESULTS

Summary data for lengths of femora, tibiotarsi, and tarsometatarsi, and for height and mass by site or region, as defined above, is presented in Appendix 1. Exemplary length frequency histograms of this data are shown in Fig. 3. Summary statistics of mass data derived from femur length are plotted graphically in Fig. 4.

The length data shows that North Island populations of *Dinornis* from the Late Glacial deposits at Te Aute, and from Holocene assemblages from closed forest habitats in the Waitomo – Waikaremoana region and Makirikiri, each have similar mean values for males and females. However, the population from Takapau Road, which is in a lowland dune-swale shrubland forest mosaic area, had mean values for both females and males considerably larger than for the other North Island populations despite also being of late Holocene age.

The absolute size range was usually greater for females than males and larger samples had greater variation. The assemblage of individual skeletons from Waitomo-Waikaremoana had more females than males, but the CVs were broadly similar between the sexes indicating a similar relative size range for each sex. In contrast, the large collection from Makirikiri had over twice as many females as males and variation within females was 2-3 times that shown by males (CVs females 9.22-12.55 *vs.* 3.4-5.17 for males). The small number of males in Takapau Road precludes meaningful comparisons of absolute size range with the females, but the size variation of females was similar to that in the Makirikiri sample.

The South Island populations had some differences from those in the North Island. The size distributions of the sexes were essentially abutting in the South Island samples, whereas they were more widely separated in the North Island. Secondly, the South Island exhibits more inter-population variation. While females in the higher rainfall zones of northwest South Island from less than 600 m altitude were of similar size to females from the Waitomo – Waikaremoana region, the males were larger, and not as differentiated in size from the females as in the North Island populations. For individuals from altitudes above 600 m in the northwest South Island (mainly Takaka Hill, Mt Owen, and Mt Arthur), females had smaller mean masses than those at lower altitude and the size of males overlapped that of females. In these instances sex was determined genetically. Males had more slender leg bones than females but, as the range of femur lengths overlapped and as mass is here based on femur length, the ranges of calculated body mass necessarily overlap. But the more slender elements of the males suggest the algorithm may over-estimate mass of males in these cases. The size variation for each sex in Northwest South Island birds, in areas both above and below 600 m altitude, was similar, as indicated by CV values, mirroring the situation for North Island birds in the Waitomo – Waikaremoana region. Both the males and females in eastern South Island were larger than their equivalents in northwest South Island, thus paralleling the trend seen in the North Island between the wetter climate regions with closed forests and the drier climate experienced around the Takapau Road site. The size variation observed in each sex for the Eastern South Island sample was also very similar, that is each had similar CV values, in marked contrast to the situation for Makirikiri. This suggests that a collecting and or preservation bias may have resulted in fewer of the smaller bones of males being recovered in the Makirikiri sample: imperfect bones are noticeably under-represented in this collection.

Basically populations with the largest samples have the greatest absolute size ranges, e.g., Makirikiri and Eastern South island, but the average mass for Makirikiri is similar to that of the Waitomo – Waikaremoana sample which is from a similar habitat.

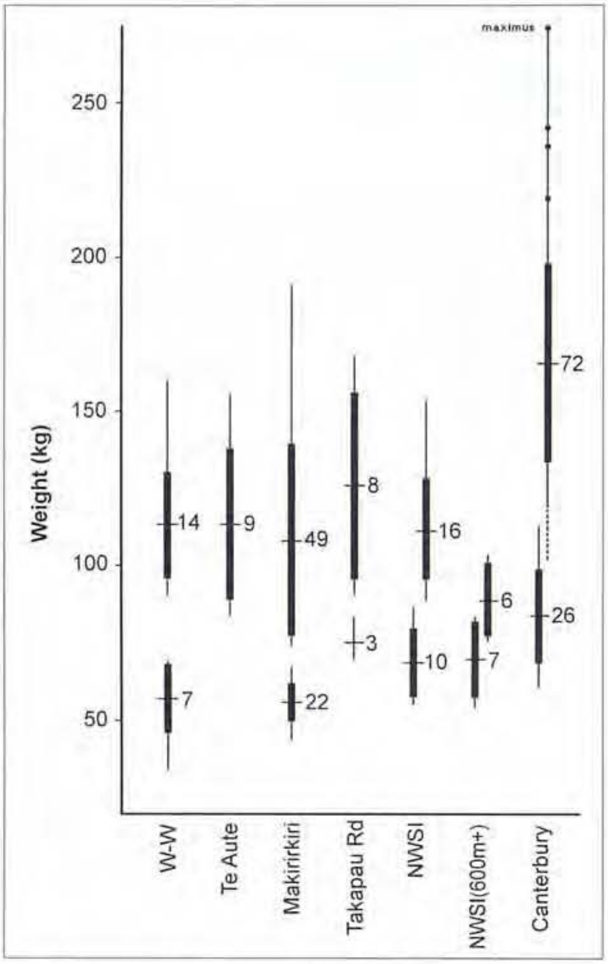

Fig. 4. A plot of weight data derived from femur length for named sites and regions. Each plot shows mean (small horizontal bar), standard deviation (filled box), range (line), and *n*. Males (smaller) are plotted separately to females, data derived from Appendix 1. W-W is Waitomo-Waikaremoana region, NWSI is northwest South Island. The dots adjacent to the plot for NWSI (600m+) represent data points for known sexed individuals determined genetically. The plot for females from Canterbury includes the data for the four largest individuals (dots on the range line) showing how much of the extreme in range is accounted for by few individuals. The largest individual ever documented is the type of *Dinornis maximus.*

Fig. 4. Diagrama de dades de pes derivat de les llargàries de fèmurs per a les localitats i regions esmentades. Cada diagrama mostra la mitjana (petita barra horitzontal), la desviació típica (rectangle ple) l'interval (línia) i n. Els mascles (més petits) es presenten separats de les femelles. Dades obtingudes a partir de l'apèndix 1. W-W és la regió Waitomo-Waikaremoana, NWSI és el noroest de l'Illa del Sud. El diagrama per a les femelles de Canterbury inclou les dades dels 4 individus més grans (punts a la línia d'interval) i mostra com gran part dels extrems de l'interval es deu a pocs individus. L'individu més gran mai documentat és el tipus de Dinornis maximus.

Discussion

The existence of clear bimodal size distributions for *Dinornis* within discrete geographic areas supports the hypothesis that only a single species with strong sexual dimorphism is present in each island, as advocated by Bunce *et al.* (2003) based on genetic evidence. North Island birds are referred to *D. novaezealandiae* and South island birds to *D. robustus*. The data clearly show that the mean size of males and females moves in unison across the landscape. It also reveals considerable size variation between geographic regions of each of North and South islands. The size distributions of North Island males and females characteristically have a greater separation than do their South Island counterparts where size distributions of each sex more or less abut or even overlap (as measured by femur length) in one region.

Across the central North Island, the size of individuals appears to have remained remarkably similar over time, if the late Glacial Te Aute sample is representative of older faunas. However, birds in the Waitomo – Waikaremoana and Makirikiri populations were markedly smaller than those in the contemporary Takapau Road deposit. The former populations lived in a closed-canopy lowland podocarp forest (McGlone, 1988) whereas the Takapau Road site is in a coastal dune – swale area where scrub-forest mosaic vegetation was likely. These vegetation differences reflect a combination of average rainfall, propensity for summer drought and soils. In the Waitomo – Waikaremoana region rainfall is presently 1500-2000 mm whereas at Makirikiri rainfall is about 900 mm, but summer drought is rare and a closed-canopy forest prevailed during the Holocene. In contrast, on the Horowhenua Coast about Takapau Road rainfall is 750-1000 mm (NIWA data 1971-2000), but summer drought is common, which combined with well-drained sand substrates and wet interdune swamps would have resulted in a variety of vegetation types.

The northwest South Island below 600 m originally had similar vegetation and climate characteristics (wet, > 2000 mm rainfall, closed-canopy podocarp forest) to that in the central North Island, and the birds were of similar size to birds from that region. But at higher altitudes, it is as if *Dinornis* encountered a maximum size limit and so mean female size was reduced markedly compared to lowland equivalents, but males were only marginally smaller. In direct contrast, in lowland eastern regions, it is as if size limiting factors were relaxed and so while both males and females were both larger than western counterparts, females exhibited a greater size increase. Individual females from this region achieve the largest size for the species *D. robustus*. In these eastern lowlands rainfall is typically 500-750 mm (NIWA data 1971-2000) and a grassland - scrub – forest mosaic existed in the late Holocene.

Therefore size variation in *Dinornis* appears strongly correlated with palaeo-vegetation characteristics. At this stage we can only speculate that the drier regions with grass-scrub-forest mosaics provided an on average more nutritious browse than wet closed-canopy forests. Conversely, the upland montane forests of *Nothofagus* and their bounding subalpine zones provided the least nutritious food. Perhaps now that we can perceive *Dinornis* as a highly variable species, the causes of this variation may be able to be traced with interpretations of diet by isotope analyses.

Moreover, now that the sexes are able to be recognised perhaps the sex composition in different sites may reveal something of the behaviour of these birds. Surely the extent of this reversed sexual dimorphism will have necessitated complex mating behaviour at the least. Such behaviour did not involve violence as no part of the skeleton appears adapted towards combat, unlike in a cassowary, which has a lengthened ungual spur on digit 2, which provides an effective weapon in defence. However, does this RSD also suggest differential resource partitioning among the sexes. For example, male cassowary not only incubates the eggs but look after the young while they grow in the absence of the females (Marchant & Higgins, 1990).

Perhaps this RSD is integral to understanding the distribution of *Dinornis* fossils in Pyramid Valley swamp. Most assemblages or sites, e.g., Bell Hill Vineyard, where collector bias was eliminated, have a male to female ratio of about 1:1, but in Pyramid Valley there were only five males (femur length < 340 mm) and the other 47 adult birds were female. Pyramid Valley differs from other swamp entrapment sites in another vital way: it was a shallow lake wherein birds only became trapped in drought conditions (summer) when water levels receded and birds were able to walk out over the lake sediments and break through a crust of peat into the gyttja below (Holdaway & Worthy, 1997). The apparent absence of males is not explained by the site somehow not trapping smaller moas as the much smaller *Emeus crassus* is abundant. Moreover, there is a parallel paucity of juvenile *Dinornis* in the deposit, only 9 of 63 birds in total (Holdaway & Worthy, 1997), yet all other typical spring-hole type swamps, where entrapment is essentially random throughout the year, have roughly equal proportions of males and females and a high number of juveniles. For example, Bell Hill Vineyard is only a couple kilometres from Pyramid Valley but has roughly equal proportions of sexes (unpubl. data). The highly seasonal frequency of entrapment in Pyramid Valley and the near absence of males suggests that males and females were segregated over summer. Perhaps there is a parallel with cassowary in that females are separated from the males and young for part of the year, and if so it suggests that the larger females controlled prime habitat around water in times of stress such as summer.

CONCLUSION

On islands, paradigms constructed from data taken from continental situations may be inappropriate. Here we have demonstrated that intraspecific size variation in the genus *Dinornis* is greater than that for any other bird. Such variation is due to extreme reversed sexual dimorphism and significant geographic variation. It is not surprising that in the "land of birds", New Zealand has produced another insular extreme, with not only the tallest bird, but one with the greatest degree of reversed sexual dimorphism known in the avian world.

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Appendix 1. Summary statistics for bone lengths mm (Fem, femora; Tib, Tibiotarsi; Tmt, tarsometatarsi). Height as sum of leg bone lengths provides an estimate of height of the back, and weights based on femur length (Prang *et al.*, 1979). Height is only computed from lengths from constituent bones of individual skeletons. Sexes were defined by gaps in bimodal distribution of data for each region. Cut-off length values (mm) are given in the row by the sex.

***Apèndix 1**. Resum estadístic per a les llargàries dels ossos, en mm (Fem, fèmurs; Tib, tibiotars; Tmt, tarsometatarsos). L'alçària, com a la suma de les llargàries dels ossos del membre, que subministra una estima de l'alçària al dors, i el pes està basat en la llargària del fèmur (Prang* et al., *1979). L'alçària només es computa a partir de les llargàries d'ossos que formen part d'esquelets individualitzats. Els sexes es defineixen a partir dels buits a la distribució bimodal de les dades per a cada regió. A les fileres es donen els valors límits per sexe.*

Waitomo – Waikaremoana region

	FemL	TibL	TmtL	Height	Weight
Females	>290	>570	>310		
Mean	339.9	709.8	371.9	1413.8	113.5
Standard Error	4.44	11.24	7.79	26.11	4.31
Standard Deviation	16.61	42.06	24.62	82.55	16.14
Minimum	315	660	328	1324	91
Maximum	385	810	421	1616	160
Count	14	14	10	10	14
CV	4.89	5.93	6.62	5.84	14.22
Males					
Mean	264.3	504.1	276.3	1052.6	56.6
Standard Error	7.65	10.89	7.63	30.39	4.14
Standard Deviation	20.23	32.66	20.18	67.95	10.96
Minimum	222	462	247	934	34
Maximum	285	541	301	1103	69
Count	7	9	7	5	7
CV	7.65	6.48	7.30	6.46	19.34

Makirikiri. Data previously figured by Worthy (1989).

	Fem L	Tib L	Tmt L	Weight	
Females	>290	>570	>310		
Mean	333.3	713.3	381.7	109.1	
Standard Error	4.39	9.65	5.11	4.24	
Standard Deviation	30.72	76.58	47.92	29.66	
Minimum	292	580	312	74	
Maximum	411	940	530	191	
Count	49	63	88	49	
CV	9.22	10.74	12.55	27.19	
Males					
Mean	263.6	512.9	271.9	55.8	
Standard Error	2.19	4.35	3.00	1.28	
Standard Deviation	10.28	17.41	14.07	6.02	
Minimum	242	480	242	44	
Maximum	284	545	298	68	
Count	22	16	22	22	
CV	3.90	3.40	5.17	10.79	

Te Aute (Late Glacial), unpublished length data (Worthy, 2000).

	Fem L	Tib L	Tmt L	Weight	
Females	>290	>570	>310		
Mean	338.2	780.8	434.2	112.8	
Standard Error	8.83	21.19	8.79	8.24	
Standard Deviation	26.48	51.89	44.83	24.72	
Minimum	306	680	342	84	
Maximum	382	832	507	156	
Count	9	6	26	9	
CV	7.83	6.65	10.32	21.92	
Males					
Mean	229.5	460.2	260.7	37.8	
Standard Error	1.50	1.78	3.56	0.69	
Standard Deviation	2.12	4.36	16.30	0.97	
Minimum	228	455	227	37	
Maximum	231	466	295	38	
Count	2	6	21	2	
CV	0.92	0.95	6.25	2.57	

Takapau Road (Late Holocene) authors' unpublished data.

	FemL	TibL	TmtL	Height	Weight
Females	>310	>640	>330		
Mean	352	734	405	1516	126
Standard Error	10.74	28.78	14.46	90.60	10.65
Standard Deviation	30.39	81.40	43.37	181.19	30.14
Minimum	315	650	351	1321	91
Maximum	392	855	472	1719	168
Count	8	8	9	4	8
CV	8.63	11.09	10.72	11.96	23.89
Males					
Mean	294	545	295	1129	75
Standard Error	5.78	5.07	7.50	7.00	4.18
Standard Deviation	10.02	10.13	10.61	9.90	7.24
Minimum	286	530	287	1122	70
Maximum	305	552	302	1136	83
Count	3	4	2	2	3
CV	3.41	1.86	3.60	0.88	9.62

Northwest South Island (<600m asl)

	FemL	TibL	TmtL	Height	Weight
Females	>305	>645	>330		
Mean	337	695	369	1429	111
Standard Error	4.33	12.18	6.04	33.62	4.10
Standard Deviation	17.34	45.57	21.77	88.96	16.41
Minimum	312	650	341	1348	89
Maximum	380	786	403	1567	154
Count	16	14	13	7	16
CV	5.14	6.55	5.91	6.22	14.76
Males					
Mean	285	563	283	1140	70
Standard Error	5.01	11.99	6.89	31.36	3.40
Standard Deviation	15.84	41.53	24.85	89.83	10.77
Minimum	262	505	248	1031	55
Maximum	310	642	325	1267	87
Count	10	12	13	8	10
CV	5.56	7.37	8.77	7.88	15.48

Northwest South Island (>600m asl): (Takaka Hill, Mt Arthur, Mt Owen). Specimens sexed by DNA (Appendix 2) and relative stoutness as bone lengths overlap.

	FemL	TibL	TmtL	Height	Weight
Females					
Mean	311	645	336	1278	89
Standard Error	6.09	16.48	10.28	26.82	4.85
Standard Deviation	14.91	43.61	25.19	65.69	11.89
Minimum	295	605	304	1205	76
Maximum	331	725	370	1356	105
Count	6	7	6	6	6
CV	4.79	6.76	7.51	5.14	13.41
Males					
Mean	285	543	278	1113	70
Standard Error	6.66	14.94	9.15	32.74	4.54
Standard Deviation	17.63	42.27	25.87	86.62	12.01
Minimum	263	506	254	1040	55
Maximum	307	609	319	1229	85
Count	7	8	8	7	7
CV	6.18	7.78	9.32	7.79	17.17

Canterbury (Pyramid Valley, Bell Hill, Glenmark, Cheviot, Kapua, Enfield). Lengths separating the sexes are as shown except for a single 'female' with a femur of length 328 mm (CM Av9532), which is shorter than expected for the associated tibiotarsi and tarsometatarsi. The femur may be abnormally short or the 'skeleton' a composite of more than one individual, which is likely for a Glenmark specimen.

	FemL	TibL	TmtL	Height	Weight
Females	>341*	>700	>365		
Mean	389	844	449	1688	166
Standard Error	3.17	8.92	4.95	19.01	3.85
Standard Deviation	26.94	67.92	39.32	124.63	32.63
Minimum	328	718	372	1419	102
Maximum	468	992	538	1888	275
Count	72	58	63	43	72
CV	6.93	8.05	8.75	7.38	19.64
Males					
Mean	304	589	313	1250	84
Standard Error	3.85	6.46	4.80	73.24	2.99
Standard Deviation	20.02	43.32	25.38	179.40	15.27
Minimum	273	510	264	935	61
Maximum	340	693	363	1391	113
Count	27	45	28	6	26
CV	6.58	7.36	8.11	14.35	

Appendix 2. Specimens used in the analysis, indicating morphological species attribution used here, collection locality, and sex determined from DNA either by Bunce *et al.* (2003) or Huynen *et al.* (2003).

Apèndix 2. *Espècimens emprats a l'anàlisi, indicant l'atribució específica morfològica que hem fet servir, la localitat de recol·lecció i el sexe determinat pel DNA a partir de Bunce* et al. *(2003) o Huynen* et al. *(2003).*

Waitomo-Waikaremoana area

Cat No	Species	Sex Bunce	Sex Huynen	Collection locality
AIM B6316	*D. struthoides*		M	Waikaremoana
AIM B6349	*D. struthoides*			Waikaremoana
AIM B6353	*D. struthoides*			Mangaotaki
AIM B6828	*D. novaezealandiae*			Waikaremoana
AIM B6829	*D. novaezealandiae*			Waikaremoana
AIM B6833	*D. novaezealandiae*			Waikaremoana
AIM B6839	*D. novaezealandiae*			Waikaremoana
AIM B6920.1	*D. novaezealandiae*			Mangaotaki
AIM B6952	*D. novaezealandiae*			Mangaotaki
AIM B7037.8	*D. novaezealandiae*		F	Mangaotaki
AIM B7168	*D. struthoides*			Waikaremoana
AU6393.18	*D. giganteus*			Cave, Murchies Farm, Waitomo
B. Reeve colln	*D. struthoides*	M		Waikaremoana
MNZ S240	*D. struthoides*			Cave, Tahora
MNZ S25761	*D. giganteus*	F		Waikaremoana
MNZ S299	*D. novaezealandiae*	F		Waikaremoana
MNZ S37874	*D. struthoides*	M		Gabrielle's cave
MNZ S37875	*D. struthoides*	M		Gabrielle's cave
MNZ S421a	*D. novaezealandiae*			Waikaremoana
MNZ S421b	*D. novaezealandiae*	F		Waikaremoana
MNZ S422	*D. struthoides*			Waikaremoana
MNZ S422	*D. struthoides*			Waikaremoana
Turangi	*D. giganteus*			Cave, Turangi, Lake Taupo
WO30.41	*D. novaezealandiae*			Briars Cave, Waitomo

Te Aute

Dinornis struthoides: MNZ S108, MNZ S24342, S110, S158, S158, S108, S109, S158, S35084, CM Av8512, CM Av8777, CM Av8817, CM Av8846, CM Av32693, OM Av4004.
Dinornis giganteus: MNZ S109, S111, S112, S113, S115, S24385, S24386, S24461, S24585, S35091, S35093, S35094, S35095, S35096, S35097, S35098, S35100, S35103, S35104, S35105, CM Av8770, CM Av8771, CM Av8778, CM Av8785, CM Av8786, CM Av8920, CM Av8980.

Makirikiri

Data previously summarized and figured by Worthy (1989) based on specimens in the Wanganui Museum and MNZ S145. Data previous attributed to *Dinornis novaezealandiae* and *D. giganteus* were combined for females in this study.

Takapau Rd

D. giganteus MNZ S1013, S1014 M?, S1015, S24377.
D. novaezealandiae MNZ S1016, S1017, S1018, S1019, S1019a, S1023, S1022, S24365.
D. struthoides MNZ S1025, S24363, S24364.

Northwest South Island, less than 600m

Cat No	Species	Bunce sex	Site
CM Av12589	*D. giganteus*		Cave, Paturau, West Coast
CM Av29320	*D. giganteus*		Unique Wonder cave, West Coast
Hochstetter' specimen, Wien	*D. novaezealandiae*		Cave, Aorere Valley
In situ	*D. struthoides*		Moonsilver Cave
MNZ S23526	*D. struthoides*		Honeycomb Hill Cave
MNZ S23654	*D. struthoides*		Honeycomb Hill Cave
MNZ S24338	*D. struthoides*		Buller area cave
MNZ S24339	*D. struthoides*		Buller area cave
MNZ S24350	*D. struthoides*		Buller area cave
MNZ S24350	*D. struthoides*		Buller area cave
MNZ S24350	*D. struthoides*		Buller area cave
MNZ S24350	*D. struthoides*		Buller area cave
MNZ S24350	*D. struthoides*		Buller area cave
MNZ S24462	*D. struthoides*		Honeycomb Hill Cave
MNZ S25765	*D. novaezealandiae*		Honeycomb Hill Cave
MNZ S25766	*D. novaezealandiae*		Honeycomb Hill Cave
MNZ S25768	*D. novaezealandiae*		Honeycomb Hill Cave
MNZ S27135	*D. struthoides*		Moonsilver Cave
MNZ S27136	*D. novaezealandiae*		Moonsilver Cave
MNZ S27137	*D. novaezealandiae*		Moonsilver Cave
MNZ S28075	*D. struthoides*		Madonna Cave, West Coast
MNZ S28088	*D. struthoides*		Madonna Cave, West Coast
MNZ S28114	*D. giganteus*		Madonna Cave, West Coast
MNZ S28115	*D. novaezealandiae*		Madonna Cave, West Coast
MNZ S28115	*D. novaezealandiae*		Madonna Cave, West Coast
MNZ S28115	*D. novaezealandiae*		Madonna Cave, West Coast
MNZ S28115	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28116	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28116	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28116	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28119	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28119	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28119	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28225	*D. struthoides*	M	Maximus Cave
MNZ S28381	*D. struthoides*		Metro Cave, West Coast
MNZ S32677	*D. novaezealandiae*		Moonsilver Cave
MNZ S32678	*D. novaezealandiae*		Moonsilver Cave
MNZ S33517	*D. struthoides*		Commentary Cave
MNZS24351	*D. novaezealandiae*		Buller area cave
MNZS24351	*D. novaezealandiae*		Buller area cave
MNZS24351	*D. novaezealandiae*		Buller area cave
MNZS24351	*D. novaezealandiae*		Buller area cave
MNZS24351	*D. novaezealandiae*		Buller area cave

Northwest South Island, greater than 600m

Cat No	Species	Bunce sex	Site
MNZ S34095	*D. giganteus*	F	Cave, Hodge Ck, Mt Arthur
AIM B723	*D. novaezealandiae*		Cave, Takaka Hill
MNZ S211	*D. novaezealandiae*	F	Cave, Takaka Hill
MNZ S23342	*D. novaezealandiae*	F	Cave, Mt Owen
MNZ S32667	*D. novaezealandiae*	F	Cave, Ellis Basin, Mt Arthur
MNZ S38981	*D. novaezealandiae*		Takaka Fossil Cave
MNZ S38988	*D. novaezealandiae*	F	Takaka Fossil Cave
MNZ S23570	*D. struthoides*	M	Mt Owen
MNZ S27891	*D. struthoides*		Cave, Paynes Ford, Takaka Valley
MNZ S32715	*D. struthoides*		Struthoides Cave, Takaka Hill
MNZ S32716	*D. struthoides*		Struthoides Cave, Takaka Hill
MNZ S33517	*D. struthoides*		Hodge Ck cave system, Mt Arthur
MNZ S38990	*D. struthoides*		Takaka Fossil Cave
MNZ S39003	*D. struthoides*	M	Takaka Fossil Cave
MNZ S39004	*D. struthoides*	M	Takaka Fossil Cave

Canterbury Region.

Cat No	Species	Sex Bunce	Sex Huynen	Site
AMNH7301	*D. struthoides*			Pyramid Valley
AMNH7303	*D. giganteus*			Pyramid Valley
CM Av13778	*D. giganteus*			Pyramid Valley
CM Av13779	*D. giganteus*	F		Pyramid Valley
CM Av14448	*D. giganteus*		F	Pyramid Valley
CM Av14449	*D. giganteus*	F		Pyramid Valley
CM Av14451	*D. giganteus*			Pyramid Valley
CM Av14549	*D. giganteus*			Pyramid Valley
CM Av15024	*D. giganteus*			Pyramid Valley
CM Av15025	*D. giganteus*			Pyramid Valley
CM Av15026	*D. giganteus*			Pyramid Valley
CM Av15028	*D. struthoides*			Pyramid Valley
CM Av20118	*D. giganteus*			Pyramid Valley
CM Av20123	*D. giganteus*			Pyramid Valley
CM Av20124	*D. giganteus*			Pyramid Valley
CM Av23466	*D. giganteus*	F		Pyramid Valley?
CM Av8415	*D. struthoides*			Pyramid Valley
CM Av8416	*D. giganteus*			Pyramid Valley
CM Av8417	*D. giganteus*		F	Pyramid Valley
CM Av8418	*D. giganteus*	undet (tmt)	F	Pyramid Valley
CM Av8419	*D. giganteus*			Pyramid Valley
CM Av8420	*D. giganteus*			Pyramid Valley
CM Av8421	*D. giganteus*	F		Pyramid Valley
CM Av8422	*D. giganteus*			Pyramid Valley
CM Av8423	*D. giganteus*			Pyramid Valley
CM Av8436	*D. giganteus*			Pyramid Valley
CM Av8464	*D. giganteus*			Pyramid Valley
CM Av8466	*D. giganteus*			Pyramid Valley
CM Av8467	*D. giganteus*			Pyramid Valley
CM Av8468	*D. giganteus*		F	Pyramid Valley
CM Av8469	*D. giganteus*			Pyramid Valley
CM Av8470	*D. giganteus*			Pyramid Valley
CM Av8471	*D. giganteus*			Pyramid Valley
CM Av8473	*D. giganteus*			Pyramid Valley
CM Av8475	*D. struthoides*			Pyramid Valley
CM Av8476	*D. giganteus*			Pyramid Valley
CM Av8477	*D. giganteus*			Pyramid Valley
CM Av8478	*D. giganteus*			Pyramid Valley
CM Av8479	*D. giganteus*			Pyramid Valley
CM Av8480	*D. giganteus*			Pyramid Valley
CM Av8484	*D. giganteus*			Pyramid Valley
CM Av8486	*D. giganteus*			Pyramid Valley
CM Av8487	*D. giganteus*			Pyramid Valley
CM Av8488	*D. giganteus*			Pyramid Valley
CM Av8489	*D. giganteus*			Pyramid Valley
CM Av8490	*D. giganteus*			Pyramid Valley
CM Av8491	*D. giganteus*			Pyramid Valley
CM Av8492	*D. giganteus*		F	Pyramid Valley
CM Av8493	*D. giganteus*			Pyramid Valley
CM Av8494	*D. giganteus*			Pyramid Valley
CM Av8495	*D. struthoides*			Pyramid Valley
CM Av8547	*D. giganteus*			Pyramid Valley
CM Av8756	*D. struthoides*			Enfield
CM Av8757	*D. struthoides*			Enfield
CM Av8758	*D. struthoides*			Kapua
CM Av8759	*D. struthoides*			Glenmark
CM Av8760	*D. struthoides*			Enfield
CM Av8761	*D. struthoides*			Kapua
CM Av8762	*D. struthoides*			Kapua
CM Av8763	*D. struthoides*	M		Kapua
CM Av8764	*D. giganteus*			Kapua
CM Av8766	*D. struthoides*	M		Kapua
CM Av8767	*D. struthoides*			Glenmark
CM Av8768	*D. struthoides*			Kapua
CM Av8773	*D. struthoides*			Glenmark
CM Av8774	*D. struthoides*			Kapua
CM Av8781	*D. struthoides*			Kapua
CM Av8787	*D. struthoides*			Glenmark
CM Av8788	*D. giganteus*			Glenmark
CM Av8790	*D. giganteus*			Kapua
CM Av8791	*D. giganteus*			Kapua
CM Av8804	*D. giganteus*			Kapua
CM Av8805	*D. struthoides*			Kapua
CM Av8806	*D. struthoides*			Kapua
CM Av8807	*D. struthoides*			Enfield
CM Av8809	*D. struthoides*			Enfield
CM Av8811	*D. struthoides*			Glenmark
CM Av8821	*D. struthoides*			Glenmark
CM Av8823	*D. struthoides*			Kapua
CM Av8824	*D. struthoides*			Kapua
CM Av8871	*D. struthoides*			Kapua
CM Av8872	*D. struthoides*		M	Glenmark
CM Av8976	*D. struthoides*			Glenmark
CM Av8978	*D. giganteus*			Kapua
CM Av8979	*D. giganteus*			Glenmark
CM Av8983	*D. novaezealandiae*			Kapua
CM Av8984	*D. giganteus*			Glenmark
CM Av8985	*D. giganteus*			Enfield
CM Av8986	*D. struthoides*			Kapua
CM Av8987	*D. struthoides*			Glenmark
CM Av8988	*D. struthoides*			Glenmark
CM Av8990	*D. giganteus*			Enfield
CM Av8992	*D. giganteus*			Kapua

CM Av8993	*D. struthoides*			Kapua
CM Av8994	*D. giganteus*			Enfield
CM Av8995	*D. struthoides*			Kapua
CM Av8997	*D. struthoides*			Glenmark
CM Av8998	*D. struthoides*			Enfield
CM Av8999	*D. giganteus*			Enfield
CM Av9001	*D. giganteus*			Glenmark
CM Av9003	*D. giganteus*			Enfield
CM Av9005	*D. giganteus*			Enfield
CM Av9006	*D. giganteus*			Enfield
CM Av9007	*D. struthoides*			Enfield
CM Av9008	*D. giganteus*			Kapua
CM Av9009	*D. giganteus*			Kapua
CM Av9010	*D. giganteus*			Kapua
CM Av9011	*D. giganteus*			Kapua
CM Av9012	*D. giganteus*		F	Enfield
CM Av9013	*D. giganteus*			Kapua
CM Av9015	*D. giganteus*		F	Kapua
CM Av9016	*D. giganteus*		F	Glenmark
CM Av9017	*D. giganteus*			Enfield
CM Av9018	*D. struthoides*			Enfield
CM Av9019	*D. struthoides*			Glenmark
CM Av9020	*D. struthoides*			Enfield
CM Av9021	*D. struthoides*			Enfield
CM Av9022	*D. giganteus*			Enfield
CM Av9023	*D. giganteus*		F	Enfield
CM Av9024	*D. giganteus*			Kapua
CM Av9025	*D. giganteus*			Kapua
CM Av9026	*D. struthoides*			Kapua
CM Av9031	*D. struthoides*			Enfield
CM Av9032	*D. giganteus*		F	Enfield
CM Av9034	*D. giganteus*			Enfield
CM Av9035	*D. giganteus*			Enfield
CM Av9036	*D. giganteus*			Kapua
CM Av9037	*D. struthoides*		M	Kapua
CM Av9040	*D. struthoides*			Kapua
CM Av9041	*D. struthoides*			Enfield
CM Av9042	*D. struthoides*			Enfield
CM Av9043	*D. struthoides*			Kapua
CM Av9044	*D. struthoides*			Enfield
CM Av9083	*D. struthoides*			Glenmark
CM Av9436	*D. struthoides*	undet		Glenmark?
CM Av9440	*D. struthoides*	undet		Glenmark?
CM Av9434	*D. struthoides*			Glenmark?
CM Av9435	*D. struthoides*			Glenmark?
CM Av9437	*D. struthoides*			Glenmark?
CM Av9438	*D. struthoides*			Glenmark?
CM Av9439	*D. struthoides*			Glenmark?
CM Av9441	*D. struthoides*			Glenmark?
CM Av9442	*D. struthoides*			Glenmark?
CM Av9443	*D. struthoides*			Glenmark?
CM Av9444	*D. struthoides*			Glenmark?
CM Av9511	*D. giganteus*		F	Glenmark
CM Av9529	*D. giganteus*			Glenmark
CM Av9531	*D. giganteus*			Glenmark
CM Av9532	*D. giganteus*	undet		Glenmark
CM Av9535	*D. struthoides*			Glenmark
CM Av9543	*D. struthoides*		M	Glenmark?
CM SB47	*D. giganteus*	F		Cheviot
CM SB 51	*D. giganteus*			Cheviot
CM SB54	*D. giganteus*			Cheviot
CM SB53	*D. giganteus*			Cheviot
CM SB50	*D. giganteus*			Cheviot
CM SB 50	*D. giganteus*			Cheviot
CM SB47	*D. giganteus*			Cheviot
CM SB214	*D. giganteus*			Cheviot
CM SB49	*D. giganteus*			Cheviot
CM SB51	*D. giganteus*			Cheviot
CM SB49	*D. giganteus*			Cheviot
CM SB48	*D. giganteus*			Cheviot
CM SB47	*D. giganteus*			Cheviot
CM SB48	*D. giganteus*			Cheviot
CM SB52	*D. giganteus*			Cheviot
MNZ S34088	*D. giganteus*	undet		Pyramid Valley
MNZ S39875	*D. giganteus*	F		Bell Hill Vineyard
MNZ S39946.1	*D. struthoides*			Bell Hill Vineyard
MNZ S39946.2	*D. struthoides*			Bell Hill Vineyard
MNZ S39946.3	*D. struthoides*			Bell Hill Vineyard
MNZ S39946.4	*D. struthoides*			Bell Hill Vineyard
MNZ S39445	*D. giganteus*			Bell Hill Vineyard
MNZ S39954	*D. giganteus*			Bell Hill Vineyard
MNZ S39959	*D. giganteus*			Bell Hill Vineyard
MNZ S39960	*D. giganteus*			Bell Hill Vineyard
MNZ S39961	*D. giganteus*			Bell Hill Vineyard
MNZ S39962	*D. giganteus*			Bell Hill Vineyard
MNZ S40074	*D. struthoides*			Bell Hill Vineyard
MNZ S40075	*D. struthoides*			Bell Hill Vineyard
MNZ S40076	*D. struthoides*			Bell Hill Vineyard
MNZ S40077	*D. struthoides*			Bell Hill Vineyard
MNZ S40078	*D. struthoides*			Bell Hill Vineyard
MNZ S40124	*D. giganteus*			Bell Hill Vineyard
MNZ S40136	*D. struthoides*			Bell Hill Vineyard
MNZ S40137	*D. struthoides*			Bell Hill Vineyard
MNZ S40187	*D. struthoides*			Bell Hill Vineyard
MNZ S40189	*D. giganteus*			Bell Hill Vineyard
MNZ S40232	*D. struthoides*			Bell Hill Vineyard
MNZ S40333	*D. struthoides*			Bell Hill Vineyard
MNZ S40335	*D. struthoides*			Bell Hill Vineyard
MNZ S40336	*D. struthoides*			Bell Hill Vineyard
MNZ S40337	*D. struthoides*			Bell Hill Vineyard
MNZ S40338	*D. struthoides*			Bell Hill Vineyard
MNZ S40339	*D. struthoides*			Bell Hill Vineyard
MNZ S40341	*D. struthoides*			Bell Hill Vineyard
MNZ S40342	*D. struthoides*			Bell Hill Vineyard

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