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NEW DATA ON THE EXTINCT ENDEMIC RODENTS *TYRRHENICOLA* AND *RHAGAMYS* (RODENTIA, MURIDAE) OF CORSICA (FRANCE) WITH SPECIAL EMPHASIS ON THEIR DENTAL MORPHOLOGY AND ADAPTATION

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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.

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 alre-
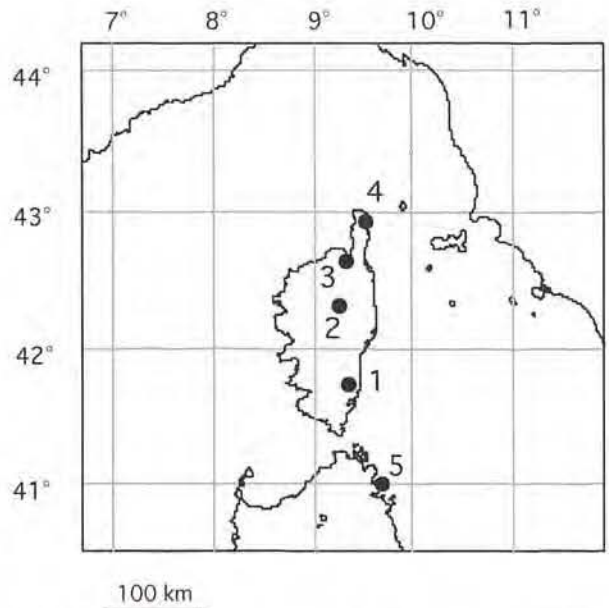

Fig. 1. Location map of the Pleistocene (Holocene excluded) fossil mammal bearing localities considered in the present paper. Corsica: 1, Punta di Calcina, 2, Corte, 3, Castiglione (several sites), 4, La Coscia. Sardinia, 5, Capo Figari.

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.
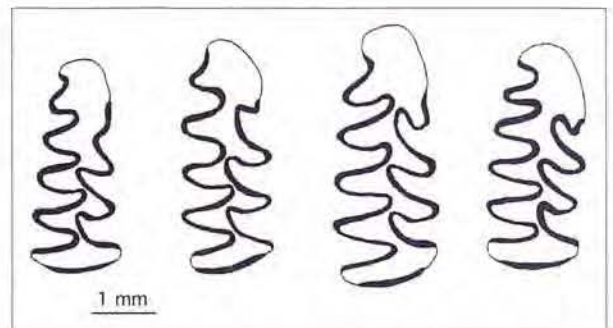

Fig. 2. *Microtus* (*Tyrrhenicola*): primitive (1) and derived (2, 3, 4) morphotypes of first lower molar.

Fig. 2. Microtus (Tyrrhenicola): *morfotipus primitiu (1) i derivats (2, 3, 4) del primer molar inferior.*

ady 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*).
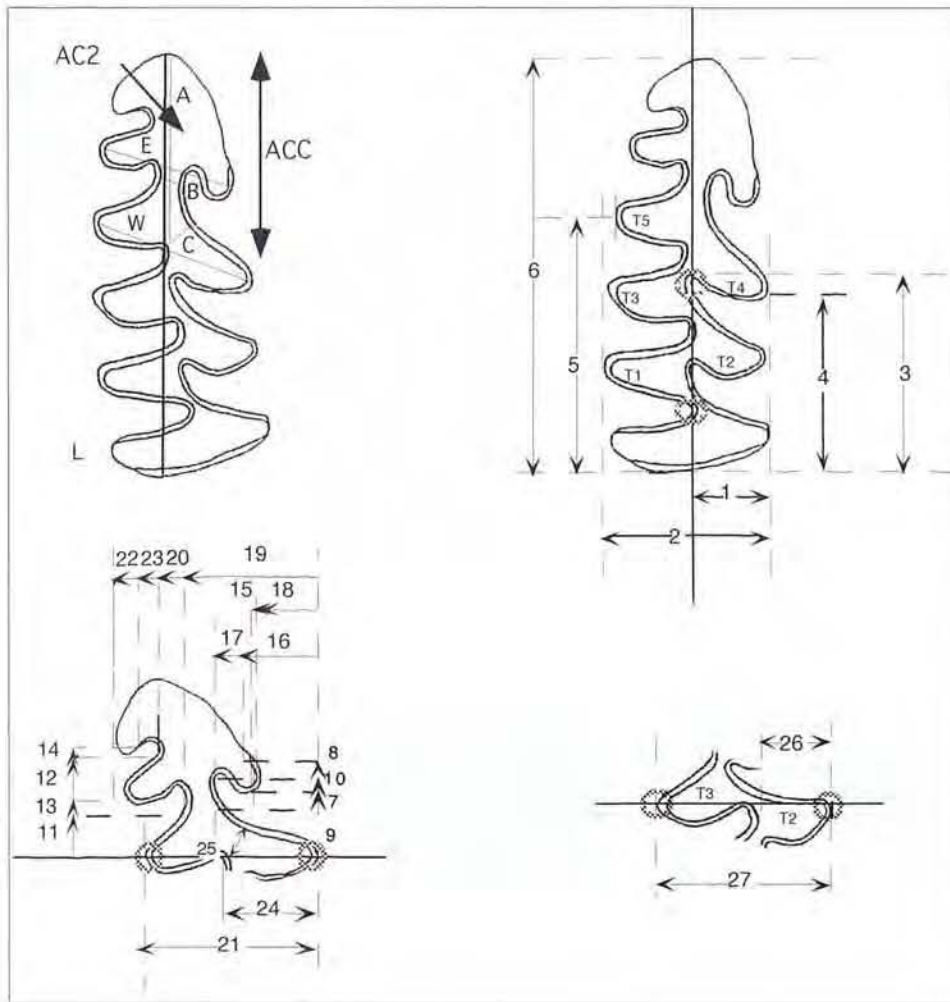
Fig. 3. *Microtus (Tyrrhenicola).* A: measurements according van der Meulen (1973) and Pereira (2001). L, total length, A, length of the anteroconid complex, W, length of the pitymyan rhombus, E, width of AC2, B, closure of AC2, C, width of the pitymyan rhombus (T4-T5). B: Brunet-Lecomte (B). See Brunet-Lecompte (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 suc-
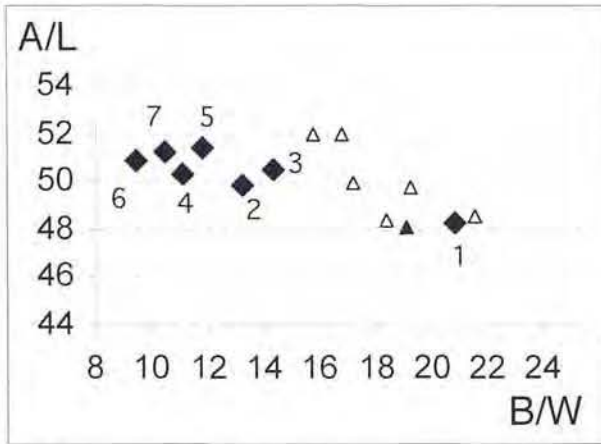
Fig. 4. *Microtus (Tyrrhenicola)*. Distribution pattern of Corsican populations (squares) and Sardinian ones (triangles) according relative for lower first molar, length of the anteroconid complex (A/L) and closure of the anterior cap (B/W). For Corsica, data *in* Pereira et al. (2001), for Sardinia, 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).*

cession 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.

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 index 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
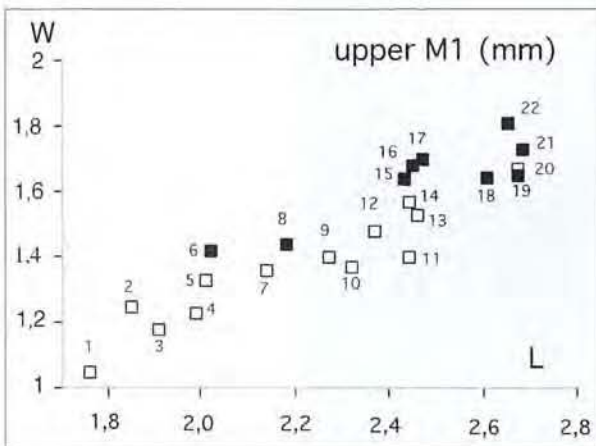

Fig. 5. Variation of first upper M1 mean size in the *Rhagamys* lineage. *Rhagapodemus primaevus*: 4, Lissieu (Hugueney & Mein, 1965), 5, Maramenna (Kotlia *et al.*, 1998); *Rhagapodemus ballesioi*: 1, Hautimagne (Mein & Michaux, 1970), 3, Gundersheim (Fejfar & Storch, 1990); *Rhagapodemus hautimagnensis*: 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 M¹ 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).
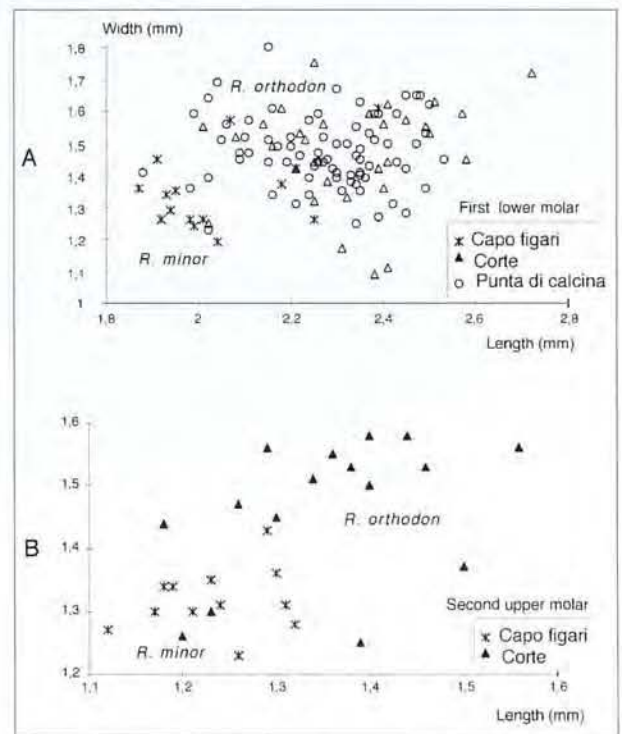

Fig. 6. Scatter diagram for first lower molar (a) and upper second molar (b) of *Rhagamys* samples from Capo Figari (Sardinia), Punta di Calcina and Corte (Corsica); data from Pereira (2001) and Pereira et al. (2001).

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).

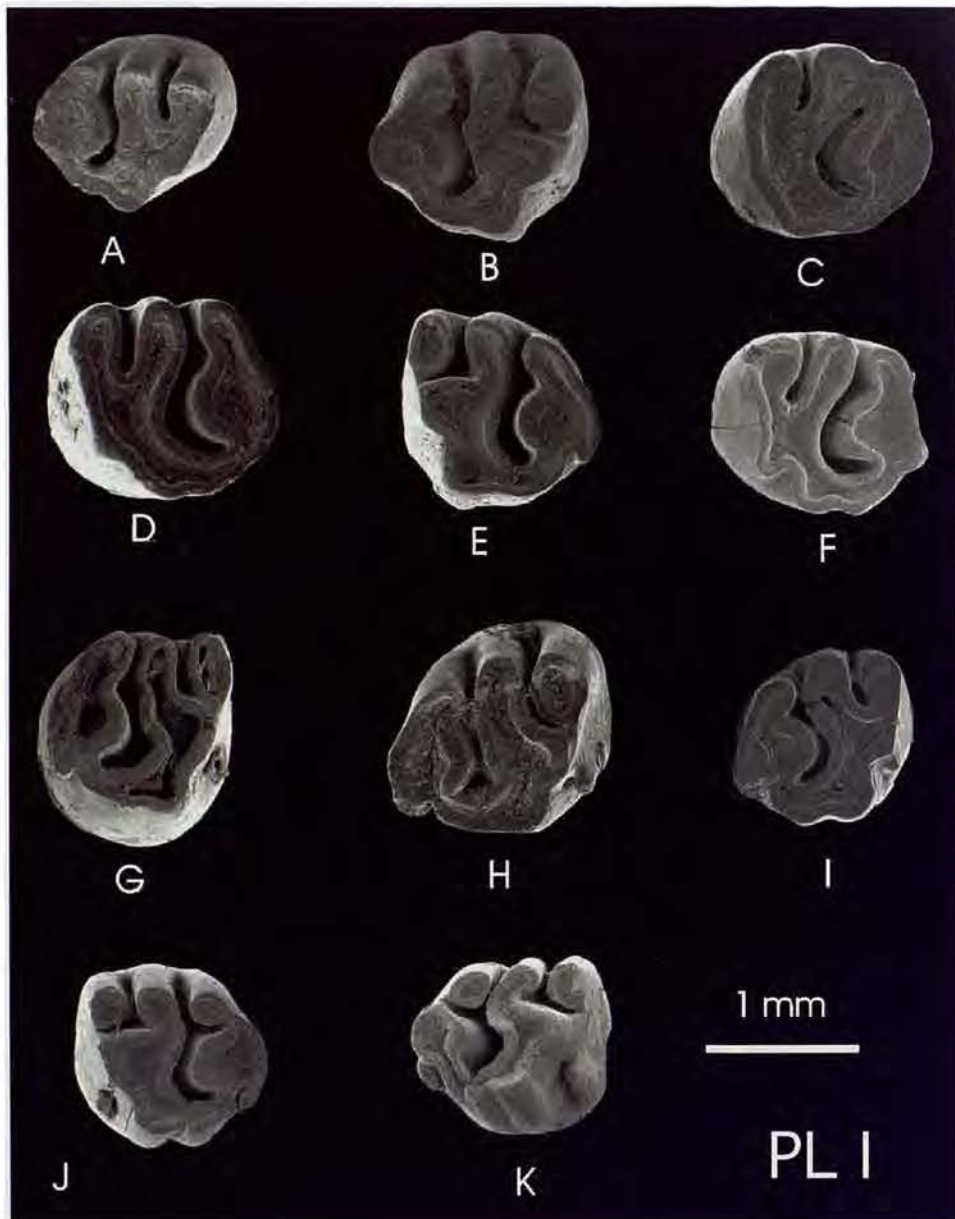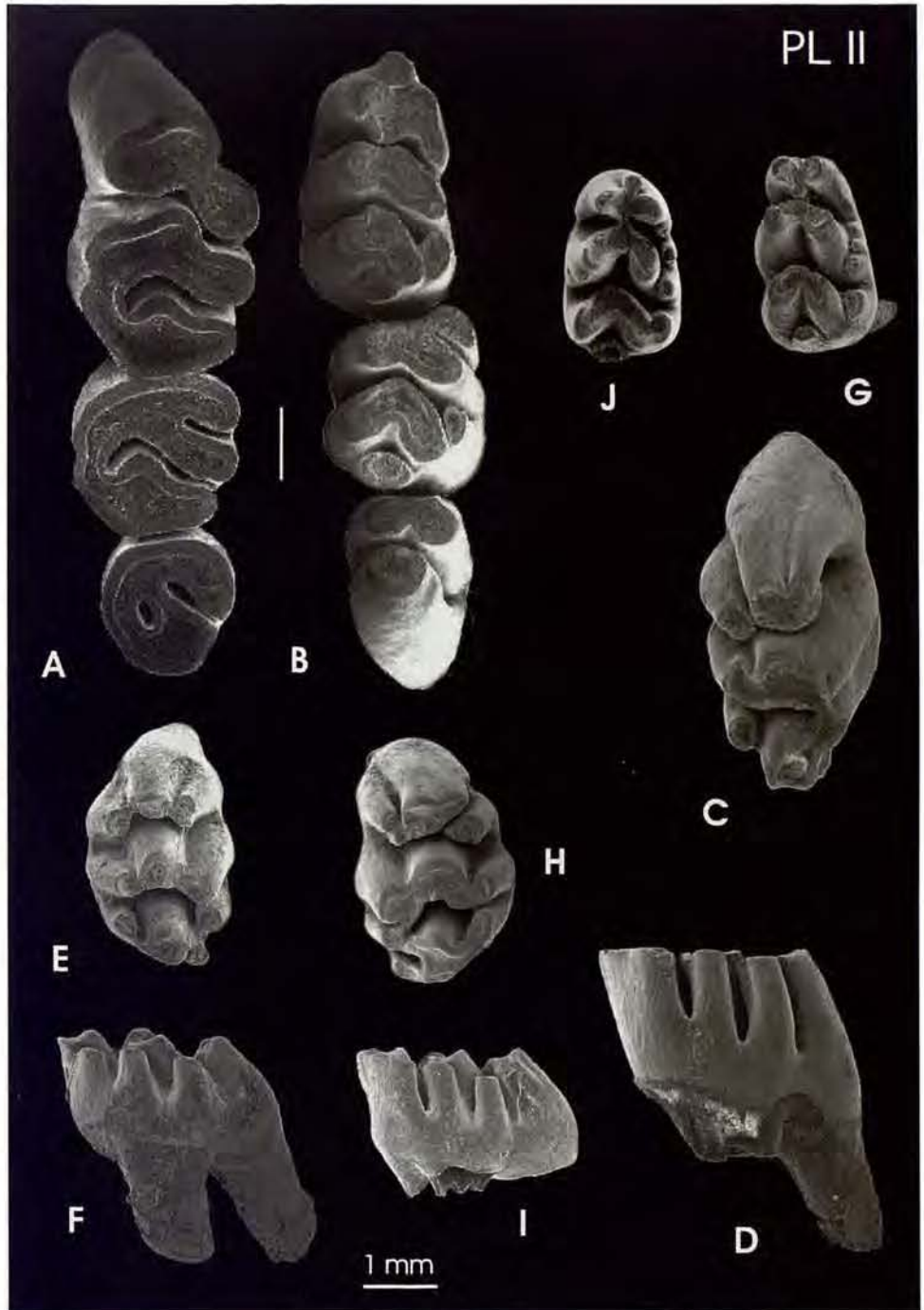Pecorini *et al.* (1974). They concluded that the *Rhagapo-
demus* of Mandriola must be assigned to a new species
they named *Rhagapodemus azzarolii. Rhagapodemus
azzarolii* is smaller and less evolved than *Rhagamys
minor.* Its ancestor would be the continental *Rhagapode-
mus ballesioi,* and *Rhagapodemus 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 pro-
blem was raised because Martin-Suarez & Mein (1998)
consider *Rhagamys minor* as a member of the genus
Rhagapodemus. They propose to use of the genus *Rha-
gamys* only for the most derived species *Rhagamys
orthodon* a conclusion not shared by Angelone & Kotsa-
kis (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 documen-
ted 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 gro-
wing, only maximum values given by teeth from juvenile
individuals can be used to calculate such indexes. For
Rhagapodemus azzarolii, crown height has been estima-
ted from the hypsodonty ratio given in the original publi-
cation. Molars do not show a rise in hypsodonty from *R.
azzarolii* either to *R. orthodon* or *R. minor.*

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 M² (Plate 1) progressively disappear whereas others, as the posterior one on M¹ and M², 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 Euro-

pean 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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