

PLEISTOCENE HIPPOPOTAMUSES OF MEDITERRANEAN ISLANDS: LOOKING FOR ANCESTORS

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Resum

Al registre fòssilífer 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 P² and P³. 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 P²-P³ 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 first 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 length
LPOc	prosthion - occipital condyle length
LCN	canine alveolus - nuchal crest length
LnnOr	nasal notch - orbital cavity length
LCOr	canine alveolus - orbital cavity length
HZOr	zygomatic arch - orbital height
HOpA	opisthion - akrocranium height
HBA	basion - akrocranium 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 occipital condyles
BTI	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 symphysis
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 - sigmoid incisure height
HGvco	gonion ventralis - coronoid process height
H3M	height of the horizontal ramus at level of M/3
H4P	height of the horizontal ramus at level of P/4
H2P	height 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	length 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 Barrington 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.

HIPPOTAMUS 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*

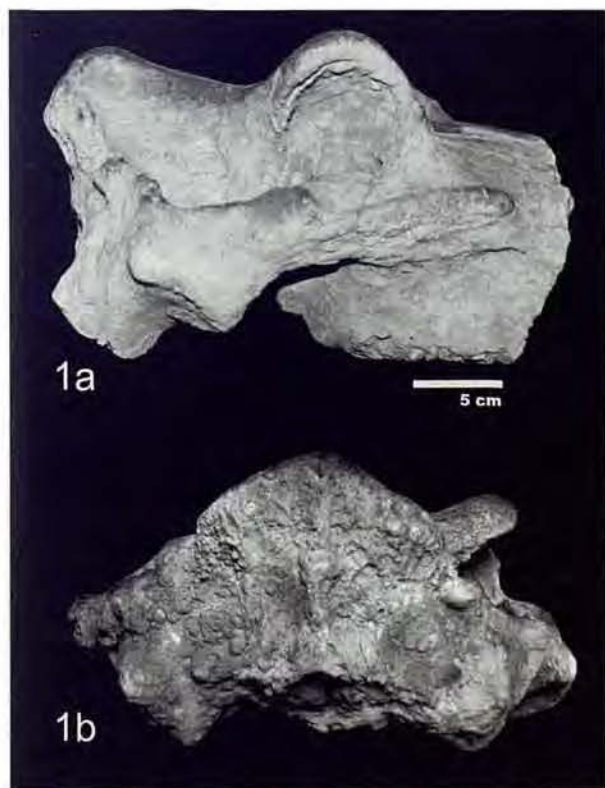


Plate 1. Cranium of *Hippopotamus pentlandi* from Sicily. 1a: lateral view. 1b: occipital view (specimen stored in the Museo di Paleontologia, University of Catania, Italy).

Làmina 1. Crani d'*Hippopotamus pentlandi* de Sicília. 1a: vista lateral. 1b: vista occipital (espècimen conservat al Museu de Paleontologia, Universitat de Catània, Itàlia).

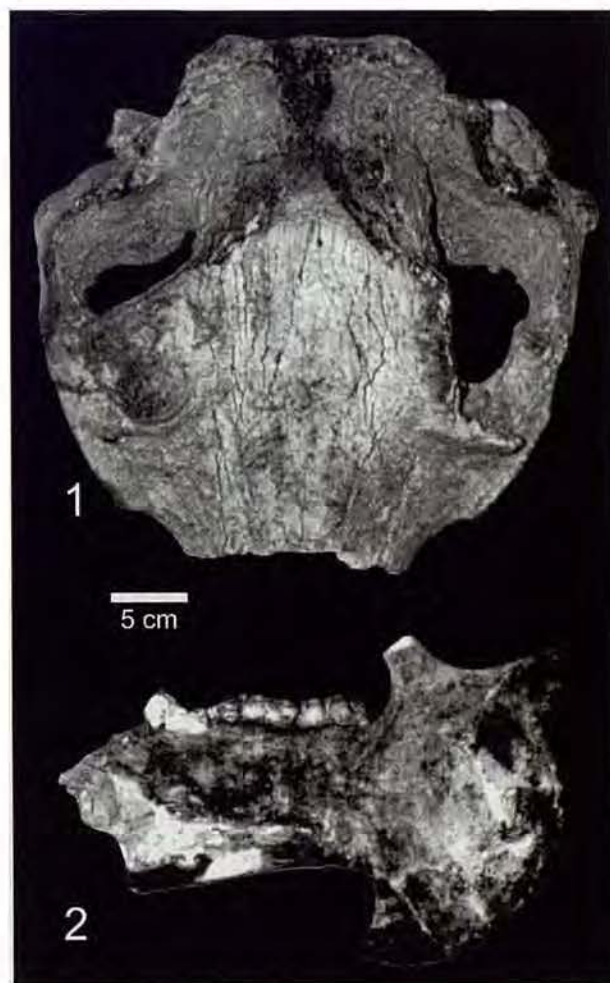


Plate 2. *Hippopotamus pentlandi* from Sicily. 1: cranium in dorsal view (specimen stored in the Museo di Paleontologia, University of Catania, Italy). 2: mandible in lateral view (specimen stored in the Museo Civico di Storia Naturale, Milan, Italy)

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 (espèimens 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 (espèimens conservats al Natural History Museum, London, UK; escala: 5 cm). *Hippopotamus creutzburgi*. 7, fragment de maxil·lar (espèimen conservat al Natural History Museum, London, UK; escala: 2,5 cm).

antiquus. M¹ is wider and shorter than in *H. antiquus* and *H. amphibius*; M² is similar to *H. amphibius*, while it is internally shorter and posteriorly wider than *H. antiquus*; M³ 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. M₂ is shorter than *H. amphibius* and is shorter and larger than *H. antiquus*. M₃ has similar proportions to *H. amphibius*, while is wider than *H. antiquus* and with a shorter posterior tubercle. M₂ and M₃ 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 M₃ of some individuals of *H. pentlandi*. The M₂ comma shaped entoconides 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													
<i>H. pentlandi</i>	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
<i>H. pentlandi</i>	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			
<i>P. minutus</i>	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
<i>P. minutus</i>	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. Mestres dels crànis.

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^1 has a short posterior style, while the hypoconulid of M_3 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 M_3 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*. M_2 is wider than *H. antiquus* and M_3 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. Mandibula 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. M₃ presents a comma shaped hypoconide.

Lateral view

As in *H. amphibius*, the horizontal branch is high, the sigmoid 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													
<i>H. pentlandi</i>	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
<i>H. pentlandi</i>	H4P	H2P	<i>H. creutzburgi</i>		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		
<i>P. minutus</i>	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 bet-

ween *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													
<i>H. pentlandi</i>	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
<i>H. pentlandi</i>	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		
<i>H. melitensis</i>	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	
<i>H. creutzburgi</i>	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	
<i>P. minutus</i>	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.

Taulla 4. Misure 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 length. Derivation from *H. pentlandi* is probable, but a previous spread, although improbable, cannot be excluded.

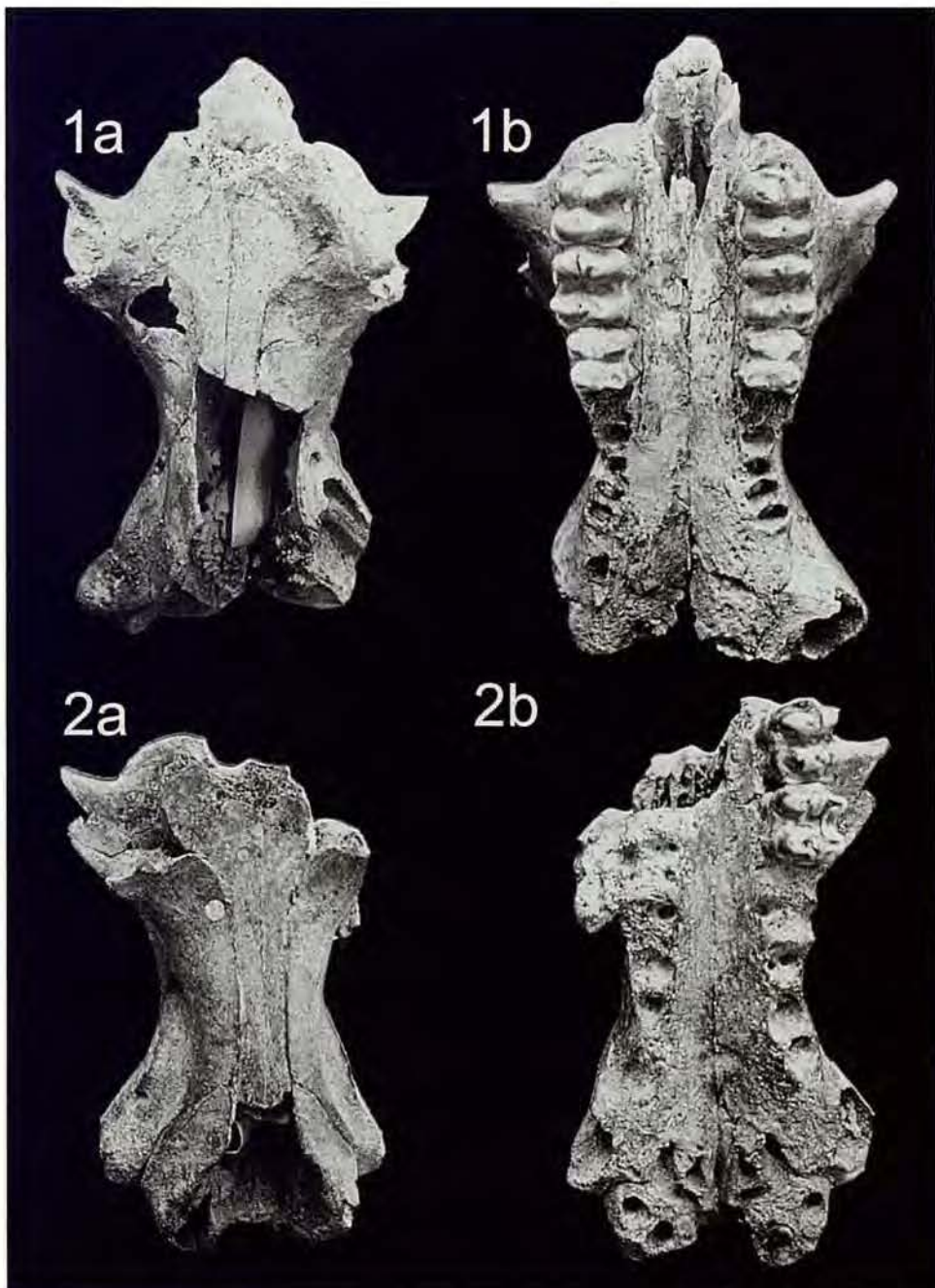
The debate about the phylogeny of *H. creutzburgi* divided the authors, some of them being inclined to a derivation from *H. amphibius* (Boekschoten & Sondaar, 1966; Kuss, 1975), others being in favour of a relationship

with *H. antiquus* (Sondaar, 1971; Coryndon, 1977; Dermitzakis & Sondaar, 1979; Capasso Barbato *et al.*, 1982; Caloi & Palombo, 1983; Faure, 1983). The presence of *H. creutzburgi parvus*, a smaller subspecies derived from *H. creutzburgi*, 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 P² and P³, characteristic of *H. antiquus*, is very interesting in presence of the general shortage of the tooth row, where the molars decrease with respect 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 hypoco-nulide, 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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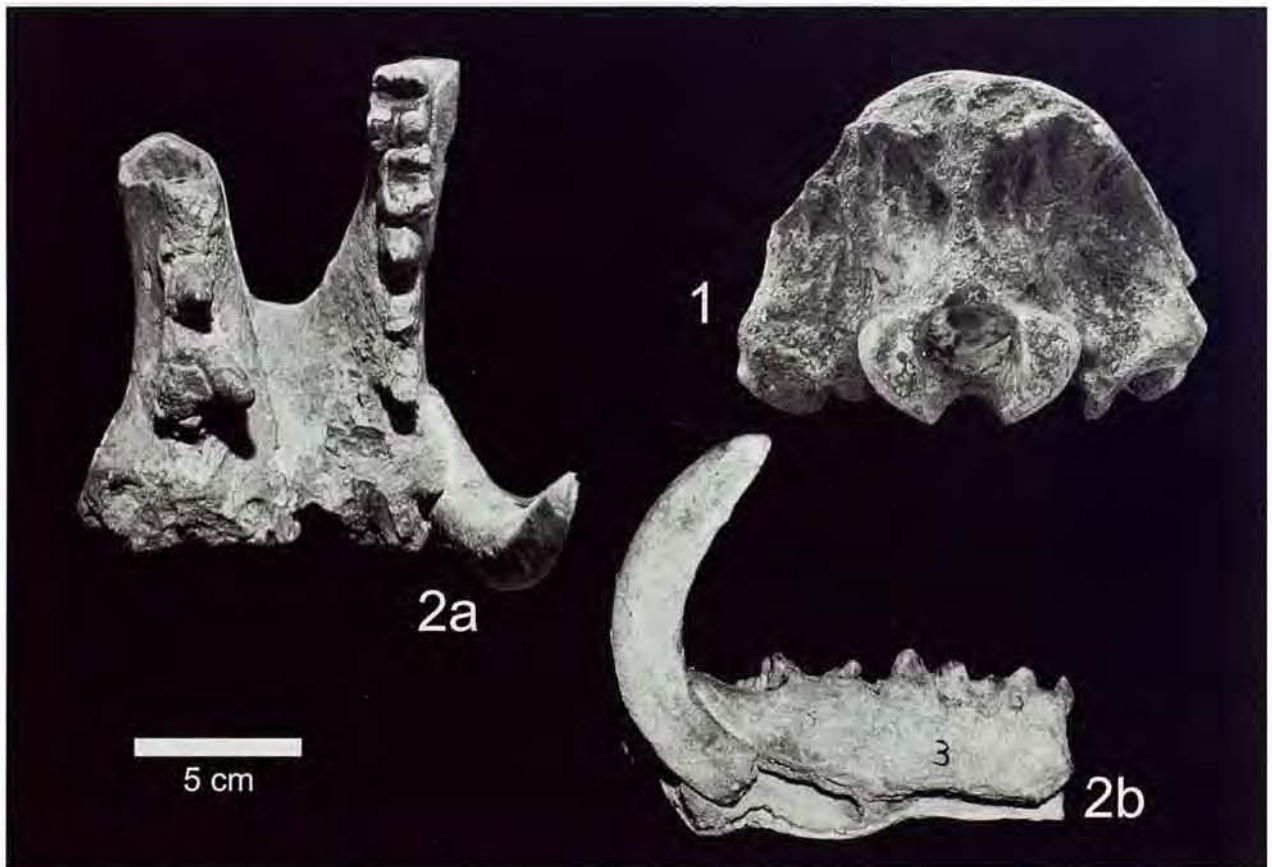


Plate 6. Cranium of *Phanourios minutus*: 1, occipital view. Mandible of *Phanourios minutus* (specimen stored in the Natural History Museum, London, UK). Mandible of *Phanourios minutus*: 2a, dorsal view. 2b, lateral view (specimen stored in the Natural History Museum, London, UK).

Làmina 6. Crani de *Phanourios minutus*: 1, vista occipital. Mandibula de *Phanourios minutus* (espècimen conservat al Natural History Museum, London, UK). Mandibula de *Phanourios minutus*: 2a vista dorsal. 2b, vista lateral (espècimen conservat al Natural History Museum, London, UK).

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LOWER TEETH													
<i>H. pentlandi</i>	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
<i>H. pentlandi</i>	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	
<i>H. melitensis</i>	M/3OL	M/3IL	M/3AB	M/3PB	M/3LPt	<i>H. creutzburgi</i>	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	
<i>H. creutzburgi</i>	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
<i>H. creutzburgi</i>	M/3PB	M/3LPt	<i>P. minutus</i>	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.

Taula 5. Mesures de les dents inferiors.

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