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CHASMAPORTHETES MELEI N. SP., AN ENDEMIC HYAENID (CARNIVORA, MAMMALIA) FROM THE MONTE TUTTAVISTA FISSURE FILLINGS (LATE PLIOCENE TO EARLY PLEISTOCENE; SARDINIA, ITALY)

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Abstract. Occurrence of large carnivores in island ecosystems is unusual, especially in the case of top predators. Here, a new endemic hyaenid species, *Chasmaporthetes melei*, from the late Late Pliocene to earliest Pleistocene fissure fillings of Monte Tuttavista, Orosei, Sardinia, is described. Although smaller, *C. melei* is morphologically comparable with the Plio-Pleistocene Eurasian hunting-hyena *Chasmaporthetes lunensis*, a possible ancestor of the Sardinian species. *C. melei* displays all the characteristic feeding adaptations of *Chasmaporthetes*, including a derived enamel structure similar to the condition in extant bone-crushing hyaenas. *C. melei* was an active predator that nonetheless included a relatively large amount of bone in its diet.

Riassunto. La presenza di carnivori di grande taglia in ecosistemi insulari rappresenta una circostanza rara, in particolar modo nel caso di predatori al vertice della catena trofica. Nel presente lavoro viene descritta una nuova specie endemica di ienide, *Chasmaporthetes melei* rinvenuta nei riempimenti carsici di Monte Tuttavista, Orosei, Sardegna, che hanno restituito numerosi resti di vertebrati Plio-Quaternari. Sebbene contraddistinto da una taglia inferiore, *C. melei* possiede una morfologia simile a quella di *C. lunensis* del Plio-Pleistocene dell'Eurasia, specie dalla quale *C. melei* potrebbe essere derivato. *C. melei* condivide con le altre specie del genere *Chasmaporthes* un caratteristico adattamento dell'apparato masticatorio, compreso una struttura derivata dello smalto dentario, simile, anche se meno specializzato, a quella presente nelle iene attuali a dieta ossifraga. *C. melei* era un predatore attivo la cui dieta includeva una elevata quantità di ossa.

Introduction

The Plio-Pleistocene vertebrate record of Sardinia is represented by a succession of "faunal complexes", highlighting repeated immigration events of taxa from the European mainland and evolution of endemic lineages (Esu & Kotsakis 1983; Van der Made 1999; Sondaar 2000). The occurrence of taxa also recorded from other European localities, allows for correlation of the Sardinian faunal complexes with the European biochronological scale.

The study of a recently discovered fossil fauna from Monte Tuttavista (Orosei) is bringing to light new and unexpected phases of the Plio-Pleistocene origin and evolutionary history of Sardinian fossil vertebrates (Rook et al. 2003; Abbazzi et al. 2004).

The fossil site, discovered by Mr. G. Mele in 1995, is located few kilometers South of Orosei, on the slopes of Mt. Tuttavista, where several quarries exploit Mesozoic limestone (Ginesu & Cordy 1997). The prompt and careful sampling carried out by personnel from the Nuoro Executive Office of "Soprintendenza per i beni archeologici per le provincie di Sassari e Nuoro" allowed the recovery of an abundant vertebrate fauna from the complex network of karstic fissures brought to light by the ongoing quarrying activity. Interpretation of the mammal fossil fauna from Monte Tuttavista allowed recognition of four time-successive faunal complexes, based on stage of evolution and faunal turnover (Abbazzi et al. 2004).

Notable among the carnivores from Monte Tuttavista, is the first record in Sardinia of hyaenids and of

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the large-sized mustelid *Pannonictis*. Occurrence of large carnivores in island ecosystems is unusual, especially in the case of top predators. Island faunal assemblages are typically impoverished and ecologically unbalanced, being commonly predator-less (cfr. MacArthur & Wilson 1963; Sondaar 1977, 1987). The identification of a large-sized hyaenid in the oldest faunal complex of Mt. Tuttavista forces reconsideration of the palaeoecologic and paleobiogeographic history of the Plio-Pleistocene Sardinian mammal assemblages (Abbazzi et al. 2004).

Abbreviations

Museums and institutions - F:AM, Frick collection, American Museum of Natural History, New York. IGF, Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Firenze. MAN, Museo Archeologico, Nuoro. MNHN, Muséum National d'Histoire Naturelle, Paris. MZF, Museo di Storia Naturale, Sezione di Zoologia, Firenze. NHMB, Naturhistorisches Museum, Basel.

Tooth measurements – CL, mesio-distal length of canine. CW, bucco-lingual width of canine. P_xL, mesio-distal length of premolar. P_xW, bucco-lingual width of premolar. P4meL, mesio-distal length of P4 metastyle. P4paL, mesio-distal length of P4 paracone.

Material and methods

The hyaenid from Monte Tuttavista has been compared with material of *Chasmaporthetes lunensis* from Olivola, Upper Valdarno (IGF, NHMB, MNHN), Roccaneyra (NHMB), Saint-Vallier (MNHN), Shansi (F: AM 99788 cast kept at IGF) and with published data on all currently recognized species of this genus. The comparative material analyzed in this study included two extant species, *Hyaena hyaena* and *Crocuta crocuta* (MZF), both showing derived adaptation to bone-crushing, and belonging to the sister group of the *Chasmaporthetes* clade (Werdelin & Solounias 1991). Comparisons of the metric characters of the specimens were carried out by means of scatter and ratio diagrams, after transformation of the raw data into $\log_{10}$. Besides the morphological and metric study of the skull and tooth gross anatomy, features of the tooth enamel were considered. Aspects of the outer enamel surface, and the pattern produced by enamel prism decussation (Hunter-Schreger Bands, HSB), as visible from the tooth surface, were analyzed. Both characteristics can be observed under a light microscope, without preparation of the specimen (non-invasive techniques). Hunter-Schreger bands, in particular, are visible as horizontal wavy alternating dark and light band (Fig. 1), an effect due to the different direction of prisms within each band with respect to the incident light. Differences in HSB complexity among carnivores have been shown to be related to distinct feeding habits (Rensberger 1995; Stefen 1997).

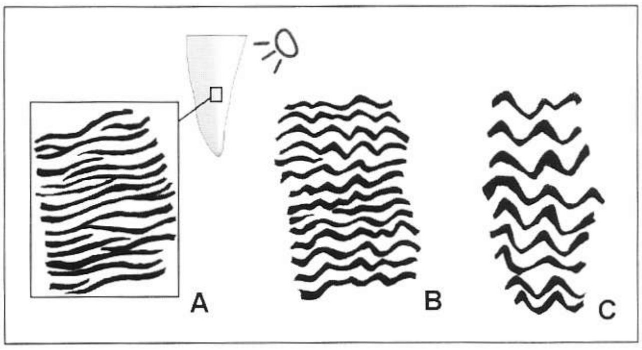

Fig. 1 - Diagrammatic representation of HSB morphology in carnivores. When observed through the outer enamel surface under incident light, HSB appears as alternating light and dark bands(as an example, an upper canine and the position of the light source are sketched). Three different HSB morphologies are known to occur in carnivores (Stefen 1997): A, HSB feebly undulated, representing the primitive condition for the group; B, HSB characterized by undulation with acute angles; C, steeply folded HBS forming a "zigzag" pattern. The different degree of folding of HSB is functionally related to the amount of bone consumed in the diet (see text).

Systematic paleontology

Order **Carnivora** Bowdich, 1821

Suborder Aeluroidea Flower, 1869

Family Hyaenidae Gray, 1869

Genus *Chasmaporthetes* Hay, 1821

Chasmaporthetes melei n. sp.

Fig. 2

1997 *Chasmaporthetes* sp. - Cordy & Ginesu, p. 40
2003 *Chasmaporthetes* n.sp. - Rook et al., p. 19-20
2004 *Chasmaporthetes* n.sp. - Abbazzi et al., p. 694, fig. 10

Holotype. MAN 65729, partial skull with mandible in anatomical occlusion.

Repository. Museo Archeologico, Nuoro, (Sardinia, Italy).

Type locality. Monte Tuttavista quarry area (Orosei, Sardinia). The specimen comes from an unregistered fissure filling.

Referred age. Latest Pliocene or earliest Pleistocene.

Origin of name. In honor of Mr. Giampietro Mele, Sardinian naturalist, who in 1995 identified the Mt. Tuttavista fossiliferous area and discovered the *Chasmaporthetes* specimen.

Diagnosis. *Chasmaporthetes* of small size (the smallest known representative of the genus); mandibular body shallow; relatively large canines; lower premolars relatively short.

Description

Material - The specimen consists of the anterior portion of the skull (premaxillary, maxillary, nasal, and frontal bones) and the lower jaws, still in occlusion (Fig. 2).

The skull is still partially embedded in the rock matrix, with only the left side completely exposed. The left mandible has been prepared and separated from the skull; the right mandible is still embedded in the rock matix and only the anterior portion of the body and the canine are

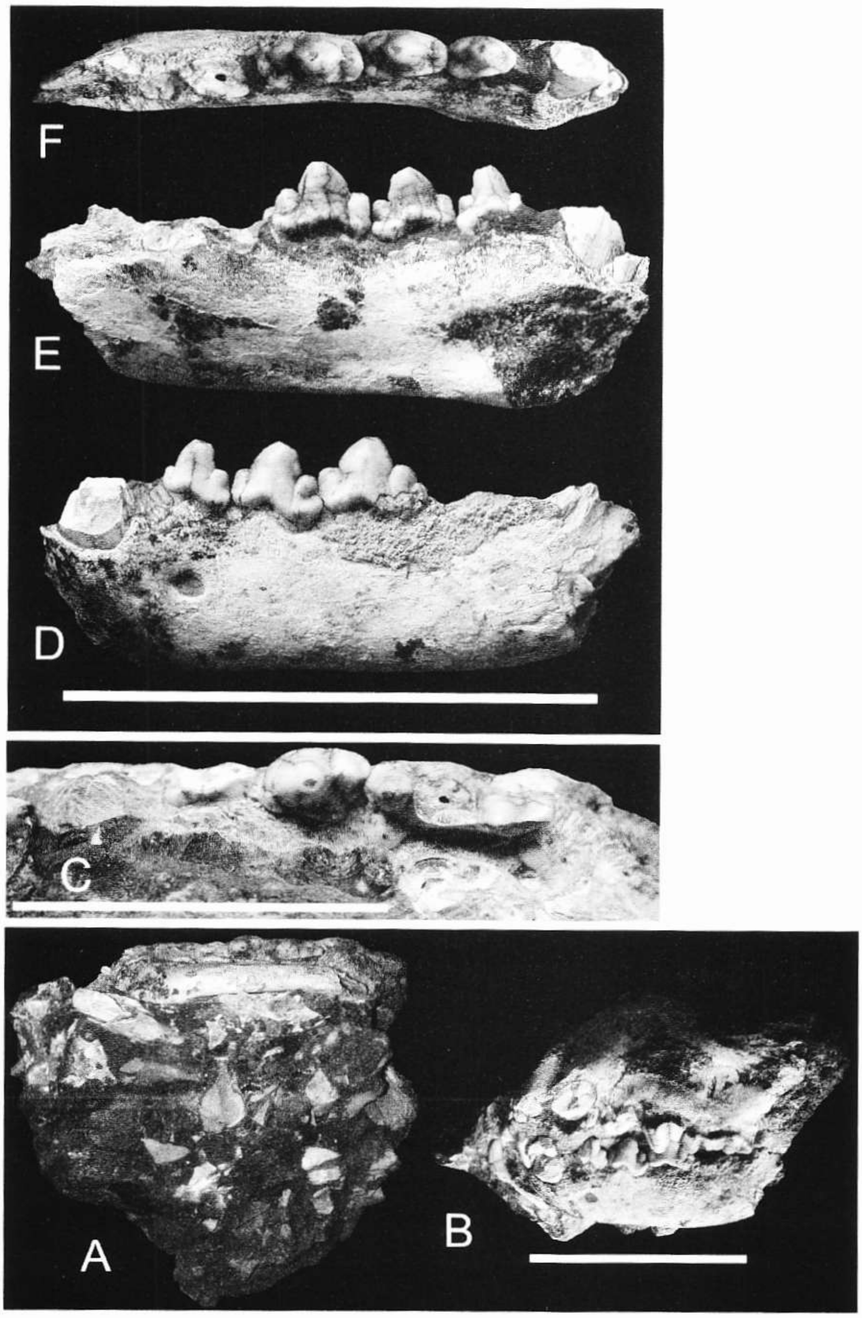

Fig. 2 - *Chasmaporthetes melei* from Mt. Tuttavista, Orosei, Sardinia, MAN 65729 (holotype). A-B, the bone breccia block still encrusting the specimen in (A) ventral (note the base of the left mandibular ramus and the symphyseal region and lower canine of the right one) and (B) left lateral views. C, left upper dentition, occlusal view. D-F, left mandibular corpus in labial (D), lingual (E) and occlusal (F) views. Bar scale represents 10 cm.

observable. Specimen MAN 65729 is an adult individual, with all permanent teeth fully erupted and showing moderate wear (premolars with dentine exposed on the main cone). Its size is comparable to that of a striped hyaena, *Hyaena hyaena*.

Skull - The rostrum is relatively short. In lateral view the frontal profile, although broken in the superior part, seems stepped (Fig. 2B). The maxillary is very deep. The area of the infraorbital foramen is covered by sediment and thus the foramen is not visible. The zygomatic process of the maxillary is broken.

Upper teeth - Of the upper incisors (Figs. 2B-C), the left I1-I3 (I3 and I2 broken at the crown base) and right I1-I2 are exposed. The canine is broken at the very base of the crown. The preserved part nevertheless indicates a very large tooth. The P1 is broken and very small. The P2 is lacking most of its crown and preserves no morphological details. The P3 is the largest of the anterior premolars. It has a very small anterior accessory cusp, mesio-lingually placed and appressed to the P3 main cone. The posterior accessory cusp is very large. Lingually there is a low and broad cingulum. The P4 has a large parastyle. The tip of the paracone is missing. The protocone is stout and relatively small. It is mesio-lingually directed, but its mesial margin is well posterior to the mesial margin of the parastyle. The metastyle is sig-

Measurements		MAN 65729
upper teeth		
	CL	17.52
	CW	-
	P2L	15.62
	P2W	-
	P3L	18.89
	P3W	11.45
	P4L	29.17
	P4W	(13.96)
	P4paL	10.84
	P4meL	12.33
lower teeth		
	cL	14.99
	cW	11.32
	p2L	13.04
	p2W	8.75
	p3L	17.15
	p3W	10.00
	p4L	20.05
	p4W	10.25
mandible		
	height of body	30.15
	width of body	14.60

Tab. 1 - Tooth and mandible measurements (in mm) of *Chasmaporthetes melei* from Monte Tuttavista, Orosei. Uncertain values are shown in brackets.

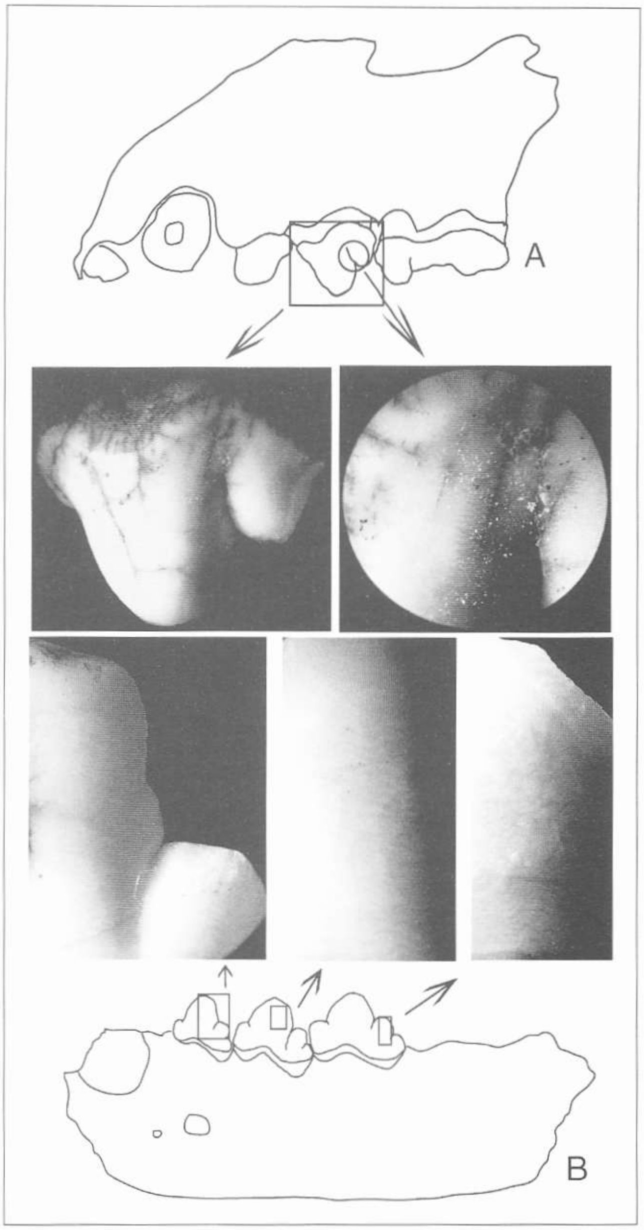

Fig. 3 - HSB morphology in *Chasmaporthetes melei* (MAN 65729) from Mt. Tuttavista, Orosei, Sardinia. A, upper teeth (P3); B, lower teeth (p2, p3, p4).

nificantly longer than the paracone (Tab. 1), and occupies 42% of P4 total length. There is a very small M1 lingual to the P4 metastyle. There is definitely no M2.

Mandible - The left mandible preserves the body and the very base of the coronoid process, while the ascending ramus is completely missing (Figs. D-F). The mental portion is very deep. The ventral margin of the symphysis is sub-vertical. There is a double mental foramen, positioned just below the p2. The corpus mandibulae is relatively shallow (low height to width ratio) and its height decreases slightly posteriorly. The ventral margin of the body is rather straight. The anterior end of the masseteric fossa is visible on the labial side, just behind the m1 alveolus.

Lower teeth - The lower tooth row is straight and the cheek teeth show full mesio-distal contact (Fig. 2F). The i3 is the only preserved incisor. The canine is broken at its base. This tooth, like the upper one, is very large (estimated measurements L 14.99 mm, W 11.32 mm) relative to the premolars. There is no p1. All premolars (p2-p4) have very large anterior and posterior accessory cusps. The p4 is large and massive. It has a large postero-lingual cingulum, carrying a very small cingulum cusp. The m1 crown is completely broken, and only the cross-section of the roots is visible in occlusal view. Judging from the size of the alveolus, the length of the lower carnassial was equal to that of the p4. Behind the m1 there are no visible traces of an m2.

Enamel structure - The outer enamel surface of all teeth is characterized by a feeble wrinkling.

All preserved teeth (both upper and lower) show acute-angled HSB (Fig. 3) along most of their height. At the level of the tooth cervix the HSB are less intensely folded, giving rise to an undulating pattern.

Discussion

Affinity and origin of *Chasmaporthetes melei*

The dental formula and tooth morphology (especially that of P4 and p2-p4) allow the attribution of MAN 65729 to the hyaenid genus *Chasmaporthetes*, an attribution also supported by the HSB morphology (see below).

Several species have been described on the basis of *Chasmaporthetes* material from both the Old World and North America (*C. borissiaki*; *C. bielawskyi*; *C. lunensis*; *C. kani*; *C. nitidula*; *C. australis*; *C. exitelus*; *C. ossifragus*; *C. johnstoni*). We follow here basically the opinion of Kurtén & Werdelin (1988) and Sotnikova (1994) (also summarized by Werdelin et al. 1994), in considering all the Eurasian forms attributable to the geographically and chronologically wide-ranging species *C. lunensis*, using subspecfic names for the definition of groups representing the extremes of morphologic ranges of a taxon with such a wide geographic and temporal distribution.

For instance, Galiano & Frailey (1977) erected the new species *C. kani* on a mandible (F:AM 99788 from Shansi, China) as a form of larger size. In fact the specimen is relatively large, but the metric range observable in the Shansi and Yushe samples (cfr. Qiu 1987; Kurtén & Werdelin 1988) is fully comparable with the dimensional range of populations from Transbaikalia and Mongolia (cfr. Sotnikova 1994) and the European *C. lunensis* (Figs. 4 and 5). Apart from size, one of the morphological aspects often used in diagnosing specific differences are the relative dimensions of the anterior accessory cusps of the lower and upper second and third premolars. Since rudimentary cusps are extremely variable within populations, their use as taxonomic indicators is misleading.

Within the late Miocene – Pleistocene fossil record of the genus, the following species are retained as valid.

Chasmaporthetes exitelus (late Miocene; Gansu, China) is the oldest representative of the genus. It is known from only one specimen (holotype, AMNH 26369), a palate, whose distinctive characteristic is that it is markedly narrow relative to other species of *Chasmporthetes* (Kurtén & Werdelin 1988). Dental dimensions are comparable with later species. The P4 is noted to be relatively large in the original diagnosis, although falling within the range (highest value) of Asian *C. lunensis* (Fig. 4).

Chasmaporthetes australis (Late Miocene; Langebaanweg, South Africa) is characterized by large size (Figs. 4, 5 and 7), especially of the upper carnassial, and by the distinct anterior accessory cusp on the fourth lower premolar (Werdelin et al. 1994).

Chasmaporthetes borissiaki (Pliocene; Europe; France and Moldova) is, by size and morphology, very close to *C. lunensis* (Figs. 4, 5 and 7), from which it differs in its very shallow mandibular ramus (Fig. 6). However, since the type specimen is a young individual, the peculiar proportions of the mandibular body of *C. borissiaki* could represent a juvenile character. Indeed, given the number of shared characters, a synonymy with *C. lunensis* cannot be ruled out (Werdelin pers. comm., 2003).

Chasmaporthetes lunensis (Late Pliocene – Early Pleistocene; Europe, Middle East and Asia: Spain, France, Italy, Germany, Turkey, Moldavia, Tazdjikistan, Transbaikalia, Mongolia, China). The status of this species and its synonymies are summarized by Werdelin & Solunias (1991). The species had the widest geographical and chronological range within the genus.

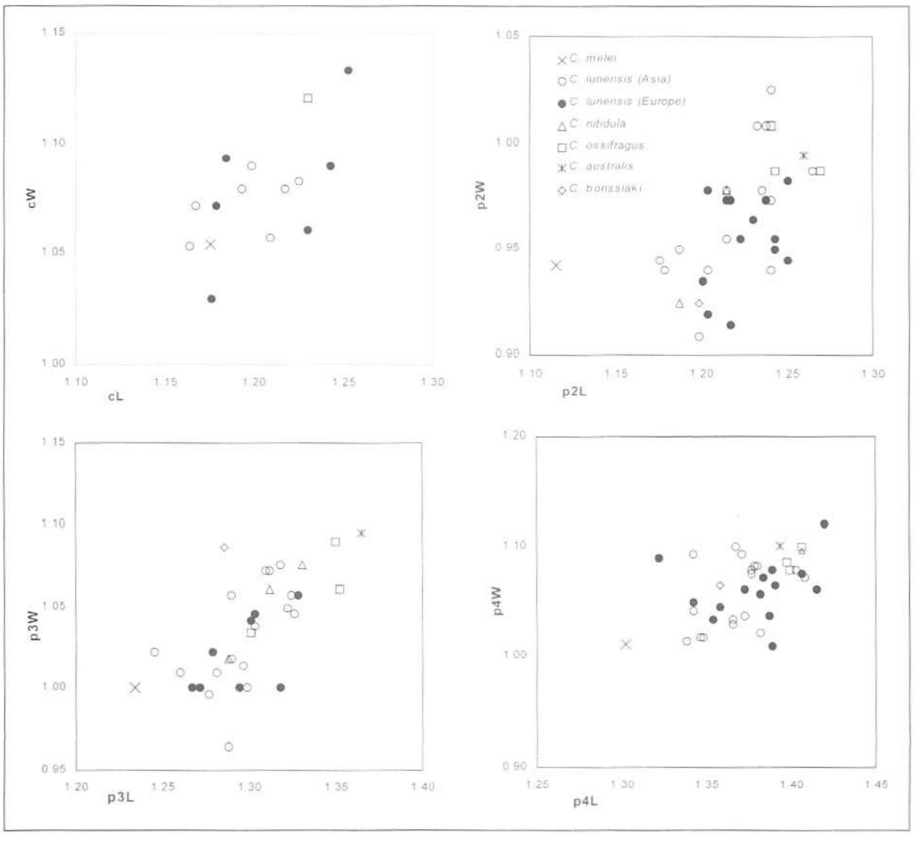

Fig. 4 - Bivariate scatter diagrams of lower teeth (length against width) in Old and New World *Chasmaporthetes* species. The axes are logarithmic.

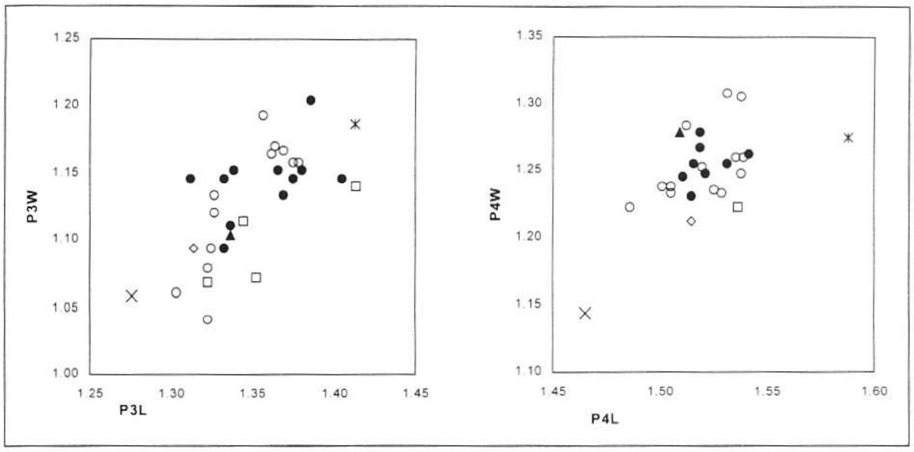

Fig. 5 - Bivariate scatter diagrams of upper teeth (length against width) in Old and New World *Chasmaporthetes* species. The axes are logarithmic. Symbols are as in Figure 4, with the addition of solid triangle for *Chasmaporthetes exitelus*.

Chasmaporthetes nitidula (Late Pliocene; Swartkrans, South Africa; Olduvai, Kenya). It was first described as *Lycyaena nitudula* (Ewer, 1955), and then included within the genus *Chasmaporthetes* by Galiano & Frailey (1977) (see also Kurtén & Werdelin 1988). Dimensionally (Fig. 4, 5 and 7) material attributed to this species does not differ from *C. lunensis*. A unique morphology observable in this species is the notable height of the premolar cusps and the greatly enlarged accessory cusps.

Chasmaporthetes ossifragus (Late Pliocene – Early Pleistocene; North America). Again, there are no strong differences from *C. lunensis*, although specimens included in this species all tend to be larger in size and with narrower dentition (especially upper teeth; Fig. 4). A further trait characterizing the North American species is the particularly elongated lower carnassial (Fig. 5) and a particularly high mandibular ramus (shadowed area in Fig. 6).

C. melei differs from all other considered *Chasmaporthetes* species in its smaller size, the relatively larger canines and narrower P4 (Figs. 5-7). The proportionally larger canines of *C. melei* could be the result of allometric scaling due to the size reduction, which in turn could be an adaptation to the insular ecosystem. A scaling effect could also account for the more gracile proportions of the mandible compared to the condition in other species except *C. borissiaki* (the latter, however, is based on a young individual).

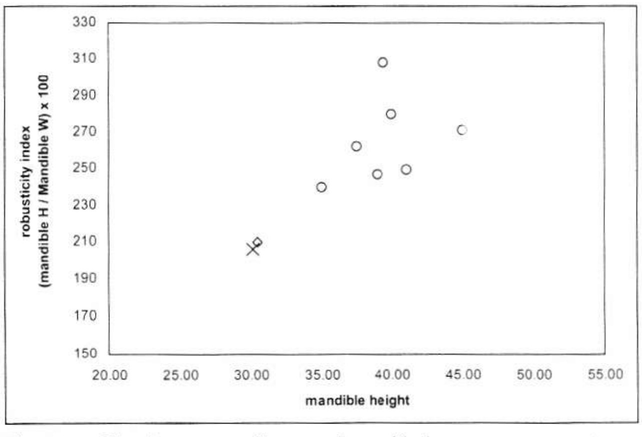

Fig. 6 - Bivariate scatter diagram of mandibular measurements (mandibular body height against robusticity index) in Old world *Chasmaporthetes* species. Symbols as in Figure 4. The grey area shows the range of mandible height in *C. ossifragus* (45.00-51.00mm), for which no data on mandible body width were available.

C. melei is more derived than primitive *Chasmaporthetes* species such as *C. exitelus* and *C. borissiaki*, in possessing a shorter and wider muzzle and, possibly, a markedly stepped frontal profile. *C. melei* shares most of its characters with *C. lunensis*, suggesting a close relationship with this species. The distinctive characters described above for *C. melei* are apomorphic with respect to the condition in *C. lunensis*. This would support the hypothesis that *C. melei* originated from a population of *C. lunensis*, or a form close to it, that migrated to Sardinia from the European mainland. The dispersal event to Sardinia which gave origin to *C. melei* should have occurred between the Middle Pliocene (Early Villafranchian) and no later than the early Early Pleistocene, the last occurrence of *C. lunenis* in Europe being in assemblages referable to the Tasso F.U. of the late Villafranchian (Inferno, Upper Valdarno, Italy; Schernfeld, Eichstätt, Germany; Werdelin & Solounias 1991; Qiu 1987). Such an interpretation is consistent with the chronological framework inferred for the older faunal complex from Monte Tuttavista (Rook et al. 2003; Abbazzi et al. 2004).

Enamel structure and mode of life

Among carnivores (Carnivora) the outer tooth surface is either smooth or wrinkled. A smooth surface is considered to be the plesiomorphic condition for the group and occurs in those taxa that show a relatively generalized carnivoran dentition (e.g. Viverridae and Canidae). On the other hand derived hyaenids, especially those species highly adapted to an ossiphagous diet, are characterized by a wrinkled outer enamel surface. This feature tends to be lost with wear, but the original external furrowing can be detected also in highly worn teeth using a light microscope. Our observation of European late Villafranchian *C. lunensis* samples demonstrates that the species is polymorphic

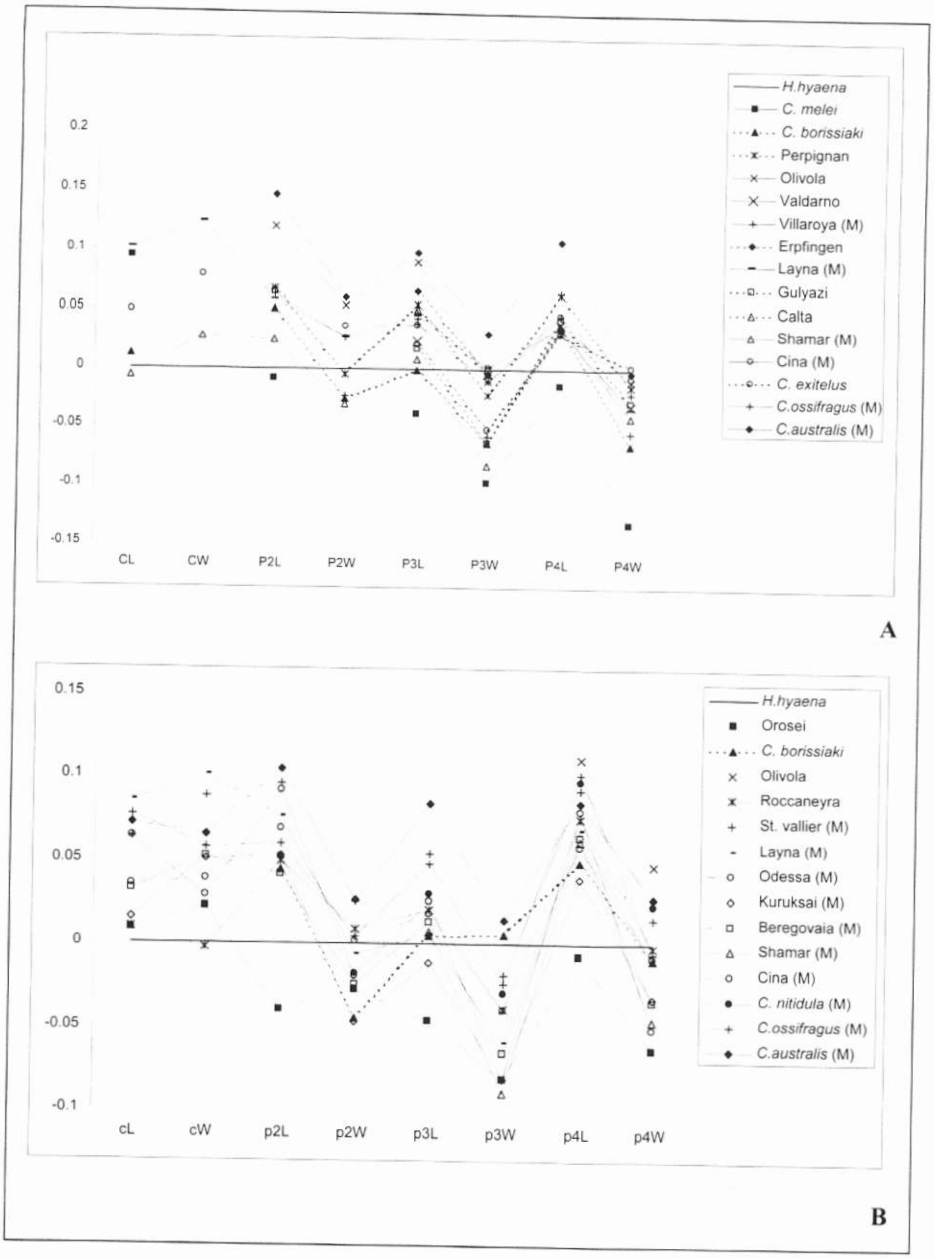

Fig. 7 - Ratio diagrams of upper (A) and lower (B) teeth of selected European and Asian *C. lunensis* samples (indicated by locality) and New and Old world *Chasmaporthetes* species. Recent *Hyaena hyaena* taken as reference.

with respect to this character. Specimens from St.Vallier and Olivola are characterized by a smooth surface, while the specimen from Inferno, Upper Valdarno has a wrinkled tooth surface (Ferretti 1999, and unpublished data).

Chasmaporthetes melei from Mt. Tuttavista has an outer tooth surface characterized by a feeble wrinkling, similar to the condition of *C. lunensis* from Inferno.

Derived bone-crushing hyaenas have complex HSB which produce a characteristic zig-zag pattern when observed from the tooth surface. Such complex HSB have been shown to be a mechanical adaptation to withstand the very high stresses produced by bone consumption (Rensberger 1995; Rensberger & Stefen 1995). Carnivores that customarily do not include bone in their diet, consistently have simpler HSB, characterized by only weak undulations. Villafranchian *Chasmaporthetes* from Europe is characterized by complex HSB, similar to those of bone-crushing hyaenas (e.g. *Crocuta*), but with less intense folding (Ferretti 1999). This suggests a lesser specialization to bone consumption in *Chasmaporthetes*. Thus, though *Chasmaporthetes* was surely capable of breaking large bones, its feeding habits relied more on hunting than on scavenging, which is consistent with the cursorial adaptations of the postcrania (Berta 1981).

The enamel structure of *C. melei* from Mt. Tuttavista is fully comparable with that of congeneric European forms. In particular, the occurrence of acute-angled HSB throughout the dentition of *C. melei*, suggests a feeding behavior similar to that proposed for other *Chasmaporthetes* species (Ferretti 1999).

Conclusions

The comparative study of the hyaenid specimen from the Mt. Tuttavista fissure fillings has led to the identification of a new species of the genus *Chasmaporthetes*: *Chasmaporthetes melei*. Although definitely smaller, *C. melei* is morphologically comparable to *Chasmaporthetes lunensis*, the Plio-Pleistocene hunting hyena of Europe and Asia, a possible ancestor of the Sardinian species. The smaller size of *C. melei* with respect to species from the mainland could represent an adaptation to the Sardinian insular ecosystem. *C. melei* displays all the characteristic feeding adaptations of *Chasmaporthetes*, including a derived enamel structure similar to, though less specialized than that of extant bone-crushing hyaenas. *C. melei* was an active predator that nonetheless included a relatively large amount of bone in its diet. The *Chasmaporthetes* remains from Mt. Tuttavista thus testifies the rather exceptional occurrence of a large active predator within an insular ecosystem.