CYNOTHERIUM MALATESTAI, SP. NOV. (CARNIVORA, CANIDAE), FROM THE EARLY MIDDLE PLEISTOCENE DEPOSITS OF GROTTA DEI FIORI (SARDINIA, WESTERN MEDITERRANEAN)

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Cynotherium sardous Studiati, 1857, is the best known endemic carnivor can from the Late Pleistocene deposits of Sardinia and Corsica (western Mediterranean). This medium-sized canid displays a peculiar mixture of craniotal features, some of them being customarily related to hypercarnivory (e.g., unicuspid talonid on m1), whereas others (such as the reduced sagittal crest and the long temporal lines) are presumably related to pedomorphism (Eisenmann, 1990). Cynotherium sardous was probably a predator specializing in small mammals, such as the ochotonid Prolagus sardus Wagner, 1829, and maybe even birds. Postcranial features, especially the short limb bones, argue against an inference of good running capabilities for this taxon, which would have been able to hold its body close to the ground when stalking instead (Malatesta, 1970; Eisenmann and van der Geer, 1999; Caloi and Palmombo, 2000; Abbazzi et al., 2005; Lyras and van der Geer, 2006; Lyras et al., 2006; Palombo, 2006; Novelli et al., 2009).

Here we describe new dentognathic remains of Cynotherium from the Pleistocene (>0.5 Ma) deposits of Grotta dei Fiori in Sardinia (Melis et al., 2013; Palombo and Rozzi, 2014). The new material is assigned to a new species of Cynotherium, and on its basis the phylogeny of this genus is reevaluated.

Institutional Abbreviations—EVT, Estació de Vallparadís (Terrassa, Barcelona, Spain), housed in the Institut Catalá de Paleontologia Miquel Crusafont (Sabadell, Barcelona, Spain); MPUR, Museum of Paleontology University of Rome (Rome, Italy); RMCA, Royal Museum for Central Africa (Tervuren, Belgium).

AGE AND GEOLOGIC SETTING

Grotta dei Fiori Cave (GFC) is located on the western side of the Rio Cannas Valley, near the town of Carbonia and about 10 km west of the Golfo di Palmas coast (Fig. 2). This cave is situated within the Paleozoic relief delimited by the Cixerri graben to the north and the Carbonia-Giba-Narcao graben to the southeast. Tectonic activity and underground water circulation affected the morphology of the GFC, which has a maximum depth of about 45 m and extends for about 800 m², mainly within the Dolomia Rigata of the Gonnese Formation (Lower Cambrian; Fig. 2).

The cave was originally infilled by red clay sediments, which are still locally present on the ceiling of the chambers, but subsequently emptied completely due to increased water circulation mostly as a result of Early Pleistocene tectonic activity. During the late Early and Middle Pleistocene, the cave was partially refilled by rockfall, sploethems, and alluvial deposits, which were subsequently eroded during the late Pleistocene (Melis et al., 2013). Three sedimentary sections (SA, SC, SD) are distinguished in the GFC (Melis et al., 2013). The fossil remains reported here come from layer C14, on top of the SC section and just below a flowstone radiometrically (U-Th) dated to >0.5 Ma (Melis et al., 2013; Palombo and Rozzi, 2014) (Fig. 2). Layer C14, about 0.75 m in thickness, is composed of a coarse chaotic assortment of angular and subangular limestone and metamorphic rock fragments within a clayey and sandy-clay loam matrix (Melis et al., 2013).
FIGURE 1. Chronological range chart of mammalian taxa recorded in the Pleistocene and Holocene local faunal assemblages from Sardinia (updated and modified from Palombo and Rozzi, 2014).

FIGURE 2. A, Location map of Grotta dei Fiori within Sardinia; B, cave map of the Grotta dei Fiori system, showing the location of the various sections (modified from Melis et al., 2013): SA, section A; SC, section C; SD, section D; EA, entrance A; EB, entrance B; EC, entrance C; C, stratigraphic sketch of section C (modified from Melis et al., 2013): 1, clayey sediments; 2, mud cracks; 3, sandy-clay-loam sediments; 4, angular and subangular clasts of carbonate and metamorphic rocks; 5, flowstone; 6, fossil remains.
SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family CANIDAE Fisher von Waldheim, 1817
Genus CYNOTHERIUM Studiati, 1857

CYNOTHERIUM MALATESTAI, sp. nov. (Figs. 3, 4)

Cynotherium sardous Studiati, 1857: Melis et al., 2002:8.
Cynotherium sardous Studiati, 1857: Pavia and Bedetti, 2003:164.
Cynotherium sardous Studiati, 1857: Boldrini, 2008:55.
Cynotherium aff. sardous Studiati, 1857: Palombo et al., 2008:101.
Cynotherium sardous Studiati, 1857: Boldrini et al., 2010:124.

Holotype—MPUR/V4200a (Fig. 3A–C), right hemimandible with c1 and p2–m2, housed in Museum of Paleontology of the Sapienza Università di Roma (Rome, Italy).

Paratypes—MPUR/V4200b, left partial hemimandible with i1–i3, c1, p4, and m1; MPUR/V4200a, right hemimandible with c1 and p2–m2; MPUR/V4201, partial left mandibular corpus with alveoli of m1–m3; MPUR/V4202, left humerus; MPUR/V4203, right humerus; MPUR/V4204, proximal fragment of left ulna; MPUR/V4205, left second metatarsal; MPUR/V4206, left fifth metatarsal.

Type Locality—Grotta dei Fiori, section C, layer C14 (Sardinia, Italy).

Chronostratigraphic Distribution—More than 0.5 Ma (?late Early Pleistocene and/or Early Middle Pleistocene).

Geographic Distribution—Exclusively known from the type locality.

Etymology—Named in honor of Prof. Alberto Malatesta, in recognition of his contribution to the study of Cynotherium sardous.

Diagnosis—Medium-sized canid species, intermediate in size between Xenocyon lycaonoides and Cynotherium sardous. Mandibular corpus deep and robust. Long diastemata between p2 and p3 and between p3 and p4. p2 without accessory cusps. p3 and p4 with moderately developed distal accessory cusps. m1 with unicuspid talonid and a vestigial transverse hypoconid crest. m2 with unicuspid trigonid.

Measurements—See Tables 1 and S1.

Description—The mandibular corpus is stout and deep, whereas the ramus is high, with the mandibular condyle not surpassing the occlusal level and being shifted posteriorly relative to the angular process. The angular apophysis is projected posteroventrally. Three diastemata are present between c1 and p2, p2 and p3, and p3 and p4; the first is the longest, whereas the third is the shortest.

The i3 is not much larger than the other incisors. The canines are vertically implanted, moderately curved, and robust (massive). The p1 is absent, while p2 is high-crowned and lacks accessory cusps. The p3 is symmetrical in lateral view, bears a slightly developed distal accessory cusp and displays a small distal cingulid. The p4 has two distal accessory cusps and a marked distolingual cingulid; the distal-most accessory cusp is very small but distinct from the cingulid. The m1 has a sharp and high trigonid, with a small and non-protruding metaconid; the talonid has a large, sharp, and centrally situated hypoconid with a vestigial transverse crest but without an entoconid. The m2 trigonid displays a single cusp (protoconid), whereas the m2 talonid only shows a small and buccally situated hypoconid. The m3 alveoli can be seen in all specimens.

DISCUSSION

Comparisons with Cynotherium sardous from Dragonara Cave

The more abundant sample of Cynotherium sardous from Sardinia comes from the Late Pleistocene deposits of Dragonara Cave and was fully described by Malatesta (1970). Cynotherium malatestai, sp. nov., differs from C. sardous in its larger dimensions (Tables 1 and S1; Fig. 4) as well as its more robust and deeper mandibular corpus. Moreover, in C. malatestai, the
mandibular condyle does not surpass the occlusal level, whereas it is situated in a higher position in most of the specimens from Dragonara assigned to \textit{C. sardous} (Malatesta, 1970). Only in the largest specimens of the latter species (e.g., MPUR1/2100, MPUR1/2092, and MPUR1/2061; Malatesta, 1970:pl. 4 as d3) is the condyle situated more inferiorly as in the new species. Some other morphological traits are also variable in the Dragonara sample, including the mental foramina—that vary in number (two or three), size, and position (Malatesta, 1970:pl. 4)—as well as the presence/absence of diastemata. However, the specimens from GFC display diastemata between p2 and p3 and between p3 and p4, whereas in the Dragonara sample, the diastema between p3 and p4 is only present in a few specimens (e.g., MPUR1/2097 and MPUR1/2088) and that between p2 and p3 is present in 69% of the 35 studied hemimandibles.

With regard to the dentition, in \textit{C. malatestai}, sp. nov., p1 is absent in all the studied specimens, whereas in the Dragonara sample, it is present in 26% of the 35 studied hemimandibles. The remaining lower premolars from GFC and Dragonara show a very similar morphology, although those from the latter locality are smaller, higher, and relatively narrower (buccolingually compressed). Moreover, in a few specimens from Dragonara (e.g., MPUR1/2088; Malatesta, 1970:pl. 4 as 5g), the distal accessory cusp of p3 is clearly reduced, as in the new species. Likewise, the morphology of the lower molars is similar between the two samples, although the specimens from GFC are generally larger. Furthermore, in the two taxa, the m1 has a reduced metaconid and a centrally situated hypoconid, although the latter is sharper and more buccolingually compressed in \textit{C. sardous}, which completely lacks the vestigial transverse crest of the hypoconid that is still present in the specimens from GFC. None of the two species show any trace of the m1 entoconid. In both species, the m2 has a single trigonid cusp (protoconid) and a small and buccally situated hypoconid in the talonid, but in a few specimens from Dragonara the latter further has a small and lingually situated entoconid (e.g., MPUR1/2097 and MPUR1/2082).

Overall, the studied specimens from GFC resemble those of \textit{C. sardous} in the very hypercarnivorous morphology of the m1 and m2 talonids, with extremely reduced lingual cusps and a stable central position of the m1 hypoconid. However, the mandible from GFC differs from \textit{C. sardous} of Dragonara and Monte Tutavista (Malatesta, 1970; Abbazzi et al., 2005) in its larger size and stouter and deeper mandibular corpus. Other features that distinguish \textit{C. malatestai} from most specimens of \textit{C. sardus} might be size-related, exhibited by the largest hemimandibles from Dragonara. Taking into account the trend of progressive size reduction in some large mammal lineages under insular conditions, as well as the chronology, size, and morphological features of \textit{C. malatestai}, the newly described species may be arguably considered the ancestor of \textit{C. sardous}. 

\textbf{FIGURE 4.} Mandibular remains of \textit{Xenocyon} and \textit{Cynotherium} from the European Pleistocene compared with the extant \textit{Lycaon}. \textbf{A–B}, \textit{Xenocyon lycaonoides} from Vallparadis Estació (Iberian Peninsula): \textbf{A}, EVT22049, partial right hemimandible in buccal view; \textbf{B}, EVT22434, partial left hemimandible in buccal view; \textbf{C}, EVT22434, detail of the m1 and m2 in occlusal view. \textbf{D–F}, \textit{Cynotherium malatestai} sp. nov. from Grotta dei Fiori: \textbf{D}, MPUR/V4200a, partial right hemimandible in buccal view; \textbf{E}, MPUR/V4200b, partial left hemimandible in buccal view; \textbf{F}, MPUR/V4200a, detail of the m1 and m2 in occlusal view. \textbf{G–I}, \textit{Cynotherium sardous} from Dragonara Cave: \textbf{G}, MPUR1/2097, partial right hemimandible in buccal view; \textbf{H}, MPUR1/2082, partial left hemimandible in buccal view; \textbf{I}, MPUR1/2060, detail of the m1 and m2 in occlusal view. \textbf{J–L}, \textit{Lycaon pictus} from Congo: \textbf{J}, RMCA 46B, right hemimandible in buccal view; \textbf{K}, RMCA 2144, left hemimandible in buccal view; \textbf{L}, RMCA 11815, detail of m1 and m2.
TABLE 1. Measurements in mm of the hemimandibles of Cynotherium malatestai, sp. nov., from Grotta dei Fiori.

| Specimen      | Lat. | W  | L  | W  | L  | W  | L  | W  | L  | W  | L  | W  | L  | W  | L  | W  | L  | W  | L  | W  | L  | W  | L  | W  | L  | W  | L  | W  | L  | W  | L  | W  |
|---------------|------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| MPUR/V4200b  | Left | 11.3| 7.1| 9.58| 4.2| 12.8| 6.7| 22.5| 5.5| 6.96| 8.6| 18.8| 23.8|
| MPUR/V4200a  | Right| 11.1| 8.8| 10.9| 4.93| 12.7| 6.0| 22.2| 5.3| 6.6| 8.6| 9.91| 6.8| 18.6| 23.0|

Abbreviations: Hp2, height of the mandibular corpus behind p2; Hp4, height of the mandibular corpus behind p4; L, length; Lat, laterally; Lt, talonid length; W, width; Wt, talonid width.

Comparisons with the late Early Pleistocene European Canids

The oldest record of genus Cynotherium in Sardinia corresponds to Cava X-3 uccelli (Monte Tuttavista; Abazzi et al., 2005; Fig. 1), with a chronology presumably close to the Brunhes-Matuyama boundary. These remains are therefore older than those from GFC, based on the presence of *M. sondaari* at Cava X-3 uccelli and *Microtus* (*Tyrrhenicola*) at GFC (Melis et al., 2013). Thus far, no *Cynotherium* or any other canid has been recorded from Sardinian local faunal assemblages of the ‘Nesogoral’ faunal complex (latest Pliocene–?pre-Jaramillo Early Pleistocene (Palombo and Rozzi, 2014). This suggests that the taxon ancestral to *Cynotherium* must have arrived around the beginning of the ‘Microtus (*Tyrrhenicola*)’ faunal complex, i.e., during the marked post-Jaramillo lowering of the sea level that took place by the late Early Pleistocene (MIS24 or MIS22, ca. 0.95–0.85 Ma) (cf. Azzaroli, 1981; Esu and Kotsakis, 1983; Sondaar et al., 1986; Van der Made, 1999; Palombo, 2006, 2009, Palombo and Rozzi, 2014).

Only two medium-sized canids are recorded from mainland Europe during the latest Early Pleistocene: the large and hypercarnivorous *Xenocyon lycaonoides* (Rook, 1994; Sotnikova, 2001; Martínez-Navarro and Rook, 2003; Mouillé et al., 2006; Madurell-Malapeira et al., 2013) and the smaller canid assigned to either *Canis mosbachensis* Soergel, 1925 (Sotnikova, 2001; Mouillé et al., 2006; Martínez-Navarro et al., 2010), or to the southern European group of *Canis aff. arnensis* (Rook and Torre, 1996). *Cynotherium malatestai*, sp. nov., shows several differences from the material customarily attributed to *Ca. mosbachensis* (cf. Sotnikova, 2001). In particular, in *C. malatestai*, the mandibular corpus is stouter and longer, with a deeper masseteric fossa, the mandibular condyle is shifted more posteriorly (Table 1; Fig. 2), and there are three diastemata. Moreover, despite a similar average dental size (only the m1 of *C. malatestai* is mesiodistally shorter than that of *Ca. mosbachensis*; Table S1; Fig. 5) and a similar premolar morphology, the two species differ in some important dental traits. Thus, in *Ca. mosbachensis*, the c1 is narrower and often more obliquely oriented than in *C. malatestai*, and the p1 is almost always present in the former (e.g., Sotnikova, 2001:613). Moreover, *Ca. mosbachensis* further differs from *C. malatestai* in the occlusal morphology of the lower molars, with the m1 displaying a well-developed metaconid, a bicuspid talonid, and a fully developed transverse crest on the hypoconid and the m2 possessing a bicuspid trigonid.

Although *Xenocyon lycaonoides*, recorded from the late Early Pleistocene layer EVT7 of Valliparidis Estació (0.83 Ma; Vallès-Penedès Basin, Iberian Peninsula; Madurell-Malapeira et al., 2013), also displays some minor differences from *C. malatestai* (larger dental and mandibular size; Table S1), the two species closely resemble each other in many morphological traits. Similarities include the straight tooth rows, the vertically oriented c1, the overall occlusal morphology of the lower premolars (in spite of the more developed posterior accessory cusps in p2 and p3 in *X. lycaonoides* and the absence of p1 in *C. malatestai*), and the reduced metaconid and unicusp talonid of m1 (in particular, the reduced transverse crest of the hypoconid in the m1 talonid is characteristic of hypercarnivorous morphologies; Sotnikova, 2001). Interestingly, the m2 metaconid, absent in *C. malatestai*, is already strongly reduced in the later forms of *X. lycaonoides*, whereas the p2/p3 diastema, although more reduced than in *C. malatestai*, has been also documented in *X. falconeri* and *X. lycaonoides* (Madurell-Malapeira et al., 2013:fig. 3).

A possible phylogenetic link between *Cynotherium* with *Xenocyon* has been previously suggested by some authors (Bonifay, 1994; Caloi and Palombo, 2000; Novelli and Palombo, 2007), and Lyras et al. (2006, 2010) more explicitly proposed *X. lycaonoides*...
as the likely ancestor of C. sardous. According to this hypothesis, Cynotherium would have originated from a hypercarnivorous, Xenocyon-like mainland ancestor, having subsequently evolved paedomorphic cranial characters under insularity conditions—probably due to changes in hunting behavior related to an absence of competitors, body size reduction, and an abundance of small prey (Eisenmann, 1990; Lyras et al., 2006, 2010). If this is correct, then the larger size (compared with C. sardous) and the retention of hypercarnivorous features of C. malatestai would indicate that the new species represents an intermediate stage in the evolutionary lineage leading from X. lycaonoides to C. sardous.

This evolutionary hypothesis is supported by the progressive size reduction documented along the Cynotherium lineage, with C. malatestai, C. sardous from Dragonara, and C. sardous from Corbeddu being reduced in body mass about 21%, 40%, and 54%, respectively, compared with the latest Early Pleistocene X. lycaonoides from Vallparadis Estació (body mass estimates computed based on m1 mesiodistal length, following the allometric equations published by Van Valkenburgh, 1990). The presence of diastemata between p2 and p3 and between p3 and p4 in C. malatestai might result from the changes in the jaw muscle system due to a change in prey size at an early stage of body size reduction. This is supported by the fact that the presence of diastemata is well documented in canids that have secondarily adapted to small-prey hunting (Sillero-Zubiri and Gotelli, 1994; Lyas and van der Geer, 2006), such as the Ethiopian wolf, Canis simensis Rüppell, 1835, or the Falkland wolf, Dusicyon australis (Kerr, 1792). The latter species also has a short sagittal crest and long temporal lines, which are characters that have been previously considered to be paedomorphic by some authors (Sillero-Zubiri and Gotelli, 1994).

CONCLUSIONS

We describe a new canid species, Cynotherium malatestai sp. nov., based on previously unpublished mandibular remains from layer C14 of Grotta dei Fiori (>0.5 Ma). The attribution of the studied specimens to the endemic Sardinian genus Cynotherium is justified by the hypercarnivorous morphology of their lower dentition. However, the new material differs from the material of Dragonara Cave (attributed to the nontypical species, C. sardoun) in its larger dimensions, a stouter and deeper mandibular corpus, and the presence of several significant diastemata. These differences support the erection of a new species, which based on morphological and chronological grounds might be the ancestor of C. sardous, thus representing a likely intermediate stage of an anagenetic lineage leading from the mainland Xenocyon lycaonoides to the insular C. sardous. An origin of the Cynotherium lineage from X. lycaonoides is supported by both dental size and occusal morphology, in agreement with previous suggestions that the ancestor of C. sardous displayed a hypercarnivorous dentition and arrived at Sardinia by the end of the Early Pleistocene. The progressive size reduction and acquisition of presumably paedomorphic cranial features might be related to a dietary change, due to the abundance of the ochotomid Prolagus sardius (the only other large mammal present on Sardinia by that time being a large deer from the endemic Sardinian lineage Praemegaceros). The existence of anagenetic evolutionary patterns has been already claimed for other Sardinian endemic lineages, such as Prolagus sardius, Microtus (Tyrhenicola), and Praemegaceros (Palombo and Rozzi, 2014, and references therein). In terms of chronology and extent, the size reduction of the Cynotherium lineage would have paralleled that of the Sardinian deer Praemegaceros, going from the large-sized and slender Praemegaceros aff. Praemegaceros sardous (Van der Made and Palombo, 2006) from the Su Fossu de Cannas cave to the smallest and stouter-limbed Praemegaceros cazioti (Depéret, 1897) from Corbeddu (Palombo and Rozzi, 2014).

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