

A large tusk of *Metaxytherium* (Dugongidae, Sirenia, Mammalia) from the Late Miocene of Montebamboli (southern Tuscany, Italy): evolutionary and paleoecological implications

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ABSTRACT - An isolated large tusk, belonging to the historical finds of the Collezione di Geologia "Museo Giovanni Capellini" (Bologna, Italy) and originally identified as belonging to a hippopotamus, is here described and reassigned to the genus *Metaxytherium* (Dugongidae, Sirenia, Mammalia). According to the museum label, this specimen originates from the now-exhausted lignite deposits of Montebamboli (Tuscany, central Italy); the latter are late Tortonian to early Messinian in age and were deposited in a lacustrine environment. The Montebamboli tusk displays strong similarities with an elderly *Metaxytherium subapenninum* specimen from the Pliocene deposits of Bra (Piedmont, northern Italy) as well as with an isolated *Metaxytherium* tusk, now apparently lost, from Miocene deposits of Son Morelló (Mallorca, Spain). The Late Miocene occurrence of a large-tusked *Metaxytherium* in the Mediterranean Basin calls into question the anagenetic trend previously proposed for the Euro-North African species of *Metaxytherium*, thus also stimulating further research on the intra- and interspecific tusk size variability within this lineage. Furthermore, this specimen represents the first record of a marine species from the lignites of Montebamboli, indicating the proximity of marine settings.

INTRODUCTION

Metaxytherium is an extinct genus of generalist halitheriine dugongid sirenians that was widely distributed during the Miocene. It is paraphyletic, having likely given rise to the subfamily Hydrodamalinae in the North Pacific Ocean (Aranda-Manteca et al., 1994). During the Late Miocene, *Metaxytherium* became extinct worldwide, except in the Mediterranean Basin (Bianucci et al., 2008). In the broad Mediterranean region, *Metaxytherium* was seemingly represented by four successive chronospecies: *M. krahuletzii* Depéret, 1895 (middle Aquitanian-early Langhian); *M. medium* (Desmarest, 1822) (Langhian-Tortonian); *M. serresii* (Gervais, 1847) (late Tortonian-early Zanclean); and *M. subapenninum* (Bruno, 1839) (early Zanclean-late Piacenzian). Members of this lineage exhibit a slight increase in tusk size and a reduction in body size in *M. serresii*, followed by a noticeable increase in both body and tusk size in *M. subapenninum* (Bianucci et al., 2008; Sorbi et al., 2012). More in detail, the remains of *M. serresii* that are found in sediments deposited shortly before and after the Messinian Salinity Crisis display an incipient increase in tusk size and a reduction in body size, thus suggesting a probable ecophenotypic dwarfing due to the degradation of seagrass meadow environments on the

eve of a major upheaval of the marine ecosystems of the whole Mediterranean Sea. *Metaxytherium subapenninum*, the largest member of the genus, displays a clear trend towards increasing body and tusk sizes that was likely triggered by the progressive climatic deterioration that finally brought them to extinction about three Ma (Bianucci et al., 2008; Sorbi et al., 2012).

In the present article, we report and describe an as-yet unpublished fossil sirenian tusk from the Upper Miocene lignites of Montebamboli. This find is referred herein to *Metaxytherium*, and its paleobiological significance is briefly discussed.

Institutional abbreviations

IGF: Museo di Storia Naturale dell'Università di Firenze, sezione di Geologia e Paleontologia (Florence, Italy); MC: Museo Craveri (Bra, Italy); MGGC: Collezione di Geologia "Museo Giovanni Capellini", Università di Bologna (Bologna, Italy); PU: Museo di Geologia e Paleontologia, Università di Torino (Turin, Italy).

Other abbreviations

C.: character state as described and numbered by Domning (1994) and Sorbi et al. (2012); MSC: Messinian Salinity Crisis.

GEOLOGICAL AND PALEONTOLOGICAL SETTING

The partial sirenian tusk studied herein is stored in the Collezione di Geologia “Museo Giovanni Capellini” (Bologna, Italy), where a historical label identifies it as belonging to a hippopotamus and indicates its provenance as “Lignite di Monte Bamboli” (= Montebamboli lignite). In the XIX and early XX centuries, the Tuscan locality of Montebamboli (southwestern Tuscany, Italy) was indeed well-known for its now-exhausted lignite deposits (De Castro & Pilotti, 1933; Moratti & Bonini, 1998; Costantini et al., 2000); the latter have also yielded a conspicuous endemic fossil vertebrate assemblage, including the type of the hominoid primate *Oreopithecus bambolii* Gervais, 1872, as well as nonmarine turtles and crocodiles (Hürzeler, 1958, 1960; Harrison, 1986; Rook et al., 1996, 1999; Chesi et al., 2009) (Fig. 1). Similar fossiliferous lignite levels occur elsewhere in southwestern Tuscany and, most notably, at the nearby localities of Baccinello, Casteani and Ribolla (Azzaroli et al., 1986; Rook et al., 1996; Chesi et al., 2009; Rook, 2016) (Fig. 1). Collectively, these deposits have been assigned to the so-called “Lignitiferous Unit”, which is regarded as Late Miocene (pre-MSC) in age (Bossio et al., 1998). The studied tusk preserves shreds of a compact, black, coal-like matrix that bring support to an origin from the highly distinctive southwestern Tuscan lignites. Furthermore, it is not the only vertebrate specimen kept at Bologna to originate from the “Lignitiferous Unit”: indeed, the MGGC contains uncatalogued specimens of the softshell turtle *Trionyx* Geoffroy Saint-Hilaire, 1809 and other terrapins labelled as coming from Montebamboli (Contessi, pers. obs., 2022), as well as an *Oreopithecus* specimen from Casteani; the latter was seemingly donated to Giovanni Capellini (Gentili et al., 1998). The lignite deposits that have historically been exploited at Montebamboli are late Tortonian to early Messinian in age (Costantini et al., 2000) and testify to a lacustrine setting. That the specimen studied herein is not reworked from older marine rocks is supported by its overall aspect, which closely resembles

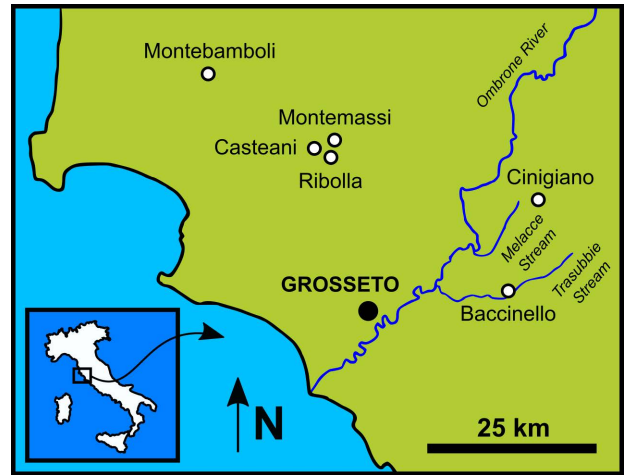


Fig. 1 - Location of the main vertebrate-bearing sites of southern Tuscany (white-filled circles). Redrawn and modified after Rook et al. (1993).

that of other vertebrate fossils from the Montebamboli lignites, as well as by the substantially organogenic nature of the host sediment, which does not contain any clast of roughly comparable size.

Though similar in age, the vertebrate assemblages from Montebamboli, Baccinello, Casteani and Ribolla are not exactly coeval, as exemplified by their different taxonomic compositions in terrestrial mammals; none of them has yielded remains of marine vertebrates up to date. In detail, the lignite fossiliferous levels described at Casteani and Ribolla preserve fossils referred to Lorenz’s (1968) vertebrate assemblage (V)1. At Baccinello, a thick stratigraphic succession preserves assemblages referred to V0, V1, V2 and V3 (Lorenz, 1968; Engesser, 1989; Rook, 2016), whereas in the rest of the Baccinello Basin, only the V1 assemblage occurs in lignite deposits. Montebamboli has yielded mammal remains that suggest an attribution to the V2 assemblage, as exemplified by the occurrence of the endemic suid *Eumaiochœrus etruscus* (Michelotti, 1861) (Azzaroli et al., 1986; Rook et al., 1996, 2011;

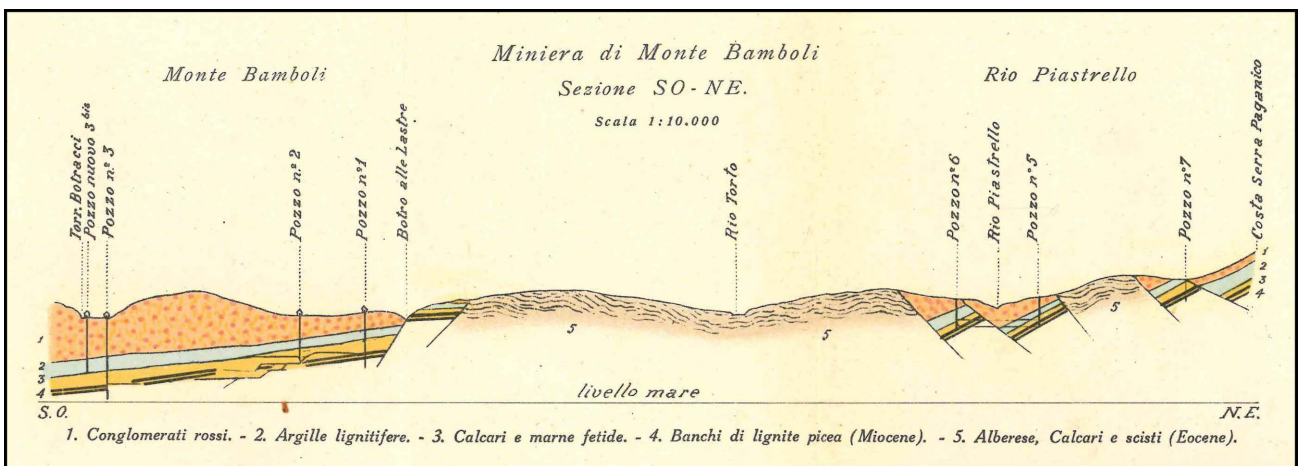


Fig. 2 - Stratigraphic scheme of the Montebamboli-Rio Piastrello area (South/ West-North/East section, scale 1:10000) showing the stratigraphic succession of Montebamboli mine as reported by De Castro & Pilotti (1933). 1: red conglomerates; 2: lignitiferous clays; 3: marly limestone with thin dark clayed levels; 4: upper and lower lignitiferous levels interlayered by a marly level; 5: marly limestone (Alberese stone, Monte Morello Formation, Eocene). “Pozzo” indicates the extractive tunnels, some of which were connected at their bases. Modified from De Castro & Pilotti (1933).

Rook, 2016). It is nonetheless important to underline that the mammal remains from Montebamboli were collected by workers during the mining activities, and as such, their exact stratigraphic provenance is uncertain. Furthermore, as the collected fossil material was probably somewhat selected by the miners themselves, it may not represent faithfully the complete fossil assemblage of the site, as some taxa could be artificially underrepresented. Considering also that at least two different lignite-bearing levels were present at Montebamboli (Fig. 2), the presence of more than one assemblage, V1 and/or V2, cannot be excluded at this historical site.

According to the chronostratigraphic calibration provided by Rook et al. (2011) for the vertebrate assemblages collected at Baccinello, V1 likely represents the 8.3-8.1 Ma time span, corresponding to the late Tortonian, whereas the age of V2 should be comprised between 7.1 Ma and 6.7 Ma, corresponding to the early Messinian. Absolute confidence about the geographic and stratigraphic whereabouts of the studied specimen would thus be needed for pinpointing its geological age. In light of these considerations, it is here conservatively assigned to the 8.3-6.7 Ma time span.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758

Order SIRENIA Illiger, 1811

Family DUGONGIDAE Gray, 1821

Subfamily HALITHERIINAE (Carus, 1868) emend. Abel, 1913

Genus *Metaxytherium* Christol, 1840

Metaxytherium sp.
(Fig. 3)

Referred Material - MGGC 8146F, an isolated left tusk preserved within lignite matrix.

Occurrence - Upper Miocene lignites exploited in the old Montebamboli mine (southwestern Tuscany, Italy).

Description - The tusk is black in color, pervasively fractured, and has been locally restored with black-colored plaster that seems to have been applied incorrectly, thus modifying the original inclination of the tusk (Fig. 3). The tusk is incomplete, lacking the base of the root. It is more than 192 mm long, mediolaterally compressed, and slightly flattened on the medial side; its cross-section is thick and shaped as a slightly eccentric ellipse (c. 141[0]) measuring 40 × 61 mm (Fig. 3a3). The root is closed. The entire crown, about 110 mm long, is covered by a thin enamel layer, less than 1 mm thick, whereas the root appears as covered by cementum (Fig. 3a2). The crown deviates anteriorly from the long axis of the root. Lateral to its apex, the crown displays a smooth and shiny wear surface that is amygdaloid in shape and measures 78 × 42 mm (Fig. 3b). The proximal termination of this wear surface is observed some 102 mm posterior to the apex of the tusk. Except for this worn-out area, longitudinal striae run throughout the outer surface of MGGC 8146F, being



Fig. 3 - MGGC 8146F in medial (a1), lateral (a2) and distal (a3) views. The dashed white line in panel (a2) indicates the approximate extent of the cementum coating along the lateral surface of the tusk. Scale bar equals 2 cm.

about 1 mm wide and separated from each other by small (about 2 mm wide) grooves (Fig. 3a1-a2). On both sides of the tooth, two broader furrows are present: that on the lateral side is located 14 mm far from the dorsal tooth edge, whereas that occurring on the medial side runs at a distance of about 20 mm from the same edge (Fig. 3a1-a2).

Comparisons and remarks - Although MGGC 8146F had originally been interpreted as originating from a hippopotamus, the Late Miocene lower canines of Mediterranean hippopotamids (genera *Archaeopotamus* and *Hexaprotodon*) differ from the studied specimen by being mesiolaterally compressed, with a triangular dorsal wear surface, as well as by showing pronounced longitudinal ridges, sometimes along with a groove on the lateral side (Martino et al., 2021). On the contrary, MGGC 8146F reveals strong affinities with an elderly specimen of *Metaxytherium subapenninum* from the Pliocene of Bra, Cuneo (Piedmont, Italy) as well as with an isolated fragmentary tusk from Miocene deposits of Son Morelló, Sancellas (Mallorca, Spain) (Fig. 4).

The Bra specimen (Fig. 4B) consists of an adult cranium (MC, unnumbered; cast IGF 12100) that preserves the right tusk embedded within its alveolus. The entire tusk is known only from a cast that is currently stored at the PU. The Bra tusk is mediolaterally compressed, about 200 mm long and slightly flattened on the medial side. The cross section of the crown is thick (35 × 55 mm) and slightly displaced from the long axis of the root, with a nearly triangular wear surface occurring on the lateral side of the crown apex. The entire crown seems to be covered by cementum, and enamel is visible on the medial side as

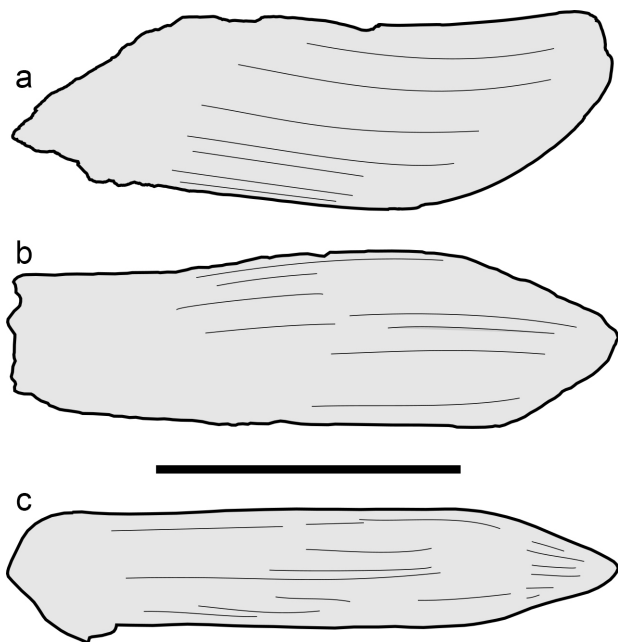


Fig. 4 - Schematic comparison between the outlines of three *Metaxytherium* tusks from the Mediterranean Neogene (line drawings). a) Left tusk of *Metaxytherium* sp. from Montebamboli (Tuscany, Italy), MGGC 8146F, in medial view. b) Left tusk of *Metaxytherium subapenninum* from Bra (Piedmont, Italy), cast kept at the PU, in medial view (reversed). c) Tusk of *Metaxytherium* sp. from Son Morelló (Mallorca, Spain), specimen apparently lost, in medial(?) view. Scale bar equals 100 mm.

a dark, thin, shiny layer. In dugongid tusks, enamel may indeed be present on the medial side only, thereby making the tusk self-sharpening (Sorbi et al., 2012).

The Mallorcan specimen (Fig. 4C) was described, illustrated and referred to the genus *Metaxytherium* by Cañigüeral (1952), but appears to be lost at present. Cañigüeral (1952) described the tusk as 200 mm long and oval in cross-section (about 40 × 20 mm wide in its median part), with an unworn enameled subconical tip that was about 30 mm long and 25 mm wide, and an open root. The latter appeared to be covered by cementum ornamented with longitudinal striae that also showed up on the crown.

In light of these comparisons, the tusk described herein is referred to the genus *Metaxytherium*. Exhibiting a closed root and a wide wear surface, both MGGC 8146F and the Bra specimen approach the maximum size values observed for the ever-growing tusks of dugongids. On the contrary, the Mallorcan tusk could be regarded as belonging to a young adult, as the root is still open and the tip unworn; thus, if it had not died somewhat prematurely, it might have attained an even greater size compared to both MGGC 8146F and MC unnumbered.

DISCUSSION AND CONCLUSIONS

Insights on the evolution of Metaxytherium

The Euro-North African *Metaxytherium* species have been interpreted as forming a lineage showing an incipient increase in tusk size and a reduction in body size in *M. serresii* (late Tortonian-early Zanclean), and a notable increase in body and tusk size in *M. serresii*'s putative descendant, *M. subapenninum* (early Zanclean-late Piacenzian) (Bianucci et al., 2008; Sorbi et al., 2012).

As the age of the Mallorcan specimen cannot be ascertained, nor is the specimen currently available for further analyses, its evolutionary significance cannot be elucidated, and the Tuscan specimen described herein can be regarded as the first well-established Late Miocene oversized tusk referred to *Metaxytherium*. In fact, Cañigüeral (1952) did not provide precise stratigraphic information for the deposits from which the Son Morelló tusk originates. He just indicated Miocene deposits in a quarry, at a depth of about five meters; furthermore, he mentioned other sirenian records referable to *Metaxytherium*, and comparable in size with *M. medium*, from other Miocene localities of Mallorca. The new sirenian record from Montebamboli reveals the occurrence of a large-tusked member of *Metaxytherium* during the Late Miocene (8.3-6.7 Ma), thus calling into question the evolutionary trend that is currently supported for the Euro-North African *Metaxytherium* species.

During the Late Miocene, the transition between *M. medium* and *M. serresii* seemingly took its place in the Mediterranean Basin. The fossil record of the former is widespread along the European coasts from the Langhian to the Tortonian, while specimens of the latter species have only been recorded in Calabria (Italy), Sahabi (Libya) and Hérault (France), in upper Tortonian to lower Zanclean deposits (Bianucci et al., 2008), respectively the geologically youngest occurrence of *M. medium* comes from the same southern Italian region (Calabria) as the oldest occurrence of *M. serresii*, hence the two records

can be easily compared stratigraphically: the former comes from the barren greyish-yellow sands of Santa Domenica di Ricàdi, referred to the Tortonian (Montcharmont Zei & Montcharmont, 1987), whereas the latter originates from upper Tortonian sands with *Clypeaster*, *Heterostegina* and pectinids of Monte Poro (Carone et al., 2013).

Carone & Domning (2007, p. 86) observed that the *M. medium* specimen from Santa Domenica di Ricàdi has an anteriorly pointed, mediolaterally broad supraorbital process with a laterally jutting posterolateral corner. This character is not present in either *M. krahuletzii* or other *M. medium* skeletons, but is the most common condition in *M. serresii*. In light of this observation, Carone & Domning (2007) regarded the Santa Domenica di Ricàdi specimen, the latest representative of its species, as possibly foreshadowing *M. serresii*.

Both these localities were investigated by Nicotera (1959) who divided the stratigraphic series exposed therein into eight levels, with *M. medium* and *M. serresii* coming from levels 3 and 7, respectively (Montcharmont Zei & Montcharmont, 1987; Carone & Domning, 2007). Level 3 is poorly fossiliferous, and as such, its absolute dating is uncertain; it can just be assigned to a Tortonian age older than level 7. The latter level correlates with Unit 2 as defined at Cessaniti (Gramigna et al., 2008), another *Metaxytherium*-bearing locality of Calabria (Carone, 1997); Unit 2 is in turn assigned to the terrestrial mammal unit MN 12, corresponding to 7.5-7.3 Ma, according to magnetostratigraphic calibrations.

Thus, the estimated chronostratigraphic range of the tusk described herein (8.3-6.7 Ma) is close to the oldest record of *M. serresii* (7.5-7.3 Ma) and, likely, to the youngest record of *M. medium*. MGGC 8146F could be consequently regarded as belonging to one of the last representatives of *Metaxytherium medium* or to another *Metaxytherium* form coeval with the dwarf species *M. serresii*; as such, it questions the model of four successive chronospecies for describing the evolution of the Euro-North African *Metaxytherium* (Bianucci et al., 2008; Sorbi et al., 2012), possibly in favor of a cladogenetic evolution within the genus *Metaxytherium* (Vélez-Juarbe & Domning, 2014).

Unfortunately, neither the record from Santa Domenica di Ricàdi nor that from Monte Poro preserve the tusks (Montcharmont Zei & Montcharmont, 1987). The only indirect information about tusk size comes from the premaxillary alveolus of the latter *M. serresii* specimen, whose depth is about half the length of the premaxillary symphysis (c. 140[1]), in agreement with the emended diagnosis for this species, and in contrast with *M. medium*, which has a shallower tusk alveolus (c. 140[0]), as well as with *M. subapenninum*, which has a bigger tusk alveolus (c. 140[2]) (Carone et al., 2013).

Sorbi et al. (2012) analyzed the intraspecific variability of tusk size in *M. subapenninum*, considering both sexual dimorphism (with adult males having larger tusks than females) and a gradual increase in tusk size to become more effective in harvesting rhizomes (thus allowing for a more nutrient-rich diet in the frame of the Pliocene climate cooling) as working hypotheses, corroborating the latter. The need to have a diet richer in rhizomes appeared to have started toward the end of the Miocene, when the onset of the MSC reduced the total seagrass biomass of the Mediterranean Sea, as supported by the incipient

increase in tusk size in *M. serresii* (Clementz et al., 2009; Sorbi et al., 2012).

As already mentioned, both MGGC 8146F and the Bra specimen are interpreted as tusks belonging to very old *Metaxytherium* specimens in which the ever-growing tusks reached their maximum size values. In light of tusk sexual dimorphism in the extant species *Dugong dugon* (Müller, 1776) (Marsh, 1980) and following the hypothesis of sexual dimorphism discussed by Sorbi et al. (2012) for *M. subapenninum*, both specimens could belong to male individuals.

The large tusk described herein backdates the evolution of large-sized tusks to the Late Miocene, and possibly also the emergence of *M. subapenninum*; this may have happened during the so-called “Tortonian Salinity Crisis” (7.8-7.3 Ma), which however is only recorded in southern Spain (Kouwenhoven et al., 2003). On the other hand, by evoking the possible coexistence between the dwarf species *M. serresii* and another congeneric large-tusked species, this new record calls into question the anagenetic trend previously proposed for the Euro-North African species of *Metaxytherium*. Further research on the intra- and interspecific tusk size variability across the Mediterranean record of *Metaxytherium* are needed to either corroborate or disprove the above hypotheses.

Paleoenvironmental and paleoecological remarks

Representing the first marine species to be ever recorded from the lignites of Montebamboli, the dugongid sirenian genus *Metaxytherium* comprises a significant addition to the mammalian faunal list from this celebrated locality. Montebamboli has previously yielded remains of the hominoid primate *Oreopithecus bambolii*, the lutrines *Paludolotra campanii* (Meneghini, 1863) and *P. maremmana* Hürzeler, 1987, the mustelid *Mustela majori* Weithofer, 1888, the ursid *Indarctos anthracitis* (a probable synonym of *Indarctos laurillardii* [Meneghini, 1863]), the bovids *Maremmia lorenzi* Hürzeler, 1983 and *Tyrhenotragus gracillimus* (Weithofer, 1888), and the suid *Eumaiocoerus etruscus* (Michelotti, 1861) (Meneghini, 1863; Gervais, 1872; Weithofer, 1888; Del Campana, 1918; Hürzeler and Engesser, 1976; Hürzeler, 1982, 1983, 1987; Ginsburg, 1999; Rook et al., 1999, 2006). Two rodents have also been reported from this locality, namely, the glirid *Anthracoqlis marinoi* Engesser, 1983 and the murid *Anthracomys majori* Schaub, 1938. The presence of the latter, coupled with the occurrence of *E. etruscus*, *M. lorenzi* and *T. gracillimus*, leads to correlate the Montebamboli fauna, as a whole, with the V2 faunal assemblage of Baccinello (Rook, 2016). The above mammals are indeed absent from V1, where less derived forms (e.g., *Maremmia haupti* [Weithofer, 1888]) and no suids are documented (Michelotti, 1861; Rook et al., 1999, 2006). As regards suids, they are part of a second wave of island colonizers from mainland Europe, differing from the bovids that would have arrived from Africa during the first colonization phase of the Tusco-Sardinian archipelago (leading to the formation of the V1 assemblage). From a paleoenvironmental point of view, *A. majori* from Montebamboli were probably strictly herbivorous and included a great proportion of grasses in its diet (Casanovas-Vilar et al., 2011). On the other hand, the presence of bovids such as *M. lorenzi* and *T. gracillimus*

suggests the presence of open and dry environments. This observation, supported also by isotopic analyses on dental enamel and on paleosoils (Matson et al., 2012; Nelson & Rook, 2016), is at odds with paleobotanical evidence (Gaudin & Strozzi, 1858; Harrison & Harrison, 1989) that suggests instead grass as a low-vegetational element of the Tusco-Sardinian paleobioprovince. However, according to Casanovas-Vilar et al. (2011), hypsodonty and enamel thickness in the Tusco-Sardinian mammals may not be related with dry and open environments but rather represent an adaptation to a specialized diet such as feeding on stems of aquatic plants. It is noteworthy that the suid *Eumaiocoerus* and the primate *Oreopithecus* are abundant at Montebamboli, thus suggesting the local presence of a swampy-marshy environment, contrary to the flood-dominated, fluvio-lacustrine sediments deposited near an uplifted delta plain in the Baccinello-Cinigiano Basin, where the two aforementioned taxa are absent or scarce (Benvenuti et al., 1999, 2001). The site of Montebamboli is also characterized by the presence of *Crocodylus bambolii* Ristori, 1890, a short-snouted crocodylian, which is also documented (as *Crocodylus* sp.) in the Apulo-Abruzzi paleobioprovince, but nowhere else in Europe (Delfino & Rook, 2008). This taxon is probably of African origin, thus suggesting a Tortonian longshore dispersal from North Africa, similar to the bovids. In spite of the substantial absence of marine taxa at Montebamboli, the discovery of a dugongid sirenian is in agreement with the general paleoenvironmental framework depicted by this peculiar vertebrate assemblage (however representative of the original oryctocoenosis). Indeed, extant dugongs are known as coastal-to-estuarine species, and the frequentation of brackish/freshwater environments has often been hypothesized for the extinct *Metaxytherium* species (e.g., Sorbi et al., 2012). That said, up to date, paleontological evidence for the presence of *Metaxytherium* in internal waters was, to our knowledge, limited to the Libyan record of *Metaxytherium serresii* from the Sahabi Basin (Domning & Thomas, 1987), where oxygen-isotope analyses indicate that these extinct sirenians were tolerant of hypersaline conditions (Clementz et al., 2009). Thus, by demonstrating the occurrence of a *Metaxytherium* tusk in a Late Miocene swamp or marsh of the Tusco-Sardinian archipelago, the present study strengthens the notion that this extinct genus of dugongids did also display some degree of freshwater tolerance.

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