**RESEARCH**

# An enigmatic giraffid from the latest Miocene of Italy: Taxonomy, affinity, and paleobiogeographic implications

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## Abstract

The origin and evolution of endemic species characterizing the *Oreopithecus*-faunal assemblages of the Tusco-Sardinian archipelago remain a matter of debate. An emblematic case is the enigmatic giraffid *Umbrotherium azzarolii*, represented by a single specimen from the type locality of Casteani (Tuscany) and by several isolated teeth and fragmentary mandibles from the locality of Fiume Santo (Sardinia). An exhaustive diagnosis of *Umbrotherium* has not been firmly established, and its systematic and phylogenetic position remain unresolved. Unpublished remains of giraffids, including an almost complete mandible, several isolated teeth, and other cranial remains are described for the first time in the present work. The specimens were collected from the locality of Botro della Canonica (Pisa), located at the northernmost portion of the Tusco-Sardinian archipelago. The new material sheds light on the morphological and morphometric variability of *Umbrotherium*, thereby enabling a comparison between specimens collected from different Tusco-Sardinian Miocene localities spanning from the V1 to the V2 *Oreopithecus*-Zone Faunas and allowing the establishment of the new species *U. engesserii* sp. nov. from Fiume Santo (Sardinia). This study also reveals that *Umbrotherium* was more closely related to *Decennatherium* than to other Late Miocene continental giraffids, suggesting a dispersal of its ancestor from the Iberian Peninsula. Accordingly, a new paleogeographic and biochronological framework is proposed herein for the Tusco-Sardinian archipelago, hypothesizing a fragmentation of the area into several domains, with sporadic reconnections, and the establishment of different faunal assemblages.

**Keywords** Morphology · Phylogeny · Island colonization · Giraffidae · Miocene

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## Introduction

Since the description of the *Oreopithecus* dental material (Gervais 1872), numerous studies have been aiming to investigate the evolution of fossil endemic mammals from the Late Neogene of the so-called Tusco-Sardinian archipelago, in the Western Mediterranean Basin (Weithofer 1888, 1889; Rook et al. 2000; Abbazzi et al. 2008; Rook 2016). Despite these efforts, no conclusive evidence has yet been provided that confidently addresses the debate about the origin of some of the species characterizing the *Oreopithecus*-faunal assemblages, such as the enigmatic giraffid-like *Umbrotherium azzarolii*. At present, the only occurrence of *U. azzarolii* is the type specimen from Casteani (around 8.3–7.7 Ma; V1 in the *Oreopithecus*-Zone Faunas) in Tuscany and from the slightly younger locality of Fiume Santo (ca. 7.1–6.7 Ma; V2 in the *Oreopithecus*-Zone Faunas) in Sardinia (Hürzeler and Engesser 1976; Rook et al. 2000, 2011; Abbazzi et al. 2008; Rook 2016). Despite the presence

of dentition and some postcranial elements, the identification of *Umbrotherium* as a giraffid has not been confirmed, and its systematic and phylogenetic position remained unresolved.

Archival research at the Natural History Museum of Basel (NMB) has enabled the rediscovery of an unpublished fauna from the latest Miocene lignite levels (V1) of Botro della Canonica (BC), 60 km south of Pisa, that contains the cranial remains of a giraffid. The new specimens are described here and compared with the type material from Casteani and the material collected from Fiume Santo to provide new considerations on the taxonomy and affinities of this endemic mammal and the relative paleobiogeographic implications.

## Geological and paleontological setting

The Upper Miocene sedimentary succession at the Baccinello-Cinigiano Basin (BCB) (southern Tuscany) is worldwide known due to the discovery of the peculiar hominoid *Oreopithecus bambolii*. This succession is characterized by four successive faunal assemblages, namely V0, V1, V2 and V3, that have yielded several mammal fossil species (Lorenz 1968; Engesser 1989). The V0 to V2 faunal assemblages belong to an endemic faunal complex (the so called "*Oreopithecus*-Zone Faunas [OZF]" sensu Bernor et al. 2001) with a high level of endemism, low taxonomic diversity, and a tendency for the development of hypsodonty (Hürzeler and Engesser 1976; Sondaar 1977; Engesser 1989; Casanovas-Vilar et al. 2011). The V3 faunal assemblage instead includes continental taxa with Eurasian affinities such as the genera *Hippotherium* and *Procapreolus* and the species *Pliorhinus megarhinus* (Lorenz 1968; Hürzeler and Engesser 1976; Engesser 1989; Rook et al. 2000, 2011; Rook 2016; Angelone et al. 2017; Pandolfi and Rook 2017; DeMiguel and Rook 2018; Pandolfi et al. 2020). The localities that yielded the giraffid remains, namely Casteani and Fiume Santo, belong to the V1 and V2 faunal assemblages, respectively. These two assemblages are rather similar in composition, but the V2 fauna includes new immigrants such as *Parapodemus* sp. II, *Eumaiochoerus etruscus*, as well as, most probably, *Indarctos anthracitis* (Rook et al. 1996, 2011; Benvenuti et al. 2001; Cirilli et al. 2016), suggesting a temporary reconnection with Europe (Benvenuti et al. 2001). Furthermore, the V2 fauna shows new species resulting from the in situ evolutionary transformation of locally endemic forms (Lorenz 1968; Hürzeler and Engesser 1976; Engesser 1989; Rook et al. 2000, 2011; Rook 2016; Angelone et al. 2017).

Archival research at the Natural History Museum of Basel allowed the collection of information about the provenance of some fossil large mammals from a locality at the northmost boundary of the Tusco-Sardinian Miocene paleobioprovince: Botro della Canonica (Pisa) (Fig. 1). This



**Fig. 1** Location of Botro della Canonica (Pisa) in Tuscany, and other latest Miocene localities mentioned in the text

locality was first mentioned by Del Campana (1918), who recorded the presence of a few isolated teeth of *Maremmia*; no other records or specimens were subsequently published from this locality. The name corresponds to a small creek located in the municipality of Montecatini Val di Cecina (Pisa), close to the medieval village of Sassa (Fig. 1). Fieldwork conducted at Botro della Canonica enabled the identification of the outcropping lignite level from which the fossils had been collected. The fossil assemblage is still under study, and it is characterized by the presence of Chelonia indet., *Oreopithecus bambolii*, *Etruria* sp., *Tyrrhenotragus gracillimus*, and *Maremmia haupti*. Overall, the fauna can be referred to the V1 faunal complex and can be biochronologically correlated with the well-known localities of Casteani, Montemassi, and Ribolla (Fig. 1).

## Materials and methods

The described material is stored in the Naturhistorisches Museum of Basel (NMB), and at the Department of Earth Sciences, University of Florence (DST). Comparisons were made with type material from Casteani, stored at the Natural History Museum, Geology and Palaeontology section, University of Florence (IGF); the specimens described by Abbazzi et al. (2008) and stored at "Soprintendenza Archeologia Belle Arti e Paesaggio per le Province di Sassari e Nuoro"; and Late Miocene representatives of fossil Giraffidae from both published papers (Geraads 1978; Hamilton

**Fig. 2** Dental nomenclature used in this work, adapted from Bärmann and Rössner (2011). From top to bottom: P4, M1, p2, m3
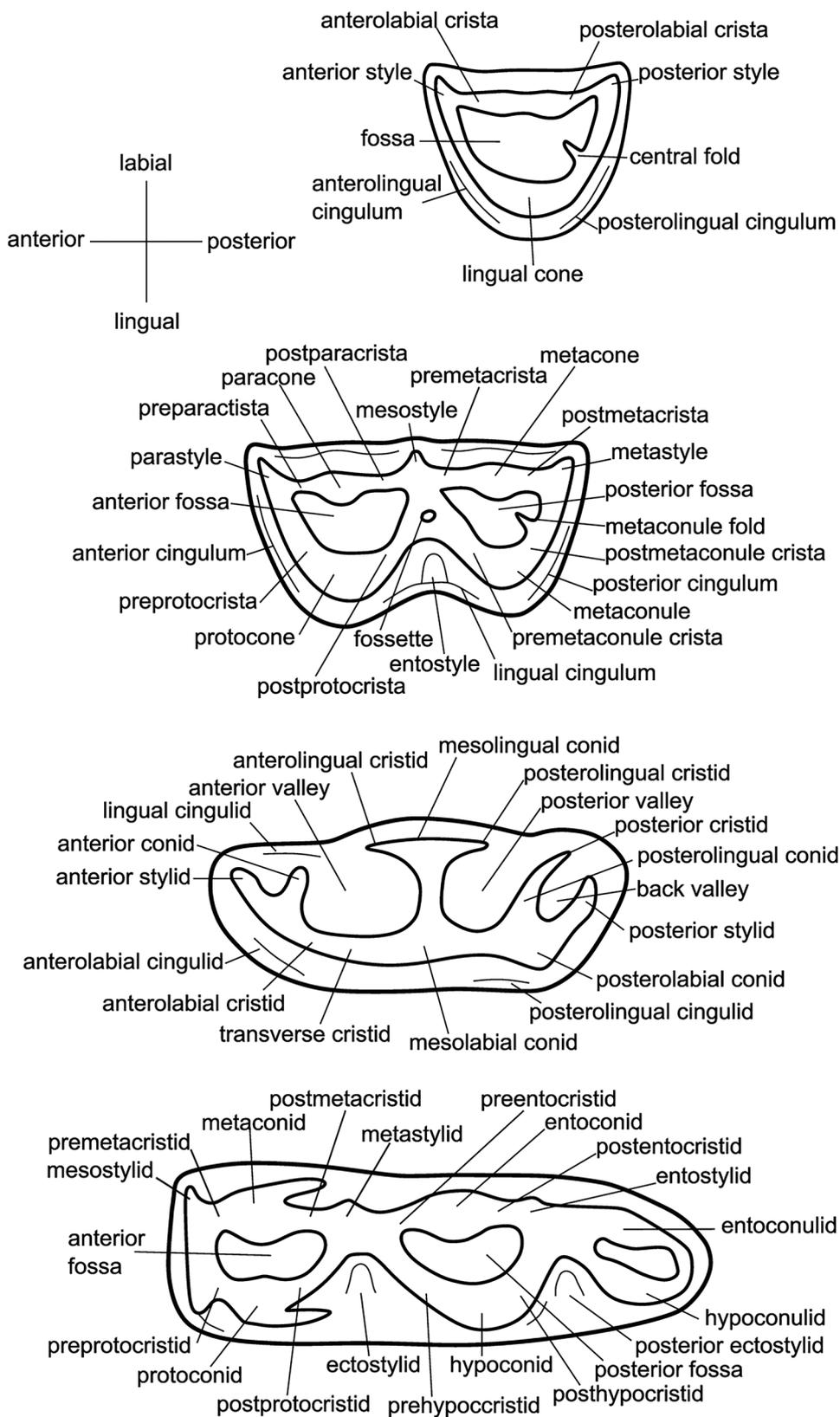
1978; Kostopoulos and Koufos 2006; Solounias 2007; Kostopoulos 2009; Ríos et al. 2017; Parizad et al. 2020; Iliopoulos and Roussiakis 2022; Laskos and Kostopoulos 2022), as well as personal observations. Dental nomenclature is based on a previous study by Bärmann and Rössner (2011) (Fig. 2). The studied specimens were measured with a digital caliper 0–150 mm/0.01, and the measurements are reported in Online Resource 1. Several of the studied specimens were acquired using the structured blue LED light 3D scanners Artec Eva and Artec Space Spider. A selection of downloadable 3D models is available in Online Resource 2.

**Institutional abbreviations**: **Bac**, Baccinello collection housed in the Naturhistorisches Museum, Basel; **DST-FS**, Fiume Santo Collection, provisionally housed at the Department of Earth Sciences, University of Florence; **FS**, Fiume Santo Collection, Soprintendenza Archeologia Belle Arti e Paesaggio per le Province di Sassari e Nuoro; **IGF**, Natural History Museum, Geology and Palaeontology section, University of Florence; **NMB**, Naturhistorisches Museum, Basel.

## Systematic paleontology

Artiodactyla Owen, 1868
Giraffidae Gray, 1821
*Umbrotherium* Abbazzi et al., 2008
1976 *Umbrotherium* Hürzeler & Engesser, p. 334 (*nomen nudum*)

**Type species.** *Umbrotherium azzarolii* Abbazzi et al., 2008

**Emended diagnosis.** Middle sized giraffid with fairly brachydont dentition. Markedly rugose enamel wall. P3 and P4 rectangular in outline, wider than long. Upper molars with a weak entostyle and cingulum. Mesostyle joins metastyle via a poorly developed cingulum; anterior lobes longer than posterior lobes. Angular lingual cones on upper molars. Parastyle well-developed on upper molars. Fusion of enamel folds between cones /conids, which occurs in very worn teeth. Bilobate lower canine with a posterior lobe smaller than the anterior one. The p4 molarized; angular lingual conids on lower molars.

*Umbrotherium azzarolii* Abbazzi et al., 2008
Figure 3
1888 *Antilope* (*Palaeoryx*?) sp. Weithofer, p. 365.
1889 *Antilope* (*Palaeoryx*?) sp. Weithofer, pp. 57, 62.
1918 *Antilope* (*Palaeoryx*?) sp. nov. Del Campana, p. 212, pl. 18.
1976 *Umbrotherium azzarolii* Hürzeler and Engesser, p. 334 (*nomen nudum*).

**Holotype.** IGF14615, an upper left series with P3–M2, Natural History Museum, Geology and Palaeontology section, University of Florence (Fig. 3a).

**Locality, horizon, and age.** Casteani (southern Tuscany), faunal assemblage V1; Late Miocene, late Tortonian, late Turolian, MN11.

**Other referred material.** NMB 306a16–3.10.93, a partial right maxilla with DP3–M1 (Fig. 3b); NMB 306a22, an isolated right P2 (Fig. 3c); NMB 306a22, an isolated right P3 (Fig. 3d); NMB 306a22, a right mandibular ramus (Fig. 3e); NMB 306a06, fragment of right mandible with



**Fig. 3** Late Miocene *Umbrotherium azzarolii* specimens from the Tuscan localities of Casteani (**a**) and Botro della Canonica (**b–f**). **a**. left P3–M2, type material of *U. azzarolii*, IGF14615 in occlusal view; **b**. right DP3–M1, NMB 306a16-3.10.93, in occlusal view; **c**. right P2, NMB 306a22, in occlusal (left) and labial (right) views; **d**. right P3, NMB 306a22, in occlusal view; **e**. right mandible with i1–m3, NMB 306a22, in lingual (upper), labial (middle) and occlusal (lower) views; **f**. right fragmentary mandible with p4–m3, NMB 306a21-31.7.98, in lingual (upper), labial (middle) and occlusal (lower) views. Scale bar equals 10 mm for **c** and **d**, and 20 mm for **a–b** and **e–f**
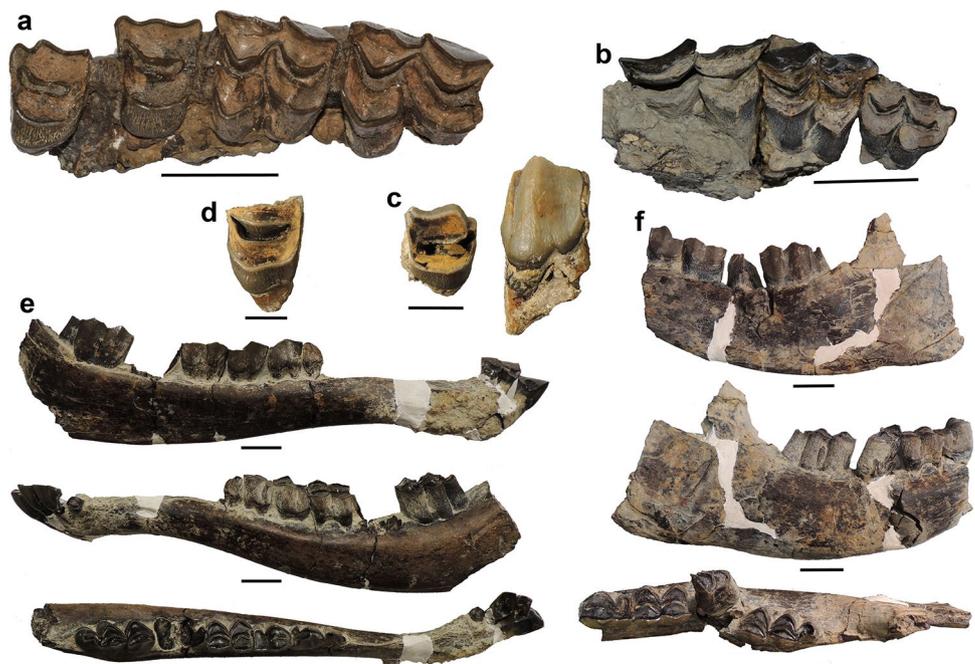
p2–m2 and fragments of m3; NMB 306a21-31.7.98, a partial right mandibular ramus with p4–m3 (Fig. 3f).

**Emended diagnosis.** Middle-sized ruminant with fairly brachydont dentition. Markedly rugose enamel wall. DP4 is fully molarized. Both DP3 and DP4 lack strong labial and lingual cingula. DP3 with strong and anterolabially directed parastyle, anterior and posterior lobes are lingually convergent. Protocone and hypocone are lingually V-shaped on DP4. P2 squared, with a posterolabial crista slightly concave, anterior and posterior styles prominent and developed till the base of the crown. P3 and P4 rectangular in outline, wider than long, with rounded lingual wall. The i1 larger than i2 and i3. Lower molars with the presence of ectostylids.

**Description.** The teeth have a markedly rugose enamel. DP3 (NMB306a16-3.10.93) is trapezoidal labially longer than lingually (Fig. 3b). There is a faint lingual cingulum below the lingual cones. The paracone fold and parastyle are well-developed. The preprotocrista reaches the parastyle; it is slightly backwards directed and the protocone is lingually rounded. The anterior fossa is bilobate in its anterior margin. The premetaconulecrista does not reach the postparacrista. The metaconule is lingually rounded. DP4 is complete and trapezoidal-shaped; the parastyle is well developed and anteriorly elongated; the paracone fold is more prominent than the metacone fold (Fig. 3b). A mesial cingulum is present. The mesostyle and the postmetacrista bend labially. The preprotocrista and parastyle are connected at this stage of wear, the protocone is V-shaped and asymmetric, whereas the metaconule is wide V-shaped. The postprotocrista is not connected with the premetaconulecrista. The premetaconulecrista and the postmetaconulecrista do not reach the labial cristae. M1 has a wide U-shaped labial profile of the posterior lobe, with the metacone fold faint (Fig. 3b). The paracone fold is slightly developed, and the labial profile of the anterior lobe is almost flat. The postmetacrista and the mesostyle are thin and bend labially. The parastyle is thin and long, almost reaching the metacone fold of DP4. The protocone and metaconule are V-shaped and the lingual cristae do not connect with the labial cristae. The postprotocrista and premetaconulecrista are separated. P2 (NMB306a22) is almost squared, slightly wider than long, with a wide and anteriorly located lingual cone (Fig. 3c). The fossa is long and narrow, and it bends labially on its anterior portion. A small enamel fold is present on the lingual-posterior margin of the fossa. The anterior and posterior styles are prominent and reach the base of the crown (Fig. 3c). The labial cone is large, and the posterolabial crista is slightly concave. P3 (NMB306a22) lacks the labial wall (Fig. 3d). The lingual cone is located on the anterior half of the lingual side of the tooth, and the lingual wall displays a faint groove on its posterior half. The fossa is long and narrow, and it bends anterior-labially on its anterior half. The right mandible NMB306a22 preserves the incisor corpus and the ramus

(Fig. 3e). The height of the ramus is regular and slightly increases below the m2–m3. The mental foramen is in the middle of the diastema (Fig. 3e). In dorsal view, the diastema has a sharp ridge, and the corpus is wider in its posterior portion. The incisor corpus preserves the c, i1, i2, and i3 (Fig. 3e). The i1 is spatulate and wider than i2 and i3, which are similar in size and rectangular-shaped. The c is asymmetric, with an anterior-labial side taller than the posterolabial one. The posterior lobe has a small cingulum on its labial-posterior side. On p2 (Fig. 3e), the anterior stylid is short and connected to the mesolingual conid by a straight anterolabial cristid. The anterior valley is relatively wide and concave in occlusal view. The p3 lacks a metaconid; the hypoconid and entoconid are fused and are obliquely oriented (Fig. 3e). The entoconid joins the protoconid. The labial wall of the hypoconid is relatively sharp. The anterior valley is wide and V-shaped in occlusal view. The p4 is molarized. The lingual wall of the metaconid is convex in occlusal view, whereas that of the entoconid is relatively flat (Fig. 3e). The anterior fossa is crescent shaped. The entoconid and hypoconid are connected at this stage of wear and the labial wall of the hypoconid is rounded. A small ectostylid is present on the labial side. The m1 is relatively worn out; the lingual cones are V-shaped and separated by a V-shaped groove; the hypoconid is asymmetric and more posteriorly placed while the protoconid is symmetric. The labial cones are slightly convex in occlusal view and are separated by a wide and faint groove. The anterior and posterior valleys are narrow and crescent shaped. The first and second lobes of the m3 resemble the m1, but the lingual cones are sharper. At this stage of wear, the protoconid is connected to the entoconid. The hypoconulid is rounded and well-developed. An ectostylid is present on m1 and m3.

NMB306a06 is a fragment of right mandible with p2–m2 and fragments of m3. The p2 is subtriangular in shape; the anterior stylid is evident and connected to the mesolingual conid by a straight anterolabial cristid. The mesolingual conid is large and posteriorly bifid at this stage of wear. The anterior valley is wide and regularly concave in occlusal view, while the posterior valley is narrow. The posterolabial and posterolingual conids are connected. The p3 is not molarized and lacks a metaconid, fusion has occurred between hypoconid and entoconid, the entoconid joins the protoconid; the paraconid and parastylid are well developed. The labial wall of the hypoconid is sharp and a deep, and a relatively wide labial groove divides the tooth into a small posterior lobe and a long and wide anterior lobe. The anterior valley is V-shaped in occlusal view. The p4 is molarized, with the metaconid in the form of an anterior–posterior wall, which joins the paraconid and lacks the transverse connection to the protoconid. A small anterior fossa is visible on the worn tooth. The entoconid and hypoconid are connected on the worn p4, and the labial wall of the hypoconid is rounded.

A deep groove in the labial side divides p4 into two unequal parts, anterior and posterior lobes, with the posterior one being strongly reduced. The m1 is much worn; the lingual conids are rounded and separated by a V-shaped groove; the hypoconid is asymmetric and more posteriorly placed, while the protoconid is symmetric. The labial conids are slightly convex in occlusal view. The anterior and posterior fossae have a crescent shape. The m3 on NMB306a06 preserves only the hypoconulid, which is rounded and well-developed, and the second lobe, with a sharp hypoconid and an almost lingually flat entoconid. The second and third lobes are lingually separated by a clear step and labially by a V-shaped groove. NMB306a21 is a fragment of right mandible with p4–m3 and a damaged m2 (Fig. 3f). The morphology of the teeth is similar to that of NMB306a22 and p4; m1 and m3 bear ectostylids.

**Remarks**. A link between the endemic *Sardomeryx* from Sardinia and *Umbrotherium* is discarded at present. *Sardomeryx* is smaller than *Umbrotherium* (Online Resource 1) and possesses some derived features, such as a tendency toward high crowned dentition and a shortened premolar toothrow (Mennecart et al. 2019). The non-molarized p3 is a feature that precludes a link to the Paleotraginae, but, according to Abbazzi et al. (2008), a primitive p3 is also documented in *Decennatherium* and *Helladotherium*, while according to Hamilton (1978) it is pretty common among many other giraffids. However, the deciduous teeth of *Helladotherium* and all other derived Sivatheriinae display labial and lingual cingula and well-developed folds and spurs (Colbert 1935; Geraads 1978, 1986; Hamilton 1978; Geraads and Güleç 1999; Kostopoulos and Koufos 2006; Kostopoulos 2009), contrary to *Decennatherium*, *Samotherium*, and palaeotragines, which display simpler morphology. The anterior lobe of DP3 is fully molariform in *U. azzarolii* and in *Samotherium* and *Decennatherium rex*, but not fully molariform in *Paleotragus* (Kostopoulos 2009; Ríos et al. 2017). In *S. boissieri*, the anterior and posterior lobes tend to converge lingually on DP3 (Kostopoulos 2009), similar to the specimen from Botro della Canonica. In *D. pachecoi*, as well as in *Umbrotherium*, DP3 has the premetaconulecrista that does not reach the postparacrista and the parastyle is strong; the anterior lobe is longer than the posterior one and both are lingually convergent (Morales and Soria 1981). DP4 is fully molarized in *Samotherium*, *Decennatherium*, *Paleotragus*, and *U. azzarolii*, whereas in *P. rouenii,* it has an angular lingual protocone and a feeble hypoconal spur. Both DP3 and DP4 are missing strong labial and lingual cingula in paleotragines, as well as in *U. azzarolii*. According to Kostopoulos and Koufos (2006) and Kostopoulos (2009), the large-sized *Paleotragus* species (*P. coelophrys*, *P. expectans*, and *P. quadricornis*) have a more labially placed parastyle on DP3, a functional style between protocone and hypocone on DP3–DP4, and a rounded lingual

protocone and hypocone on DP4. The P2 of *P. rouenii* is sub-squared, with a strong parastyle and paracone that fuse at the base of the tooth, and the protocone and hypocone are barely distinguished by a shallow groove, similar to the P2 from Botro della Canonica, while in *P. quadricornis* the parastyle is reduced (Kostopoulos 2009). The P2 of *Paleotragus* sometimes displays an enamel fold on the posterior part of the central fossa (Kostopoulos 2009). In *P. rouenii*, the P3 and P4 are similar in shape and lingually rounded, and *P. quadricornis* has an incipient lingual bilobation on both teeth, as also observed on the P3 from Casteani and Botro della Canonica. This feature also seems to be present in *Decennatherium rex* (Ríos et al. 2017). In *S. boissieri*, the parastyle and paracone are equally strong on the upper premolars. In *Samotherium* and *Decennatherium rex*, the P2–P3 are wider or slightly wider than long, almost rounded in shape, while in *D. pachecoi*, the P4 is longer than wide, and the labial cones are weak, similar to *Umbrotherium*. On the upper molars of *P. roueni*, the mesostyle is stronger than the parastyle, and in *P. quadricornis*, the upper molars have a rounded hypocone and protocone, contrary to *Umbrotherium*. The M1 in *D. pachecoi* has a strong parastyle, as observed for Botro della Canonica. Angular lingual cones are documented in *D. pachecoi* (Ríos et al. 2016, 2017), as are the non-molarized p3 and the very rugose enamel.

*Umbrotherium engesserii* sp. nov.
urn:lsid:zoobank.org:pub:47798A99-EC17-4701-94FA-B22226CA89FB
Figure 4
2008 *Umbrotherium azzarolii* Abbazzi et al., p. 434.

**Derivation of name.** Named in honor of Prof. B. Engesser, paleontologist at the Naturhistorisches Museum of Basel.

**Holotype.** FS1995#0342, a left partial mandible with p3–m3, figured in Abbazzi et al. (2008: text- fig. 8G-I), housed in the "Soprintendenza Archeologia Belle Arti e Paesaggio per le Province di Sassari e Nuoro".

**Locality, horizon, and age.** Fiume Santo (northern Sardinia), faunal assemblage V2; Late Miocene, late Tortonian, late Turolian, late MN12–earliest MN13.

**Other referred material.** Upper and lower teeth listed in Abbazzi et al. (2008: tab. 3) (Fig. 4a). DST-FS#03, left M2; DST-FS#07, right c (Fig. 4b); DST-FS#05, left p2; DST-FS#06, left m1; DST-FS#02, left m2; DST-FS#70, left unworn m3 (Fig. 4c); FS1995#0140, left worn m3 (cast) (Fig. 4d); DST-FS#01, left m3 (Fig. 4e); DST-FS#04, fragment of a third lobe of a left m3.

**Diagnosis.** Smaller species of the genus. P2 with a weak parastyle and a small and narrow lingual wall. All the lower premolars are shorter than *U. azzarolii*. Lower toothrow shorter than in *U. azzarolii*. Ectostylid absent on m1–m3. The lower molars display sharper entoconid and metaconid in lingual view than in *U. azzarolii*.

**Fig. 4** Late Miocene *Umbrotherium engesserii* sp. nov. specimens from the Sardinian locality of Fiume Santo. **a**. left mandible, type specimen FS1995#00, in occlusal (upper) and lingual (lower) views; **b**. right canine, DST-FS#07, in mesial (upper), middle (occlusal) and labial (lower) views; **c**. left unworn m3, DST-FS#70, in occlusal (upper) and labial (lower) views; **d**. left m3, FS1995#0140 (cast), in occlusal (upper) and labial (lower) views; **e**. left m3, DST-FS#01, in occlusal (upper) and labial (lower) views. Scale bar equals 5 mm for **b**, and 20 mm for all other specimens
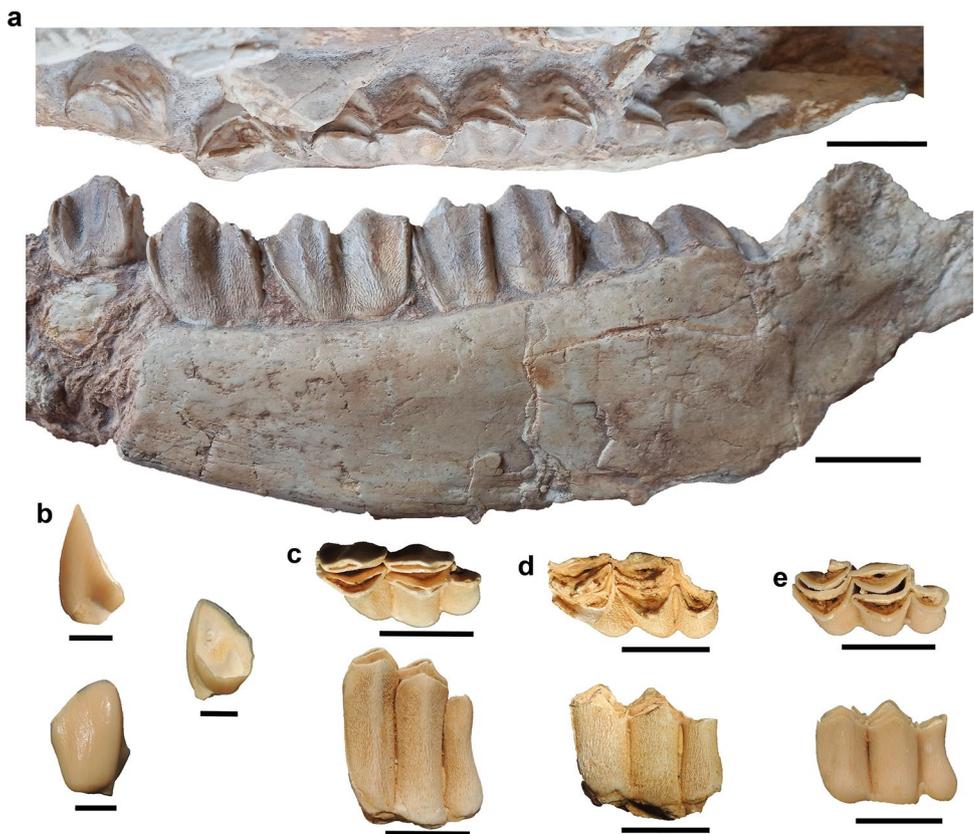


**Description.** The specimens were partially described by Abbazzi et al. (2008). Only a few characters can be added. The isolated canine is bilobate with a large anterior lobe and a small posterior one, similar to the specimen from Botro della Canonica. On P2, the parastyle is very weak; it does not reach the occlusal surface on little worn teeth and does not reach the base of the tooth. The lingual cone is small and posteriorly located on the lingual wall.

**Remarks**. The specimens from Fiume Santo exhibit the general *Umbrotherium* features but differ from the type species, being smaller (Online Resource 1; Fig. 5) and slightly morphologically different. In particular, the lower and upper teeth are more hypsodont than in *U. azzarolii* and have a simpler morphology with the absence of ectostylids on lower molars and a weaker parastyle on P2. The sharper lingual cones may be
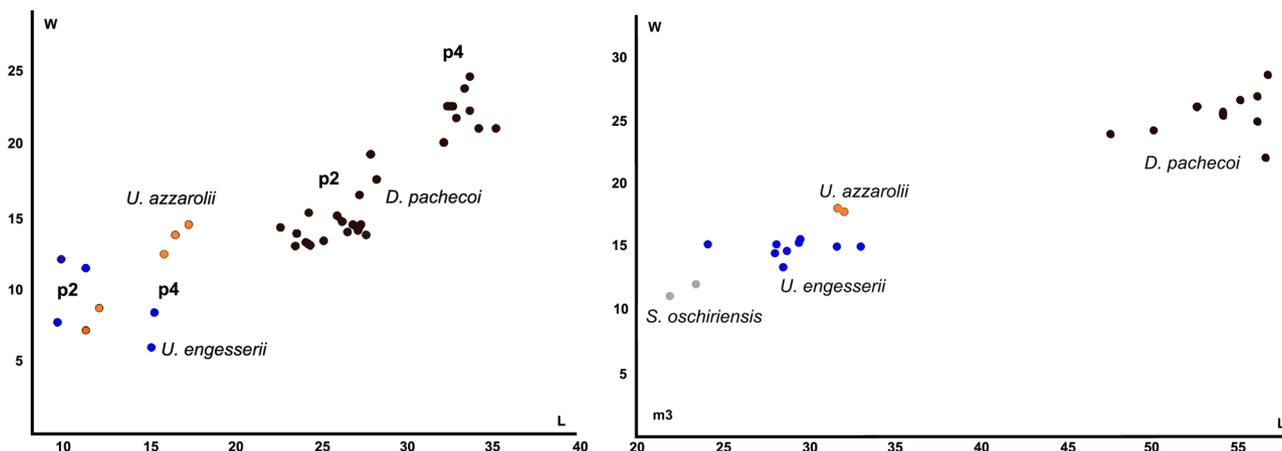


**Fig. 5** Scatterplot of p2 and p4 (left) and m3 (right) belonging to endemic giraffids from the Miocene of the Tusco-Sardinian area and *D. pachecoi* (data from Ríos et al. 2016; Online Resource 1). Abbreviations: **L**, occlusal length; **W**, maximal width. Dimensions in mm. Data are reported in Online Resource 1

related to an advanced degree of endemism (increase of hypsodonty), as observed in other taxa (Mennecart et al. 2019).

## Discussion

The remains originally referred to *Umbrotherium* by Hürzeler and Engesser (1976) were not formally described, rendering it a *nomen nudum* according to the ICZN (1999). In 2008, Abbazzi and coauthors provided an extensive description and formal definition of *Umbrotherium* based on fragmentary mandibles and isolated teeth collected from Fiume Santo (Abbazzi et al. 2008). The authors suggested an attribution to the Giraffidae family, despite the fact that the main diagnostic characters, such as the bilobate lower canines and ossicones, were not documented from either southern Tuscany or Fiume Santo. Unfortunately, the comparison between Fiume Santo and the type material from Casteani did not reveal any significant differences in morphology between the two samples, mainly because of the absence of lower dentition at Casteani. Furthermore, the differences in size within *Umbrotherium* were interpreted as sexual dimorphism by Abbazzi et al. (2008).

The abundant material from Botro della Canonica allows an extensive comparison with both Casteani and Fiume Santo, as well as a better comparison with other late Miocene European giraffids.

The presence of non-molarized p3s, the morphology of the upper premolars, and the morphological features detected on upper deciduous teeth suggest an affinity between *Umbrotherium* and *Decennatherium*, in particular *D. pachecoi*, rather than with *Palaeotragus* or *Samotherium*. Considering the common characters shared between *D. pachecoi* and *Umbrotherium*, we suggest a close relationship between these two taxa; however, further phylogenetic analyses would be helpful to validate this hypothesis. *Decennatherium pachecoi* is documented in the Iberian Peninsula during the Vallesian (mainly MN9–10), and the dispersal by the ancestor of *Umbrotherium* in Tusco-Sardinian archipelago should have taken place at least before or during the Vallesian, probably from the West (Fig. 6).

The upper permanent dentition from Botro della Canonica resembles the type material from Casteani both in proportions and morphology. The isolated P2 from Fiume Santo instead displays some differences with Botro della Canonica, showing a different degree of development of the parastyle and the lingual wall. The lower teeth from Fiume Santo also display some differences in size (in particular in the length of the toothrow),



**Fig. 6** Paleogeographic evolution of the northern Perityrrhenian area between the Serravallian and the Tortonian (modified from Benvenuti et al. 2001), with the dispersal routes of giraffids (white arrow) and the origin of the different endemic assemblages (V0–V1 and V2). Within the Tuscan domain, two subdomains are recognized: the Northern Tuscan subdomain and the Southern Tuscan subdomain. Abbreviations: **BCB**, Baccinello-Cinigiano Basin; **Bo**, Botro della Canonica; **Ca**, Casteani; **Fs**, Fiume Santo; **Mb**, Montebamboli; **Mm**, Montemassi; **R**, Ribolla; **Se**, Serrazzano. Dotted lines represent uncertain limits between land and coastal areas
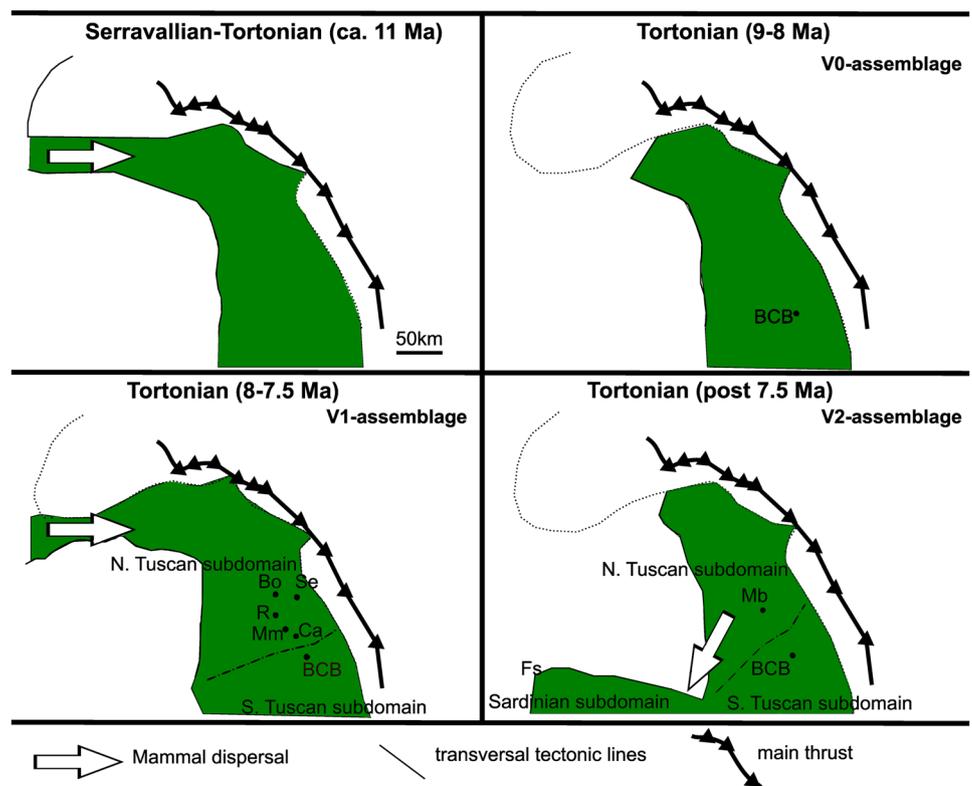
and a few differences in morphology, such as the absence of ectostylids. These characters can be related to a more advanced stage of endemism in the species from Fiume Santo and seem to be in agreement with the evolutionary transformation of endemic forms from V1 to V2 assemblages in the Tusco-Sardinian domain (e.g., *Paludolutra campanii* from *Tyrrhenolutra helbingi*, and *Maremmia lorenzi* from *Maremmia haupti*). The V2 assemblage from Fiume Santo is indeed characterized by species that show a more pronounced degree of endemic evolution with respect to the V1 assemblage from Tuscany. At Fiume Santo, the suid M3, referred to as *Eumaiochoerus* cf. *E. etruscus*, lacks the three grooves in the protocone and hypocone, and which are present and shallow in the paracone and metacone. These characters are interpreted as the result of increasing enamel thickness, a derived feature in suids under insular condition (Made 1999). The *Maremmia* from Fiume Santo resembles *M. lorenzi* from the V2 of Tuscany, but it appears to be slightly larger when compared with the material from Baccinello-Cinigiano. For this reason it was referred to as *Maremmia* cf. *M. lorenzi* (Abbazzi et al. 2008).

All this evidence suggests that the Fiume Santo assemblage could be intermediate between the classical V1 and V2 assemblages from Tuscany, but also suggests the existence of separated areas within the Tusco-Sardinian Paleobioprovince (Fig. 6). The new results obtained from the study of *Paludotona* highlighted the existence of a geographic barrier between the Fiume Santo area (Sardinian subdomain) and the Tuscany area (Tuscan subdomain), as was also hypothesized by Casanovas-Vilar et al. (2011). Furthermore, according to Angelone et al. (2017), morpho-dimensional differences between *Paludotona etruria* and *Paludotona minor* are indicative of a further fragmentation into two or more insular domains within the Tuscan subdomain (Angelone et al. 2017) as previously suggested by Engesser (1989) regarding the occurrence and intrageneric morphological comparison of *Anthracomys*. The fragmentation of the Tuscan subdomain may explain the absence of *Umbrotherium* in the Baccinello-Cinigiano Basin and its occurrences only in the northern part of the Tuscan subdomain (i.e., Botro della Canonica and Casteani) (Fig. 6). The presence of *Umbrotherium* at Fiume Santo is also suggestive of a temporary connection between the northern Tuscan subdomain and the Sardinian subdomain at the time of the arrival of *Eumaiochoerus*.

## Conclusion

New fossil material collected from the late Miocene of Tuscany and from the V1 assemblage at Botro della Canonica (Pisa) is described here for the first time. Most of this collection include cranial elements and isolated teeth belonging to the enigmatic giraffid *Umbrotherium*. Among the studied specimens, bilobate canines allowed a reference to the family Giraffidae, while deciduous teeth and new observations on upper and lower teeth allowed a linkage between *Umbrotherium* and the Iberian giraffid *Decennatherium pachecoi*. Furthermore, the new material from Botro della Canonica, together with that from Casteani, display a larger size and a different morphology with respect to the material collected at Fiume Santo, suggesting the presence of two endemic species with different levels of endemism: *U. azzarolii* from the Tuscan subdomain and *U. engesseri* sp. nov. from the Sardinian subdomain. The new results derived from the study of the Botro della Canonica giraffid would open up a new hypothesis regarding the colonization route of the Tusco-Sardinian archipelago and its paleogeographic structure. New fieldwork activities at Botro della Canonica and the revision of the material from the other Tuscan localities, such as Serrazzano and Montebamboli, are required for better investigation of the paleogeographic assessment of the area and the origin of other endemic mammals, such as the genera *Maremmia* and *Etruria*.

## Declarations

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