The Fossil Record of the Neogene Proboscidea (Mammalia) in Greece

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1 Introduction

The order Proboscidea is represented today by the largest living terrestrial mammals, the African savanna and forest elephants *Loxodonta africana* and *Loxodonta cyclotis*, respectively, and the Asian elephant *Elephas maximus*, which are all locally restricted and considered as threatened to extinction. The extant elephants are relics of a group that was once extremely diversified and widely distributed across Africa, Europe, Asia, and the Americas, especially during the Miocene (Shoshani and Tassy 1996a). Most proboscideans are characterized by the presence of tusks and molars of specialized morphology, making them easily recognizable in the fossil record and placing them among the most iconic vertebrates that have ever lived on this planet.

The earliest known proboscideans are *Phosphatherium* and *Daouitherium* from the Early Eocene of Morocco, at ~55.0 Ma (Gheerbrant et al. 1996, 2002). The cladistic position of *Eritherium* from the Late Paleocene (~60.0 Ma) of Morocco (Gheerbrant 2009) remains unresolved; it may be a stem proboscidean, or otherwise a sister group either to both Proboscidea and Sirenia or to all tethytherians (Gheerbrant et al. 2018). If *Eritherium* belongs to Proboscidea, then this species will represent the earliest proboscidean and will indicate a Paleocene emergence for the order. Since their appearance, the evolutionary history of proboscideans is marked by three major radiation events: (1) the Eocene radiation of primitive lophodont taxa, endemic in the, at that time, Afro-Arabian continent; (2) the Miocene

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radiation of gomphotheres sensu lato and stegodonts; (3) the Mio–Pliocene emergence of the family Elephantidae (Shoshani and Tassy 1996b). Not only the emergence and the subsequent first radiation of proboscideans took place in Africa, but also the other two radiations appear to have been triggered also in this continent (Sanders et al. 2010).

Proboscidean remains are common in the Neogene faunas of Greece, and especially during the late Miocene, including several taxa. They are present in almost all the large mammal fossiliferous sites of the country, with relatively abundant material. The Greek fossil record includes proboscideans from all three radiations. The first two radiations are presented in this chapter and comprise members of the families Deinotheriidae, Mammutidae, Amebelodontidae, Choerolophodontidae, Gomphotheriidae, and Stegodontidae; the third radiation of Elephantidae is the subject of the next chapter (Athanassiou this volume). For the sake of simplification, we use the informal name "Neogene proboscideans of Greece" for the taxa described in the present study, acknowledging however that the elephantid *Mammuthus* (presented in the following chapter) appeared in Greece during the late Pliocene and the fact that *Anancus*' biostratigraphic range extends to the Early Pleistocene.

2 Historical Overview

The presence of proboscideans in the Greek fossil record was recognized already from the first excavations that were carried out in the nineteenth century in the rich late Miocene vertebrate localities of Pikermi (Attica, discovered in 1836) and Samos [Aegean Sea; Forsyth-Major (1888, 1894)] and the beginning of the twentieth century in Axios valley (Central Macedonia, discovered in 1915–1916; Arambourg and Piveteau (1929)]. The first systematic studies on Miocene proboscideans included important material from these localities and were conducted, among others, by Wagner (1848, 1857), Gaudry (1862–1867), and Vacek (1877) for Pikermi; Forsyth-Major (1894), Schlesinger (1917, 1922), and Lehmann (1950) for Samos; and Arambourg and Piveteau (1929) for Axios valley ("Salonique"). These publications served (and still do) as a reference point for future research on Neogene proboscideans. In all of the abovementioned localities, the fossils occur in different stratigraphic levels from multiple quarries and unfortunately—as is the case with several historical collections—most of the fossils lack precise stratigraphic information. Subsequent important Miocene proboscidean specimens were studied in Paraskevaidis (1940) and Tobien (1980) from the middle Miocene of Chios Island, Melentis (1967, 1969) from the late Miocene of Halmyropotamos, Koufos (1980) from the late Miocene of Axios valley, Tassy (1985) from the late Miocene of Pikermi, Tsoukala and Melentis (1994) from Kassandra Peninsula in Chalkidiki, Koufos et al. (2003) from the early Miocene of Gavathas on Lesvos Island, Theodorou et al. (2003) from the late Miocene of Kerassia, Athanassiou (2004), Poulakakis et al. (2005) and Iliopoulos et al. (2014) from the late Miocene of Crete Island, and Lazaridis and Tsoukala (2014a) from the late Miocene of Kryopigi. Furthermore, the new series of excavations in Axios valley (started in 1972; Koufos

2013), Samos (started in 1993; Koufos and Nagel 2009), and Pikermi (started in 2009; Theodorou et al. 2010), as well as in Nikiti (started in 1990; Koufos and Kostopoulos 2016), which aimed in the discovery of new stratified and dated material, provided a wealth of specimens, including several proboscideans. Therefore, in the recent years the need has arisen for a complete revision and study of the taxonomy, biostratigraphy, and paleoecology of the Miocene proboscideans. This was part of the investigations of Konidaris (2013) and of subsequent studies (Konidaris and Koufos 2009, 2013a, 2016, 2019; Konidaris et al. 2014, 2016, 2017; Konidaris and Roussiakis 2019).

The Pliocene–Early Pleistocene sediments of Greece have been also intensively explored during the last decades. From this period, mammutids and gomphotheres are well-known from the recent excavations in Milia (started in 1996), which provided a wealth of proboscidean specimens (Tsoukala 2000; Tsoukala and Mol 2016) and in Sesklo (Symeonidis and Tataris 1983; Athanassiou 2016), but also from Apolakkia (Theodorou et al. 2000), Vatera (de Vos et al. 2002), and Gephyra (Crégut-Bonnoure and Tsoukala 2017).

The extensive and systematic fieldwork during the last decades in Greece has greatly increased the number of proboscidean specimens, which together with the specimens from the old collections, constitute a rich proboscidean sample. Recent advances in proboscidean taxonomy, along with biostratigraphic correlations and magnetostratigraphic calibrations, allow a more comprehensive classification and biostratigraphy of the Neogene proboscideans from Greece, which are presented in this chapter.

3 Phylogenetic Relationships

The order Proboscidea consists predominantly of fossil taxa, which complicates their classification and phylogeny, in particular of the early representatives. Based on recent findings and new cladistic analyses, Proboscidea together with the orders Sirenia (sea cows) and the Hyracoidea (hyraxes), as well as with the extinct Embrithopoda (e.g., *Arsinoitherium zitelli* from the Early Oligocene of Fayum in Egypt), belong to the clade of Paenungulata; in turn, proboscideans, sirenians, and Embrithopoda constitute the clade of Tethytheria (Gheerbrant et al. 2018) (Fig. 1). Anthracobunidae and Desmostylia, which were usually classified within tethytheres, are in fact related to Laurasian Euungulata and Perissodactyla (Cooper et al. 2014). Proboscidean synapomorphies include the well-developed zygomatic process of the maxillary, which contributes significantly to the ventral border of the orbit and to the zygomatic arch, the relatively large size of the *pars mastoidea* of the periotic, the hypoconulid in a labial position, and possibly also the loss of i3 and (d) p1 (Gheerbrant et al. 2005). Well-recognized proboscidean features, such as the large size, the presence of a trunk (proboscis), the huge-sized and pneumatized crania with retracted nasal apertures, the hypertrophy of the second incisors to form upper tusks, the graviportal stance, the shortening of the tooth row, the horizontal
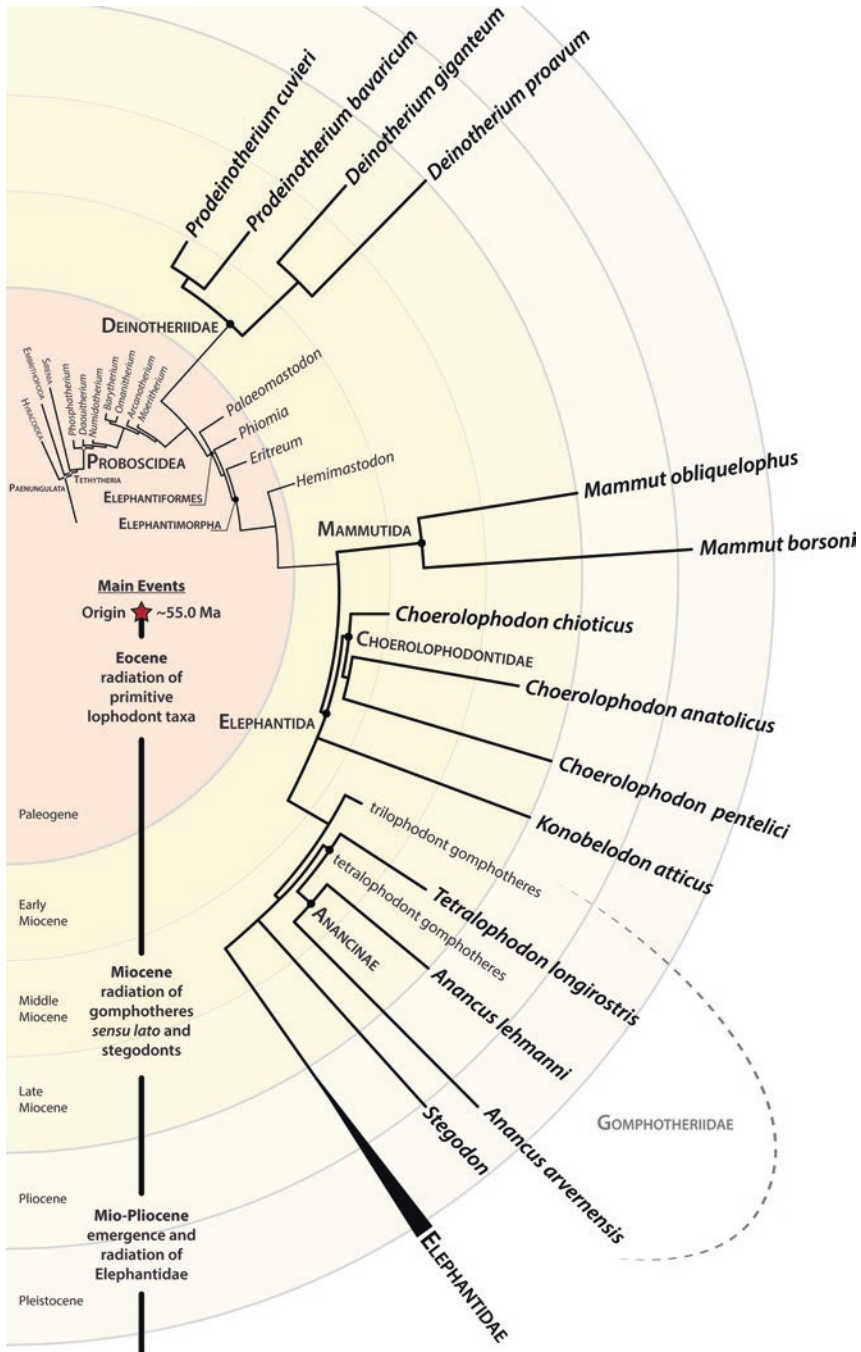
Fig. 1 Simplified cladogram showing the relationships of Paenungulata and Proboscidea based on Gheerbrant and Tassy (2009), Seiffert et al. (2012), and Gheerbrant et al. (2018)

tooth displacement, the reduction in the number of teeth with regard to the complete eutherian dentition, the enlargement and specialization of the cheek teeth, and the increase in the value of the encephalization quotient, constitute evolutionary trends within Proboscidea that evolved progressively since the Eocene (Shoshani and Tassy 1996a; Shoshani 1998, 2002; Gheerbrant and Tassy 2009; Sanders et al. 2010).

In this chapter, we mainly follow the classification proposed by Shoshani and Tassy (2005). However, we include choerolophodonts and amebelodonts in the families Choerolophodontidae and Amebelodontidae, respectively (Gheerbrant and Tassy 2009), and the tetralophodont gomphotheres *Tetralophodon* and *Anancus* of the family Gomphotheriidae in the subfamilies Tetralophodontinae and Anancinae, respectively (Sanders et al. 2010).

Focusing on the proboscidean taxa that are present during the Neogene of Greece, Deinotheriidae are more closely related to Elephantiformes, than to the more basal proboscideans (Fig. 1) based on dental features (e.g., presence of hypocone in P3 and P4 and the higher hypolophid than the protolophid in the lower molars) and postcranial traits (e.g., astragalus with long neck, enlarged lateral calcaneal facet, and reduced fibular facet) (Tassy 1994, 1996a; Gheerbrant et al. 2005). Deinotheres are unique within Proboscidea in lacking upper tusks and possessing strong and downward curved lower tusks (Gheerbrant and Tassy 2009). Apart from Deinotheriidae, all other proboscideans of the Greek fossil record belong to the monophyletic clade Elephantimorpha (Fig. 1). The monophyly of Elephantimorpha (*Eritreum*, *Hemimastodon*, Mammutida, Elephantida) is based among others on the "horizontal tooth displacement", i.e., a pattern of dental eruption, in which the cheek teeth during their use move anteriorly along the jaws and when they are completely worn, they are succeeded by teeth that emerge more distally, in a manner that is reminiscent of a "conveyor belt" (Tassy 1994, 1996a; Shoshani et al. 2006; Sanders 2018; Tassy 2018). Within Elephantimorpha, the family Mammutidae is defined by the zygolophodont molars, with sharper loph(id)s due to anteroposterior compression, and with presence of pretrite and posttrite zygodont crests instead of central conules (Tassy 1996a; Shoshani 1996).

The clade Elephantida includes taxa with bunodont molars, which are transformed into molars with lamellae in the families Stegodontidae and Elephantidae (Gheerbrant and Tassy 2009). The family Choerolophodontidae is distinguished by the fused mesoconelets and central conules and by the mesially pointed chevrons of the intermediate and third molars ("V," chevroning) formed by the more mesial position of the conelets in regard to the main cusps, especially in the distal lophids (Tassy 1996a; Sanders 2003; Konidaris et al. 2016). The straight medial border of the lower tusks and the posttrite conules on the molars are the distinguishing traits of the family Amebelodontidae; their most distinctive feature, the flattened lower tusks, is a plesiomorphic character present in *Phiomia* (Tassy 1996a; Shoshani 1996). The paraphyletic family Gomphotheriidae includes the trilophodont gomphotheres [with three loph(id)s in the intermediate molars] represented in Europe by the genus *Gomphotherium* and the tetralophodont gomphotheres [with four loph(id)s in the intermediate molars], which in Europe include the longirostrine

Tetralophodon (with rounded to pyriform lower tusks) and the brevirostrine *Anancus* (lacking lower tusks) (Tassy 1996a; Shoshani 1996).

4 Distribution

Neogene proboscidean remains are present in almost all the large mammal fossiliferous sites of Greece, from the northernmost regions of the country (e.g., Thermopigi, Dikaia) to the southern-most ones (Crete) and from the western ones (e.g., Milia, western Peloponnese) to the easternmost ones (Samos, Kos, and Rhodes Islands); they are present in both today's continental and insular Greece (Figs. 2 and 3). The earliest occurrence of Neogene proboscideans in the Greek fossil record is documented in the early Miocene of Gavathas (Lesvos Island) with the primitive deinothere *Prodeinotherium*, whereas their last occurrence is recorded in the Early Pleistocene of Vatera (Lesvos Island) with the gomphothere *Anancus* (Fig. 2). The taxonomic diversity reached its peak during the Turolian (late Miocene), when at least four proboscidean species have been recorded in Pikermi and Samos.
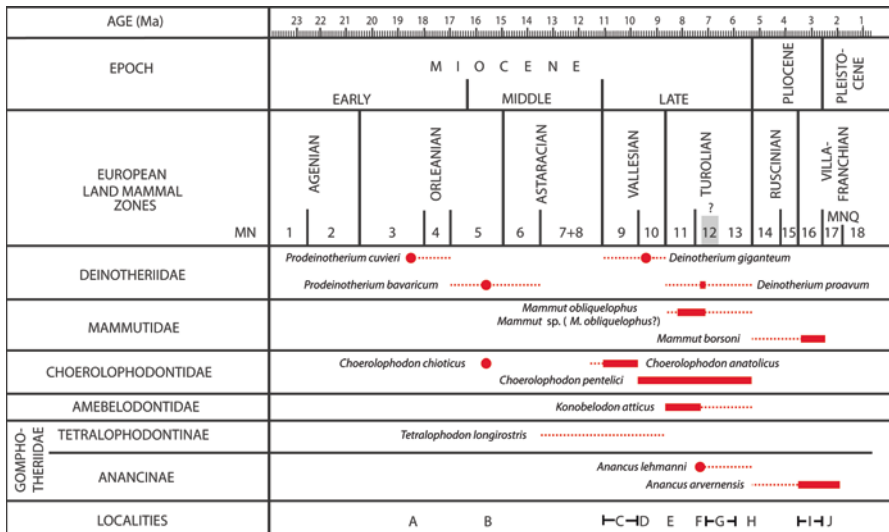

Fig. 2 Biostratigraphic distribution of the Neogene proboscideans in Greece. Solid lines indicate the biostratigraphic range of the species based on their occurrences in Greece; dots indicate single occurrences in Greece; dashed lines indicate the known biostratigraphic range based on data outside Greece; the top of MN12 is controversial and appears in grey. Selected localities with radiometric, biostratigraphical, or magnetostratigraphical data are also shown with letters: **A**, Gavathas; **B**, Thymiana; **C**, Pentalophos-1; **D**, Xirochori-1, Ravin de la Pluie; **E**, Nikiti-2, Ravin des Zouaves-5; **F**, Prochoma-1, Vathylakkos-2, Perivolaki, Pikermi, Pikermi Valley-1, 3, Mytilinii-1A, B, ?Halmyropotamos, ?Kerassia, ?Kryopigi, Chomateri; **G**, Dytiko-2, 3; **H**, Maramena; **I**, Milia, Sesklon, Gephyra; **J**, Vatera. Further details are given in the Appendix
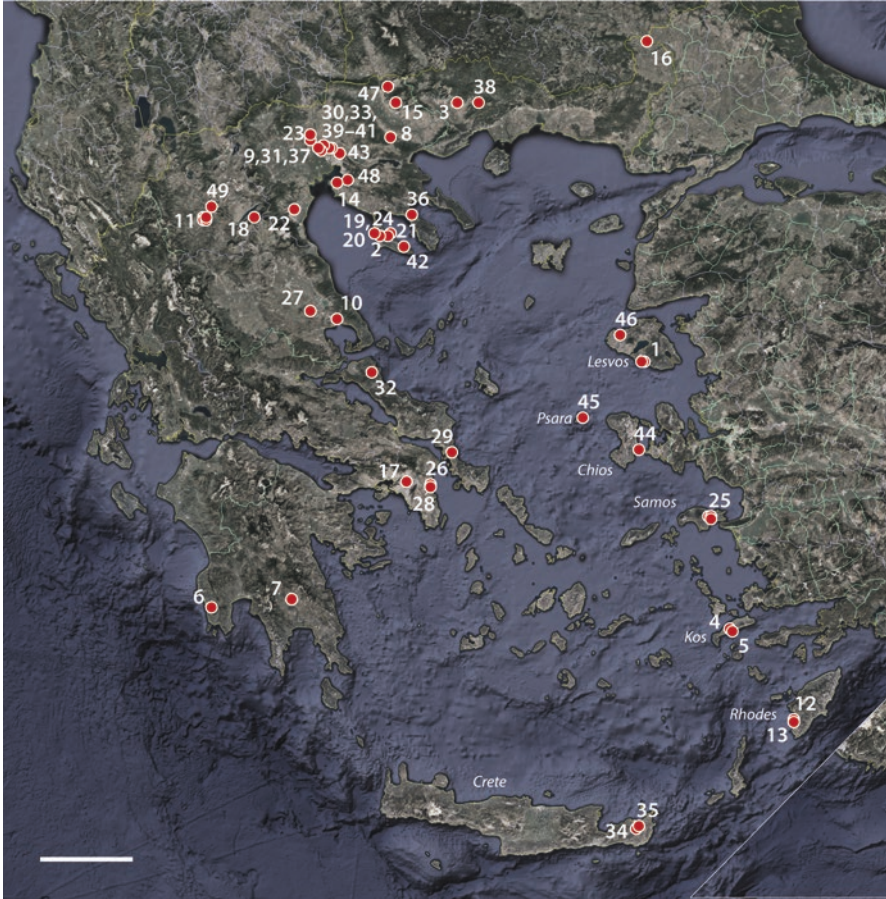
Fig. 3 Map of Greece showing the geographic distribution of the most important localities with Neogene and Early Pleistocene proboscideans. **1**, Vatera localities; **2**, Sani; **3**, Kalliphytos; **4**, Antimachia; **5**, Kardamaena; **6**, Pylos; **7**, Skoura; **8**, Nigrita; **9**, Gephyra-1; **10**, Sesklon; **11**, Milia localities; **12**, Apolakkia I; **13**, Apolakkia II; **14**, Agia Triada; **15**, Maramena; **16**, Dikaia; **17**, Pyrgos Vassilissis; **18**, Servia; **19**, Fourka; **20**, Chelona beach; **21**, sea bed of Kryopigi; **22**, Neokaisareia; **23**, Dytiko localities; **24**, Kryopigi; **25**, Samos localities; **26**, Chomateri; **27**, Perivolaki; **28**, Pikermi localities; **29**, Halmyropotamos; **30**, Prochoma-1; **31**, Vathylakkos locali- ties; **32**, Kerassia localities; **33**, Ravin des Zouaves-5; **34**, Maronia; **35**, Gela; **36**, Nikiti-2; **37**, Ravin X; **38**, Platania; **39**, Ravin de la Pluie; **40**, Xirochori 1; **41**, Ravin des Zouaves 1; **42**, Agia Paraskevi; **43**, Pentalophos 1; **44**, Thymiana; **45**, Psara; **46**, Gavathas; **47**, Thermopigi; **48**, Antonios; **49**, Siatista. See Appendix for more information. Image exported from Google Earth Pro © 2019, map data from US Dept. of State Geographer, SIO, NOAA, U.S. Navy, NGA, GEBCO, image from Landsat/Copernicus. Scale bar equals 80 km, North faces upward

Deinotheres present the widest biostratigraphic range, covering almost the whole Miocene (late MN3 until at least MN12), followed by choerolophodonts, which were present from the middle Miocene until the end of the late Miocene (MN5–13). *Choerolophodon* presents the widest temporal distribution among the genera in Greece, and where present, it is the dominant genus in terms of abundance.

5 Systematic Paleontology

Proboscidea Illiger, 1811
Deinotheriidae Bonaparte, 1845

Comments Deinotheres were specialized browsing proboscideans with low-crowned, tapir-like lophodont and bilophodont cheek teeth—apart from the trilophodont dp4/DP4 and m1/M1—and with a dental formulae 0.0.3/1.0.3 for the deciduous and 0.0.2.3/1.0.2.3 for the permanent teeth (Harris 1973; Sanders et al. 2010) (Figs. 3, 4 and 5). Deciduous dentition is replaced by the permanent one in a vertical manner, and all permanent cheek teeth are in function simultaneously. In this feature, as well as in other cranial, dental, and postcranial traits, deinotheres differ markedly from elephantimorphs. The most distinctive feature of deinotheres is the downcurved mandibular symphysis bearing the lower tusks, the latter emerging almost vertically, whereas they lack upper tusks (Harris 1973). Known from the Late Oligocene of Africa, where they persisted until 1.0 Ma, deinotheres have an evolutionary history of ~25.0 myr (Sanders et al. 2010). In Greece, deinotheres are known from several localities ranging from the early to the late Miocene and belong to the genera *Prodeinotherium* and *Deinotherium*. The original generic name *Deinotherium* Kaup 1829 (consisting of the Greek words δεινός = fearfully great, and θηρίον = wild animal/beast) is valid and not *Dinotherium* used subsequently by several authors (see also comment in Huttunen 2002). Accordingly, Harris (1973) emended the original name *Prodinotherium* Éhik 1930 to *Prodeinotherium*, which is justified and valid.

Prodeinotherium Éhik, 1930

Type Species *Prodinotherium hungaricum* Éhik, 1930.

Other Included Taxa *P. cuvieri* (Kaup, 1832a); *P. hobleyi* (Andrews, 1911); *P. pentapotamiae* (Falconer, 1868); *P. sinense* Qiu et al., 2007.

Distribution Early–early late Miocene of Africa, Europe and Asia.

Comments Based on the conservativeness and the minor evolutionary changes of deinotheres (apart from a gradual increase in size through time) several researchers recognize only *Deinotherium* as the valid European genus (e.g., Gräf 1957; Ginsburg and Chevrier 2001; Pickford and Pourabrishami 2013). Here we follow Harris

(1973), Huttunen (2002), and Aiglstorfer et al. (2014) and regard *Prodeinotherium* as a distinct genus from *Deinotherium*, based on several cranial, dental, and postcranial features. In Europe, *Prodeinotherium* includes the small and primitive deinotheres from the early until the middle Miocene (early Orleanian–early Astaracian, MN3–6). In Greece this genus is recognized with two species, *Prodeinotherium cuvieri* and *Prodeinotherium bavaricum*.

Prodeinotherium cuvieri (Kaup, 1832a)

Nomenclatural and Taxonomical History The species was erected by Kaup (1832a), who distinguished it from *Deinotherium giganteum*, based mainly on the smaller dimensions of the teeth from Chevilly (France) and Eppelsheim Formation (Germany). During the subsequent years and until today, the validity of this species is accepted by several authors (e.g., Ginsburg and Chevrier 2001; Pickford and Pourabrishami 2013), whereas others synonymize it with *Prodeinotherium bavaricum* (e.g., Gräf 1957; Huttunen 2002). The taxonomical status of the early Miocene deinotheres of Europe is not yet clarified and could be briefly summarized into the question whether *P. cuvieri*, *P. hungaricum*, or *P. petenyii* Vörös 1989 are conspecific or not, although the small dental dimensions of all three of them supports the synonymy; in this case, the type species of *Prodeinotherium* would be *P. cuvieri* (Markov 2008a: p. 144, footnote). Regardless of the specific name, dental dimensions and mandibular morphology (and perhaps also cranial and postcranial features) are in favor of a specific distinction from *P. bavaricum* (Markov 2008a).

Type Material MNHN-CHE 13 (lectotype), right and left mandibular fragments (Mayet 1908: pl. 8, figs. 3, 4).

Type Locality Chevilly, France, early Miocene, middle Orleanian, MN4.

Distribution Early Miocene (end of early Orleanian, late MN3) of Greece (Gavathas on Lesvos Island); early Miocene, middle Orleanian (MN4) of Hungary, Germany, France, and Spain.

Remarks This species comprises the smallest, earliest, and most basal deinotheres in Europe, known in Greece from a single occurrence of great importance. In particular, Koufos et al. (2003) studied tooth rows with permanent dentition from the locality Gavathas on Lesvos Island (Fig. 4), well-known for the Petrified Forest of Sigri. The authors noted that the dental morphology and the small dimensions of the Gavathas specimen indicate that it belongs to a primitive form of *P. bavaricum* (following the two European deinothere species concept of *P. bavaricum* and *D. giganteum*, accepted at that time). According to these observations and accepting here the validity of a distinct species from *P. bavaricum*—the valid name for which seems to be *P. cuvieri*—the Gavathas deinothere is provisionally attributed to *P. cuvieri*, pending complete revision of the primitive European deinotheres and new findings. The Gavathas deinothere, dated to as older than 18.4 ± 0.5 Ma (upper part of the

early Miocene, late MN3), documents the earliest occurrence of deinotheres in Europe (Koufos et al. 2003). As part of the complex "Proboscidean Datum Event," it marks the penetration of deinotheres into Europe (roughly together with the mammutid *Zygolophodon*, the gomphotheriid *Gomphotherium*, and the amebelodontid *Archaeobelodon*), after the establishment of the so-called *Gomphotherium* landbridge in the middle Burdigalian (~19.0–18.0 Ma, early MN3) (Tassy 1990; Rögl 1999; Antoine et al. 2003; Koufos et al. 2003).

Prodeinotherium bavaricum (von Meyer, 1831)
(=★*Dinotherium bavaricum aegaeum* Paraskevaidis, 1940)

Nomenclatural and Taxonomical History　The species was originally coined and described as a member of *Deinotherium* by von Meyer (1831, 1833). Almost a century after, it was transferred to *Prodeinotherium* by Éhik (1930). By being the oldest available name for the small and basal deinotheres, it has been considered by several authors (e.g., Gräf 1957; Bergounioux and Crouzel 1962; Huttunen 2002) as the senior synonym of the species *Prodeinotherium cuvieri*, *P. hungaricum*, and *P. petenyii* (but see above).

Type Material　SNSB-BSPG-AS I 220 (lectotype), right p3 (von Meyer 1833: pl. 34, figs. 12–15).

Type Locality　Georgensmünd?, Germany, middle Miocene, early Astaracian, MN6.

Distribution　Middle Miocene (late Orleanian, MN5) of Greece (Thymiana); middle Miocene (late Orleanian–early Astaracian, MN5–6) of Germany, Austria, France, Hungary, Slovakia, Spain, Bulgaria, Czech Republic.

Remarks　This species is well-known with abundant (mainly dental) material from several European localities, including at least two partial skeletons (Huttunen and Göhlich 2002; Huttunen 2004). In Greece its presence is documented with dental material from Thymiana (Paraskevaidis 1940), a vertebrate locality on Chios Island, bio- and magnetostratigraphically dated to ~15.5 Ma (middle Miocene, late Orleanian, MN5; Koufos 2006). Originally attributed to a new subspecies under the original spelling "*Dinotherium bavaricum* var. *Aegäum*," the dimensions and morphology of the teeth indicate that are within the intraspecific variability of *P. bavaricum* without the need for subspecific distinction (Besenecker and Symeonidis 1974). The species is also known from the nearby Psara Island with an isolated M1 (Besenecker and Symeonidis 1974).

Deinotherium Kaup, 1829

Type Species　*Deinotherium giganteum* Kaup, 1829.

Other Included Taxa　*D. bozasi* Arambourg, 1934; *D. indicum* Falconer, 1845; *D. levius* Jourdan, 1861; *D. proavum* (Eichwald, 1831).

Distribution Middle Miocene–Early Pleistocene of Africa, Europe, and Asia.

Comments The genus *Deinotherium* includes the large-sized deinotheres, and in Europe it is known from the middle until the late Miocene (late Astaracian–Turolian, MN7/8–13).

Deinotherium giganteum Kaup, 1829

Nomenclatural and Taxonomical History The species was erected and originally described by Kaup (1829, 1832a). Because it was the oldest available name for the large and derived deinotheres, it has been considered by several authors (e.g., Bergouniouz and Crouzel 1962; Huttunen 2002) as the senior synonym of the species *Deinotherium levius* and *D. proavum* (but for *D. levius* see: Gräf 1957; Ginsburg and Chevrier 2001; Böhme et al. 2012; Konidaris and Koufos 2019; and below for *D. proavum*).

Type Material HLMD-Din 466 (holotype), left hemimandible with tusk, m2–m3 and right mandibular fragment with symphysis and tusk fragment (Kaup 1832a: pl. 4, add. pl. 1, fig. 5).

Type Locality Eppelsheim, Germany, late Miocene.

Distribution Late Miocene (late Vallesian, MN 10) of Greece (Ravin de la Pluie); late Miocene, Vallesian (MN9–10) of Germany, Austria, France, Hungary, Spain, Bulgaria, and Turkey.

Remarks This species is well-known with abundant material from several European localities (mainly Germany, Austria, France, and Spain). In Greece it is rare, and known from only few localities and with limited specimens. Konidaris (2013) and Konidaris and Koufos (2013a) described an isolated p4 from the late Vallesian of Ravin de la Pluie in Axios valley, and Tsoukala and Melentis (1994) described an upper cheek tooth row from Agia Paraskevi in Kassandra, Chalkidiki.

Deinotherium proavum (Eichwald, 1831)

Nomenclatural and Taxonomical History The species was erected by Eichwald (1831, 1835) based mainly on the large dimensions of some teeth from Rakhny Lesovye (Ukraine). Several years later, Stefanescu (1892) coined another deinothere species with huge dimensions from Găiceana and Mânzaţi (Romania), which he named *D. gigantissimum*. During the subsequent years, although the species name *proavum* was used by several authors, it was mostly neglected in favor of *gigantissimum*, whereas others included these huge-sized deinotheres within *Deinotherium giganteum*. Nowadays, Turolian deinotheres are mostly accepted as a distinct species. Codrea (1994) pointed to the priority of Eichwald's species, which was further supported recently by Pickford and Pourabrishami (2013). Meanwhile, however, Kovachev and Nikolov (2006) erected *D. thraceiensis*, for the Ezerovo (Turolian;

Bulgaria) skeleton, yet its specific distinction is not supported by morphological and metrical data (Markov 2008b).

Type Material left p4 and m1 (holotype) (Eichwald 1835: pl. 60, figs. 1–5).

Type Locality Rakhny Lesovye in Podolia, Ukraine.

Distribution Late Miocene (Turolian) of Greece (Pikermi, Samos Island, Andriano, Halmyropotamos, Perivolaki, Maronia, Gela, Zakros, ?Kerassia); late Miocene (Turolian) of Austria, Spain, Germany, Hungary, Slovakia, Moldova, Ukraine, Romania, North Macedonia, Bulgaria, South Russia, Turkey, Afghanistan, Iran, Iraq (Konidaris et al. 2017).

Remarks During the Turolian, European deinotheres reached huge dimensions and are attributed to *D. proavum*. This species represents the terminal stage of the gradual increase in size characterizing the evolutionary history of deinotheres during the Miocene in western Eurasia. Diagnostic characters include, among others (see Tarabukin 1974; Markov 2008b; Pickford and Pourabrishami 2013; Konidaris and Koufos 2019), the large-sized cheek teeth (juvenile and permanent), the morphology of the dp2, and the strongly developed mandibular angle protruding beyond the ventral border of the horizontal ramus (Figs. 4 and 5). The species is well-known from eastern-southeastern Europe, from where several skeletons are documented (Romania, Moldova, Bulgaria, Russia, Greece). In Greece, *D. proavum* is known with the most abundant material among deinotheres. The most complete material is a partial skeleton from Gela in Crete (Fig. 5; Poulakakis et al. 2005; Iliopoulos et al. 2014). Pikermi, Samos, and Halmyropotamos yielded a very important collection of craniomandibular, dental, and postcranial remains, including a skull from Samos, which is the most complete juvenile deinotheriid skull so far in Eurasia and Africa (Konidaris et al. 2017; Konidaris and Koufos 2019) (Fig. 6).

Elephantimorpha Tassy and Shoshani in Shoshani et al., 1998
Mammutida Tassy and Shoshani in Shoshani et al., 1998
Mammutidae Hay, 1922

Comments The family includes elephantimorphs, whose cheek teeth are characterized by zygolophodonty (presence of yoke-like transverse crests), mesiodistally compressed and sharp transverse ridges, absence of accessory conules, and presence of zygodont crests (Tassy 1996a; Shoshani 1996). The intermediate molars remain trilophodont throughout the evolutionary history of the family (Tobien 1996). In Europe, two genera are present: *Zygolophodon* and *Mammut* (subfamily Mammutinae). The more basal *Zygolophodon* retains a more bunodont character on its cheek teeth, whereas in the more derived *Mammut*, the zygodont character is strongly developed (Tobien 1996). The family originated during the Late Oligocene in Africa, and migrated to Europe in the early Miocene, where it existed until the Pliocene. Mammutids migrated via the Bering Strait to North America during the

Fig. 4 Left tooth row with p3–m3 (cast of GVT-1) of *Prodeinotherium cuvieri* from the early Miocene of Gavathas, Lesvos Island (under permission from N. Zouros, copyright Natural History Museum of the Lesvos Petrified Forest). Scale bar equals 5 cm

Fig. 5 Right mandible with the lower tusk and p3–m3 (NHMC 21.4.2.27) of *Deinotherium proavum* from the late Miocene of Gela, Aghia Photia (under permission from C. Fassoulas, copyright Natural History Museum of Crete). Maximum anteroposterior diameter of the mandible: 1040 mm (Iliopoulos et al. 2014)
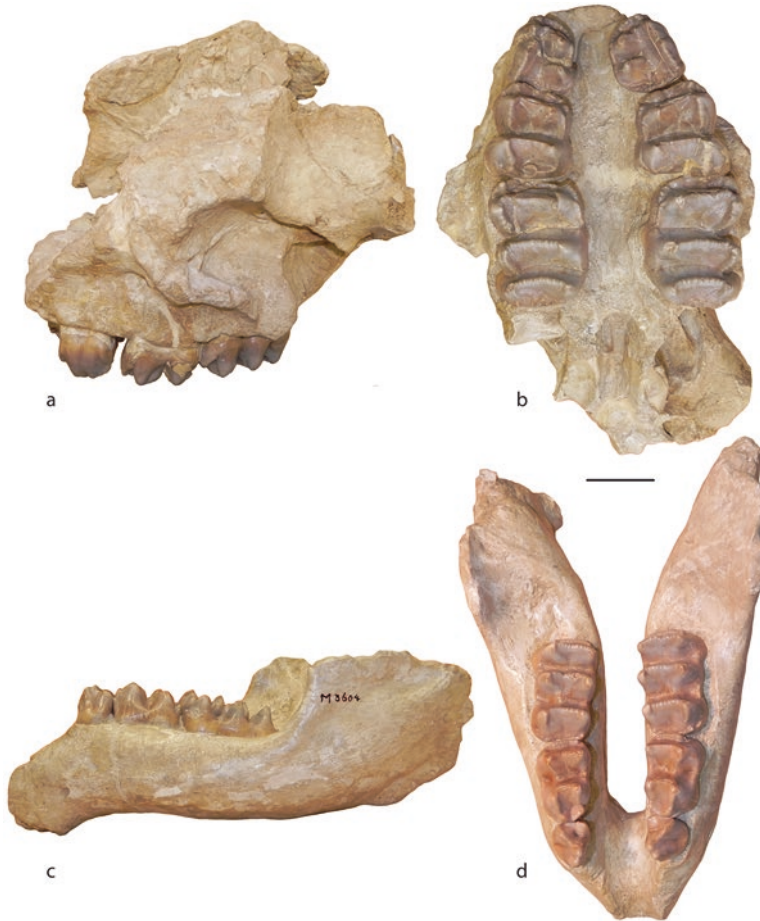
Fig. 6 Partial skull of *Deinotherium proavum* from the late Miocene (Turolian) of Samos (SMF-M 3604; copyright G. Konidaris). (**a–b**), cranium with DP2–DP4 of both sides, in left lateral and ventral view; (**c–d**), mandible with dp2–dp4 of both sides, in left lateral and dorsal view. Scale bar equals 5 cm

middle Miocene and persisted there until the Late Pleistocene (Saunders 1996). In Greece, although some occurrences have been previously attributed to *Zygolophodon*, the only so far representative of Mammutidae is *Mammut*. This genus is present in several localities ranging from the late Miocene to the late Pliocene.

Mammut **Blumenbach, 1799**

Type Species *Elephas americanus* Kerr, 1792.

Other Included Taxa *M. borsoni* (Hays, 1834); *M. matthewi* (Osborn, 1921); *M. obliquelophus* (Mucha, 1980); *M. pacificus* Dooley et al., 2019.

Distribution Late Miocene–Late Pleistocene of Europe, Asia and North America.

Comments Apart from the well-expressed zygolophodonty on the cheek teeth, the genus *Mammut* is characterized by its shortened mandibular symphysis with relatively small or even vestigial lower tusks and by its straight or upturned upper tusks that lack an enamel band (Fig. 6). In these features, it differs from *Zygolophodon*, which has a longer mandible with well-developed lower tusks, and downwardly curved upper tusks with an enamel band (Tobien 1996). In Europe, the genus is well-known from the Pliocene; however, its first representatives are recorded during the Turolian (late Miocene). It should be noted, however, that the generic name *Mammut* for the Eurasian representatives is in question, pending revision of the whole sample and comparison with the North American specimens (see discussion in Markov 2008b, and von Koenigswald and Göhlich 2019).

Mammut sp. [*M. obliquelophus*? (Mucha, 1980)]

Nomenclatural and Taxonomical History The species was erected by Mucha (1980) for a mammutid mandible from Romanovka (Ukraine). Markov (2008b) validated the species and included into it the skull remains from the Balta Sands in Podolia (Ukraine), which were attributed by Kubiak (1972) to *Mammut praetypicum* as well as material from other late Miocene localities (see discussion in Markov 2008b).

Type Material Paleontological Museum of Odessa State University, Nr. 3347, mandible with m2–m3 (holotype) (Mucha 1980: pl. 1).

Type Locality Romanovka, Ukraine.

Distribution Late Miocene (Turolian) of Greece (Pikermi, Mytilinii-1A-Samos, Ravin des Zouaves-5, Halmyropotamos, Neokaisareia, Palaio Keramidi), and from the late Miocene (Turolian) of Bulgaria, Hungary, Spain, North Macedonia, Moldova, Ukraine, Southern Russia, Spain, and China.

Remarks The late Miocene representative of European (and possibly also Asian) mammutids, *M. obliquelophus*, shows similar cheek tooth morphology as *Mammut borsoni*; however, the length of the symphysis and the size of the lower tusks are distinguishing features between the species: *M. obliquelophus* is characterized by a symphysis that is longer than the tooth row and equipped with well-developed tusks, whereas in *M. borsoni* the symphysis is much reduced and bears small tusks (Markov 2008b). Apart from the Neokaisareia partial skeleton (including an upper tusk) and the Palaio Keramidi molar of this taxon (Konidaris and Tsoukala 2020), the Greek material includes predominantly juvenile specimens (Pikermi, Ravin des Zouaves-5, Mytilinii-1A, Halmyropotamos), but it is very important, including two crania, two maxillae, two mandibles, and isolated teeth (Melentis 1967; Koufos 1980; Tassy 1985; Konidaris and Koufos 2009, 2013a; Konidaris 2013). Their

complete study is in progress, and we tentatively attribute here this material to *Mammut* sp. (*M. obliquelophus*?).

Mammut borsoni (Hays, 1834)

Nomenclatural and Taxonomical History Borson (1823) described and figured a tooth from Villanova d'Asti (Italy). Later on, Hays (1834), who had in his possession a cast of this tooth, erected the new species *Mastodon borsoni*. Osborn (1926, 1936) refers to the species as *Zygolophodon borsoni*, a binomen already used by Pohlig (1988). Meanwhile, however, Schlesinger (1922) already included the species within subgenus *Mastodon* (*Mammut*), currently elevated to the genus level.

Type Material MGPT-PU 14896 (holotype), right M3 (Borson 1823: pl. 2).

Type Locality Villanova d'Asti, Piedmont, Italy.

Distribution Late Pliocene (early Villafranchian, MN16) of Greece (Milia, Grevena) and various Pliocene localities (Ruscinian–early Villafranchian, MN14–MN16) of Europe and Asia; its presence during the middle Villafranchian (MNQ 17; Early Pleistocene) of Europe is insecure based on the current evidence.

Remarks The Borson's mastodon is best known from Milia, a locality which has yielded the richest and most important material of this species. The material consists of several partial skeletons and isolated skeletal elements, including two complete pairs of the longest upper tusks ever recorded in the world and the most complete mandible in Europe (Tsoukala 2000; Tsoukala and Mol 2016). The upper tusks are almost straight with a slight upward curvature and torsion, long but slender, they have almost circular cross-section, and they lack enamel (Fig. 7). The brevirostrine mandible bears rudimentary lower tusks of oval section and the molars show well-expressed zygolophodonty (Fig. 7a). *Mammut borsoni* is mentioned also from other localities in Greece, albeit with no precise stratigraphic information (see Appendix).

Elephantida Tassy and Shoshani in Shoshani et al., 1998
Choerolophodontidae Gaziry, 1976

Comments The family Choerolophodontidae includes bunodont trilophodont elephantimorphs, whose most distinctive dental features are the chevroning of the half-loph(id)s (mesially pointing chevrons, "V"), the choerodonty (multiplication of accessory conules), the ptychodonty (corrugated enamel), and the cementodonty (cement cover), with all these traits more-expressed in the later and more derived species. Other choerolophodont features include the upward curvature of the upper tusks that lack enamel, the long mandibular symphysis without tusks, and the strong development of the facial region of the cranium, which is elongated in comparison with the cerebral region. Choerolophodonts originated during the early Miocene, a period when they were distributed in northern/eastern Africa and South Asia.

Fig. 7 *Mammut borsoni* remains from the late Pliocene of Milia. (**a**), Mandible with lower tusks and m2–m3 of both sides (MIL 143), left ulna (MIL 141) and right tibia (MIL 142) from Milia 1; all belong to the same individual; (**b**), partial skeleton from Milia 5; (**c**), close view of the left (MIL 561) and right (MIL 560) upper tusks from Milia 5

Subsequently, during the end of the early Miocene–middle Miocene, they dispersed to Southeastern Europe and China, and possibly to North America. The last appearances of choerolophodonts are traced at the latest Miocene. In Greece, they are known from several localities ranging from the middle to the late Miocene.

★*Choerolophodon* **Schlesinger, 1917**

Type Species *Mastodon pentelicus* Gaudry and Lartet, 1856.

Other Included Taxa *C. anatolicus* (Ozansoy, 1965); *C. chioticus* Tobien, 1980; *C. corrugatus* (Pilgrim, 1913); *C. guangheensis* Wang and Deng, 2011; *C. kisumuensis* (MacInnes, 1942); *C. ngorora* (Maglio, 1974); *C. palaeindicus* (Lydekker, 1884); *C. zaltaniensis* Gaziry, 1987a.

Distribution Miocene of Europe, Africa, and Asia.

★*Choerolophodon chioticus* **Tobien, 1980**

Nomenclatural and Taxonomical History A complete skull from the middle Miocene of Thymiana on Chios Island (Greece), originally attributed to *Gomphotherium angustidens* (Tobien 1973), constitutes the holotype of *Choerolophodon chioticus*, erected by Tobien (1980). Pickford (2001), who studied cranial material from Kenya, erected the genus *Afrochoerodon*, in which he included

also the Thymiana specimen. According to Shoshani and Tassy (2005) *Afrochoerodon* constitutes a paraphyletic taxon placed within *Choerolophodon*.

Type Material AMPG-937 (holotype), cranium with I2, M1–M2, and erupting M3 of both sides, and associated mandible with m1–m2 and erupting m3 of both sides (Fig. 8).

Type Locality Thymiana, Chios Island, Greece, middle Miocene, late Orleanian, MN5.

Distribution Middle Miocene (late Orleanian, MN5) of Greece (Thymiana), and possibly from the middle Miocene of Turkey and Bulgaria.

Remarks *Choerolophodon chioticus* from Thymiana represents the earliest known choerolophodont in Europe. The skull is characterized, among others, by: moderate elongation, steeply inclined facial region and high cerebral region of the cranium; upper tusks that emerge downwards, then curve upward and at the tip inward; long and downwards deflected mandibular symphysis (Fig. 8); and, weak to moderate expressed choerodonty, ptychodonty, and cementodonty on the molars. The Thymiana cranium is less derived than the late Miocene choerolophodonts and closer to *C. kisumuensis* (Tobien 1980; Tassy et al. 1989; Pickford 2001; Konidaris et al. 2016). The distal fragment of an m3 from Thymiana, attributed by Paraskevaidis (1940: pl. 14, fig. 6) to *Trilophodon (Mastodon) angustidens*, possibly also belongs
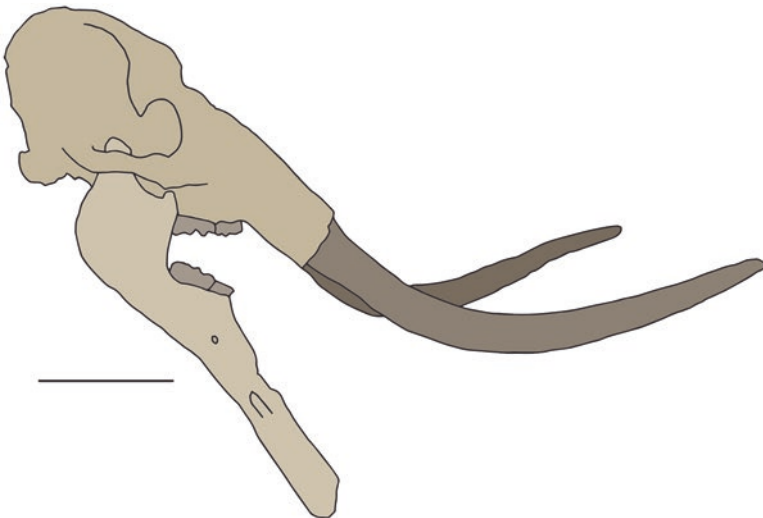

Fig. 8 Cranium with upper tusks, M1–M2 and erupting M3 of both sides, and associated mandible with m1–m2 and erupting m3 of both sides (holotype; AMPG-937) of *Choerolophodon chioticus* from the middle Miocene of Thymiana, Chios Island (copyright G. Konidaris). Scale bar equals 50 cm

to *Choerolophodon*. Study of additional material from Thymiana is in progress. Thymiana is bio- and magnetostratigraphically correlated to the middle Miocene (late Orleanian, MN 5), at ~15.5 Ma (Koufos 2006).

Choerolophodon anatolicus (Ozansoy, 1965)

Nomenclatural and Taxonomical History *Trilophodon* (*Choerolophodon*) *anatolicus* was erected as a new choerolophodont species by Ozansoy (1965) based on material from Yassiören (Middle Sinap, Turkey). However, in the subsequent years, the species was regarded as synonymous with *C. pentelici*, until Sanders (2003), who studied new material from the Sinap localities, re-established its validity. Sanders attributed to this species specimens from several other Turkish localities, including some of the material that had been attributed by Gaziry (1976) to *C. pentelici* and a mandible from Eşme Akçaköy assigned to *C. pentelici lydiensis* by Tassy et al. (1989) (see below). Recently, Konidaris et al. (2016) revised *C. anatolicus* and marked its presence for the first time outside Turkey in the Greek locality Pentalophos-1 of Axios valley.

Type Material MNHN-TRQ-1000 (lectotype), maxilla with right DP2–DP4 and left DP3–DP4.

Type Locality Yassiören, Middle Sinap, Turkey, early Vallesian, MN9.

Distribution Late Miocene (early Vallesian, MN9) of Greece (Pentalophos-1), and the late Miocene (early Vallesian–?late Vallesian, MN9–?10) of Turkey, and possibly of Moldova and Romania.

Remarks *Choerolophodon anatolicus* is diagnosed and differentiated from *C. pentelici*, among other characters, by the moderate retracted perinasal area in the cranium, the ventrally deflected mandibular symphysis in adult individuals, the small size of the deciduous teeth and the weak development of the distal cingulum in the DP3/dp3, which is connected to the second loph(id) (Sanders 2003; Konidaris and Koufos 2013a; Konidaris et al. 2016). The first and so far only record of *C. anatolicus* in Greece is traced in the early Vallesian locality Pentalophos-1 of Axios valley (Konidaris and Koufos 2013a; Konidaris et al. 2016). The material consists of juvenile and adult specimens (Fig. 9), which present more primitive morphology and smaller dimensions than the rest of the choerolophodont material from Axios valley, as well as from Pikermi and Samos, and are similar to those of *C. anatolicus* from Yassiören, Sinap 12 and Eşme Akçaköy (Turkey).

★*Choerolophodon pentelici* (Gaudry and Lartet, 1856)

Nomenclatural and Taxonomical History Gaudry and Lartet (1856) erected the species *Mastodon pentelici* based on proboscidean remains from the Turolian locality Pikermi. This material was subsequently studied in detail by Gaudry (1862–1867) (specimens of *Konobelodon atticus* were included in this study as

Fig. 9 Right mandibular fragment with m2–m3 (LGPUT-PNT-154) of *Choerolophodon anatolicus* from the late Miocene (Vallesian) of Pentalophos-1, Axios valley (copyright G. Konidaris). Scale bar equals 5 cm

well; see below), who emended also the species name *Mastodon pentelici*, although such a correction was not necessary (Tassy 1985: p. 617). Later on, Schlesinger (1917, 1922) studied choerolophodonts from Samos Island and Maragheh (Iran) and erected the subgenus *Mastodon (Choerolophodon)*, while Arambourg and Piveteau (1929) studied specimens from Axios valley. Since then, all the late Miocene choerolophodont material has been referred to this species without any distinction. Gaziry (1976) was the first, who recognized different evolutionary dental features within the late Miocene choerolophodonts of Turkey. Subsequently, Tassy et al. (1989) erected the subspecies *C. p. lydiensis* for an adult mandible from Eşme Akçaköy, a specimen, which was later transferred by Sanders (2003) to *C. anatolicus* (see above). From the fossiliferous sites of Kemiklitepe, Tassy (1994) identified two different evolutionary morphs, a primitive one in Kemiklitepe-D and a more advanced one in Kemiklitepe A-B. Recently, Konidaris (2013) examined all the choerolophodont material from Greece (old and new collections) and revised specimens from western Eurasia, and recognized the presence of two evolutionary stages within *C. pentelici*. In particular for Greece, "*C. pentelici* primitive" is correlated to the late Vallesian until possibly the early Turolian (MN10–?11; Xirochori-1, Ravin de la Pluie, Ravin des Zouaves-1, and from an unknown locality from the Turolian of Samos Island) and "*C. pentelici* advanced" from the Turolian (MN11–13; Pikermi, Samos Island, Mytilinii-1B-Samos, Andriano-Samos, Nikiti-2, Ravin des Zouaves-5, Prochoma-1, Vathylakkos-2, Ravin X and Dytiko-2, 3 (Konidaris and Koufos 2016, 2019; Konidaris et al. 2016).

Type Material MNHN-PIK-3665 (lectotype), juvenile cranium with right DP2–DP4, left I2 and left DP4, and associated mandible with right dp3–dp4 and left dp4 (Fig. 10a–d).

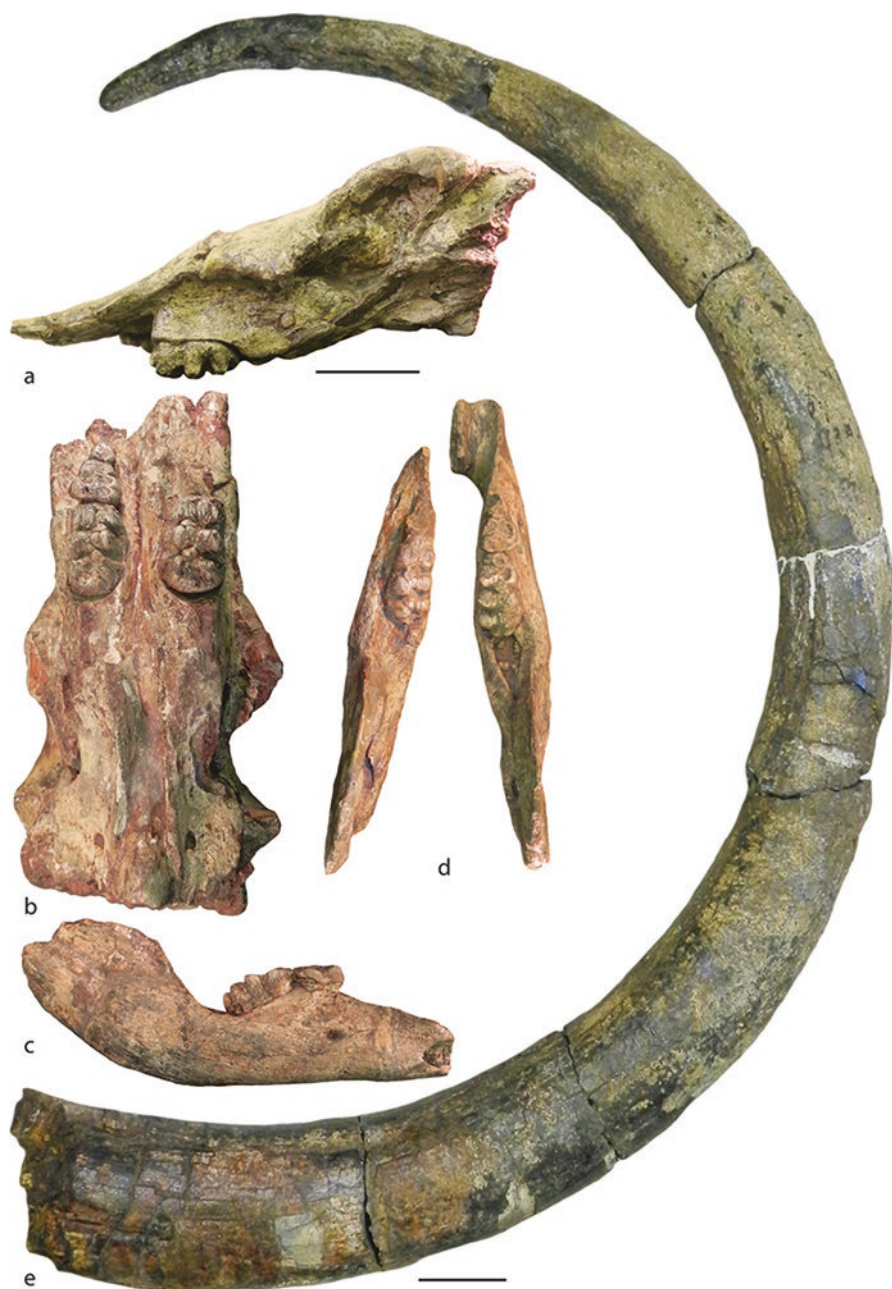**Type Locality** Pikermi, Attica, Greece, late Miocene, middle Turolian, MN12.

Fig. 10 (**a–d**), Juvenile cranium with right DP2–DP4, left upper tusk and left DP4, and associated mandible with right dp3–dp4 and left dp4 (lectotype; MNHN-PIK-3665) of *Choerolophodon pentelici* from the late Miocene (Turolian) of Pikermi; (**a**), left lateral view of the cranium; (**b**), ventral view of the cranium; (**c**), lateral view of the right hemimandible; (**d**), dorsal view of the mandible (copyright G. Konidaris); (**e**), right upper tusk (LGPUT-NIK-1776) in lateral view of *C. pentelici* from the late Miocene (Turolian) of Nikiti-2 (copyright G. Konidaris). Scale bar equals 10 cm

Distribution Late Miocene (late Vallesian–late Turolian, MN10–13) of Greece (Xirochori-1, Ravin de la Pluie, Ravin des Zouaves-1, Ravin des Zouaves-5, Nikiti-2, Prochoma-1, Vathylakkos-2, Pikermi, Mytilinii-1B, Samos Island-old collections, Andriano, Kerassia, Ravin X, Kryopigi, Dytiko-2, 3, Dikaia, Sani, ?Maramena, ?Pyrgos Vassilissis, ?Servia). Outside Greece it is known from the late Miocene (?late Vallesian–middle Turolian, ?MN10, MN11–12) of Turkey, Bulgaria, North Macedonia, Romania, Moldova, Iran, Iraq, and possibly in Ukraine and Azerbaijan.

Remarks The skull of *C. pentelici* is characterized, among other traits, by an elongated cranium with moderately inclined facial region and low cerebral region, orbits situated at the top of the cranium and far behind the last molar in function, retracted perinasal area and narrow nasal aperture, and mandibular symphysis situated ventrally at the extension of the corpus in both juvenile and adult specimens (Fig. 10a–d). The upper tusks emerge sub-horizontally and outwards and then curve upward (Fig. 10e). The deciduous teeth are large, the distal cingulum of the dp3/DP3 is well developed, and it is separated from the second loph(id) in the more advanced morphs. Choerodonty, ptychodonty, and cementodonty are well-expressed in the cheek teeth. The last appearance of *C. pentelici* is traced in the late Turolian (MN 13) localities of Dytiko in Axios valley (Konidaris et al. 2016). Schmidt-Kittler et al. (1995) note the occurrence of this species in the faunal list of Maramena (Serres basin), dated to the Miocene/Pliocene (MN13/14) boundary. If this occurrence is indeed *C. pentelici*, then the species survived until the uppermost Miocene.

Amebelodontidae Barbour, 1927

Comments The family includes predominantly bunodont trilophodont elephantimorphs (tetralophodonty in all intermediate molars has reached only the genus *Konobelodon*), commonly called "shovel-tuskers" due to the broadening and flattening of their lower tusks. However, the monophyly of the family is based on the straight medial border of the lower tusks and the posttrite conules on the molars (Tassy 1996a; see also Shoshani 1996). Based on the internal structure of the lower tusks, two groups of amebelodontids are distinguished: one with only concentric laminated dentine (*Archaeobelodon*, *Protanancus*, *Amebelodon*, *Serbelodon*, *Aphanobelodon*) and another with presence of tubular dentine or otherwise called dentinal rods (*Platybelodon*, *Torynobelodon*, *Konobelodon*) (Tassy 1986, 1996a; Konidaris et al. 2014; Wang et al. 2017a). The family originated during the early Miocene in Africa, but rapidly dispersed into Europe and Asia, and subsequently into North America; by the beginning of the Pliocene amebelodontids had vanished (Lambert and Shoshani 1998; Sanders et al. 2010). In Greece, amebelodontids are represented so far only by the late Miocene *Konobelodon*.

Konobelodon Lambert, 1990

Type Species *Amebelodon (Konobelodon) britti* Lambert, 1990.

Other Included Species *K. atticus* (Wagner, 1857); *K. cyrenaicus* (Gaziry, 1987b); *K. robustus* Wang et al., 2016.

Distribution Late Miocene of Europe, Africa, Asia, and North America; in Europe is known from the late Vallesian until the late Turolian.

Comments *Konobelodon* was originally erected as a subgenus of *Amebelodon*, which included the shovel-tuskers with tetralophodont first and second molars, and flattened lower tusks bearing internal dentinal rods from the late Miocene of North America (Barbour and Hibbard 1941; Gregory 1945; Lambert 1990) [we note here that the DP4, associated with fully tetralophodont M1 in the palate KUVP-3477 from the Rhino Hill site, Kansas, U.S.A. (Barbour and Hibbard 1941), albeit considerably worn shows an incipient fourth loph (GK observation on photos provided by C. Beard, University of Kansas); Mebrate (1987: p. 232) described the DP4 as trilophodont with a talon, Lambert (1990) mentioned it as trilophodont, while Lambert (pers. comm. 2020 to GK) as quasi-tetralophodont]. Lambert (1990) included also to the same genus/subgenus the Sahabi *Amebelodon cyrenaicus*—described by Gaziry (1987b) and considered a possible junior synonym of *Mastodon grandincisivus* by Tassy (1999) —whose lower tusk shows tubular dentine; trilophodont m1 and tetralophodont m2 were originally attributed to this taxon; however, it is uncertain whether these molars belong to the same taxon as the lower tusk (holotype) or each other (Markov 2008b; Sanders 2008). Konidaris et al. (2014) described juvenile mandibles from Pikermi belonging to a tetralophodont grade species bearing flat lower tusks with tubular dentine, as well as an adult large lower tusk with flattened-pyriform cross-section and internal dentinal rods. The upper and lower deciduous premolars (some of the lower ones associated with flat lower tusks) are both morphologically and metrically similar to those of *Mastodon atticus* (Wagner 1857; Gaudry 1862–1867; usually attributed to *Tetralophodon atticus*), and the adult lower tusk is morphologically and metrically similar to the holotype of *Mastodon grandincisivus* from Maragheh (Iran; Schlesinger 1917). Konidaris et al. (2014) revised the tetralophodont material from Pikermi (see below), noting the similarities with the lower tusks from North America, and proposed the elevation of *Konobelodon* to generic level, the synonymy between *Mastodon atticus* and *Mastodon grandincisivus*, and the inclusion of all the Turolian tetralophodont shovel-tuskers from western Eurasia to *Konobeledon atticus*. New tetralophodont amebelodontid material from China, including juvenile specimens (with striking morphological resemblance to the deciduous premolars from Pikermi, including the holotype of *Mastodon atticus*) and adult mandibles preserving the flattened lower tusks with internal dentinal tubules (Wang et al. 2016), corroborates further the attribution of the Pikermi tetralophodont material to an amebelodontid. Tassy (2016) suggested that the paratype of *K. britti* is similar to the holotype of *Torynobelodon loomisi* Barbour 1929 [*Torynobelodon* is considered a junior synonym of *Platybelodon* in Shoshani and Tassy (1996b: app. A)] and therefore that *Konobelodon* is a junior synonym of *Torynobelodon*; *Konobelodon atticus* should thus be *Torynobelodon atticus*. However, the tusk of *T. loomisi* has different cross-sectional

shape from the tusk of *K. britti*, as well as from those of *K. robustus* and *K. atticus*, e.g., from Pikermi, Maragheh and Pestszentlörinc (Hungary), having wide and straight medial border, roughly the same width in the middle and lateral parts, and with very shallow dorsal and ventral concavities. Moreover, it is unknown whether the tusk of *T. loomisi*, which is so far the single known specimen of this species, belonged to a trilophodont or tetralophodont grade species. Consequently, the current evidence does not support the synonymy between *Konobelodon* and *Torynobelodon*, and they should be considered distinct genera. Finally, the coexistence between a tetralophodont amebelodontid (here *Konobelodon*) and a derived tetralophodont taxon, such as that found in the Turolian of Crevillente 2 [Spain, Mazo and Montoya 2003; possibly related to *Stegotetrabelodon* (Tassy 2016)], or *Stegotetrabelodon* (present in the Turolian of Cessaniti, Italy; Ferretti et al. 2003), both having oval/sub-circular cross-sections with lamellar dentine in their lower tusks, cannot be excluded for Pikermi or other Turolian localities of the wider region, as discussed by Tassy (2016). Nonetheless, such evidence is so far not recorded in the Turolian of the Greco-Iranian-Afghan (*sensu* Bonis et al. 1992; Balkano-Iranian or Sub-Parathethyan) paleobiogeographic province.

★*Konobelodon atticus* (Wagner, 1857)

Nomenclatural and Taxonomical History   The type locality of the tetralophodont amebelodontid *K. atticus* is Pikermi, from where the richest material of this species is known. The species has a long and complicated taxonomical history. The presence of tetralophodonts in Pikermi was recognized early by Wagner (1857), who described a juvenile maxilla and erected the species "*Mastodon atticus* G. and L." However, Wagner (1857) attributed *Mastodon atticus* to Gaudry and Lartet (1856), but as noted by Gaudry (1862: p. 142 footnote), the only bunodont proboscidean referred by Gaudry and Lartet (1856: p. 273) was the trilophodont *Mastodon pentelicus* (= *Choerolophodon pentelici*). Few years later, Lartet (1859) transferred the Pikermi tetralophodonts to *Mastodon longirostris* (= *Tetralophodon longirostris*). Gaudry (1862–1867) included all bunodont proboscideans from Pikermi (tri- and tetralophodonts) to *Mastodon pentelici*. Subsequently, Vacek (1877: p. 32, pl. 7) attributed a third molar from Pikermi to *Mastodon atticus*, which was transferred to *Stegotetrabelodon grandincisivus* by Tobien (1978). The tetralophodont material of Wagner (1857) and Gaudry (1862–1867), as well as that described by the latter author as *Mastodon turicensis*, was included in the zygodont taxon *Turicius atticus* by Osborn (1936). More recently, Tassy (1985) referred the tetralophodonts of Pikermi to *Tetralophodon atticus*, although he later questioned this generic attribution (Tassy 2005). Konidaris et al. (2014) studied all the published tetralophodont material from Pikermi, as well as previously unpublished material from the locality originating from the old excavations, and attributed them to the amebelodontid *Konobelodon atticus* (see discussion above).

Type Material   SNSB-BSPG-AS II 182 (holotype), left maxillary fragment with DP2–DP3 (Fig. 10a).

Type Locality Pikermi, Attica, Greece, late Miocene, middle Turolian, MN12.

Distribution Late Miocene (Turolian) of Greece (Pikermi, Samos-old collections, Kerassia-4, and possibly from Platania). Outside Greece, it is known from the late Miocene (Turolian, MN11–13) of Turkey, Bulgaria, Moldova, Ukraine, Hungary, North Macedonia, and Iran.

Remarks The species is characterized, among other features, by the tetralophodont intermediate molars, the enlarged third loph in the DP3 with posttrite-pretrite connection in both transverse valleys and well-marked second ento-/ectoflexus (Fig. 11a), the large-sized and dorsoventrally flattened-pyriform adult lower tusks that have thin concentric laminated dentine layer externally and tubular dentine internally (Fig. 11b), and by the long and high mandibular symphysis (Konidaris et al. 2014). Apart from Pikermi, the species is known from Samos, Kerassia-4 and possibly from Platania (Lehmann 1950; Theodorou et al. 2003; Konidaris et al. 2014; Konidaris and Koufos 2019; Konidaris and Tsoukala 2020). It is well distributed from the early until the late Turolian of eastern Europe-western Asia and in Greece, in particular, is present possibly from the Vallesian/Turolian boundary (Platania) until the middle Turolian (Pikermi).

Gomphotheriidae Hay, 1922

Comments This paraphyletic family includes the bunodont trilophodont and tetralophodont elephantimorphs, excluding the choerolophodontids and amebelodontids, and constitutes the most diverse family within Elephantimorpha. By the early Miocene, the primitive *Gomphotherium* "*annectens* group" had already a cosmopolitan distribution in Africa, Europe, and Asia (Tassy 1996b); during the middle Miocene, gomphotheriids entered North America and persisted in South America until the beginning of the Holocene (Lambert and Shoshani 1998; Mothé et al. 2017). In Europe, gomphotheriids are represented by the trilophodont *Gomphotherium* and the tetralophodonts *Tetralophodon* and *Anancus*. In Greece, only tetralophodont gomphotheres are known so far.

Tetralophodontinae van der Maarel, 1932
***Tetralophodon* Falconer, 1857**

Type Species *Tetracaulodon longirostre* Kaup, 1832b.

Other Included Species *T. euryrostris* Wang et al., 2017b; *T. xialongtanensis* (Chow and Chang, 1974).

Distribution Middle–late Miocene of Europe, Asia, and Africa.

Comments *Tetralophodon* includes tetralophodont gomphotheres with long mandibular symphysis bearing pyriform to oval in cross-section lower tusks (in contrast to the brevirostrine and tuskless *Anancus*), consisting of concentric lamellar dentine
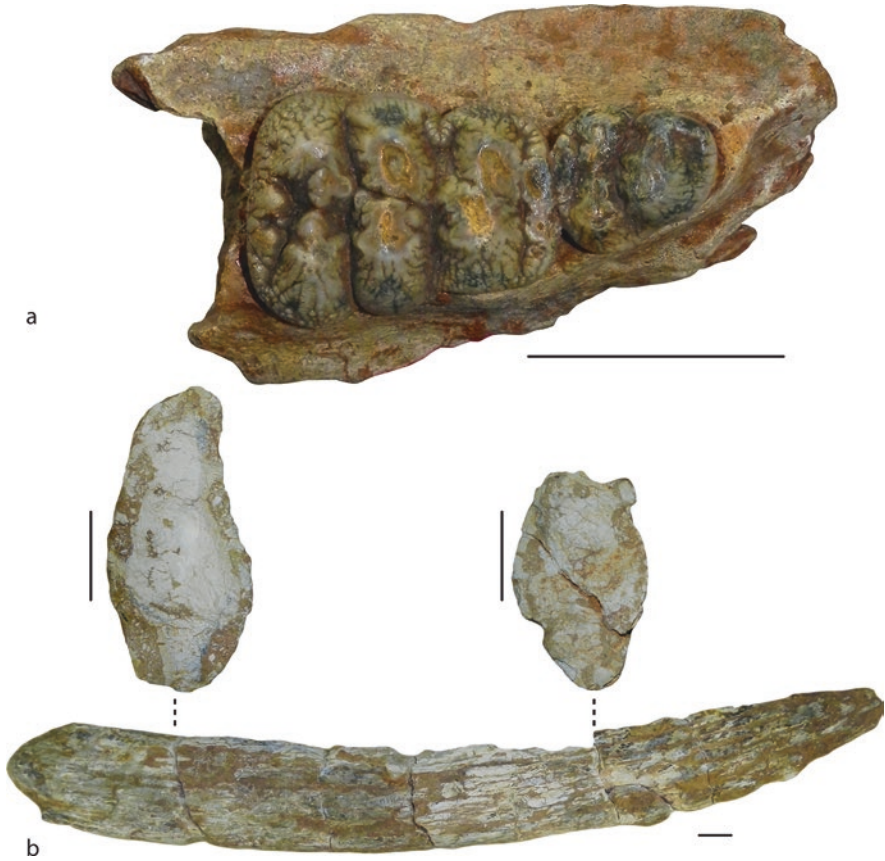
Fig. 11 *Konobelodon atticus* from the late Miocene (Turolian) of Pikermi. (**a**), Left maxilla fragment with DP2–DP3 (holotype; SNSB-BSPG-AS II 182) (copyright G. Konidaris), (**b**), right lower tusk (AMPG-PA1972/61) in ventral view with cross-sections (copyright G. Konidaris). Scale bars equal 5 cm

(no dentinal rods like *Konobelodon*), intermediate molars, and third molars that show trefoil wear patterns (not plate like pattern such as *Stegotetrabelodon*) and rounded upper tusks that lack enamel bands.

Tetralophodon longirostris (Kaup, 1832b)

Nomenclatural and Taxonomical History Tetralophodont proboscidean remains from the Eppelsheim Formation (Dinotheriensande) of the Mainz Basin in Germany were originally allocated to the species *Tetracaulodon longirostre* by Kaup (1832b) (*Tetracaulodon = Mammut*), and slightly later they were assigned to *Mastodon longirostris* (Kaup 1835). This species was subsequently included within the subgenus *Mastodon* (*Tetralophodon*) by Falconer (1857).

Type Material HLMD-Din 111 (holotype), mandible fragment with left m2–m3.

Type Locality Eppelsheim, Germany, Miocene.

Distribution ?Late Miocene (?Vallesian) of Greece (Fourka area, seabed of Kryopigi, Chelona beach). Outside Greece, this species is known from the middle–late Miocene (?early Astaracian, late Astaracian–Vallesian, ?MN6, MN7/8–9, ?MN10) of Europe.

Remarks *Tetralophodon longirostris* shows an evident variation in the dental morphology and the shape of the mandible (especially the curvature of the mandibular symphysis), which were attributed to polymorphism (Tassy 1985, 1999). Most of the known specimens originate from the Eppelsheim Formation, which was generally considered to be of Vallesian age. However, recent studies indicate the stratigraphic inhomogeneity due to reworking of the sediments and a chronological range of the fauna from the middle Miocene to the late Miocene (Böhme et al. 2012; Pickford and Pourabrishami 2013). In this aspect, the revision of all known material from Europe and the discovery of new specimens are necessary to clarify the taxonomy of the European *Tetralophodon*, and especially whether *T. curvirostris* Bergounioux and Crouzel 1960 and *T. gigantorostris* (Klähn 1922) are indeed varieties of *T. longirostris*.

In Greece, Lazaridis and Tsoukala (2014b) and Lazaridis (2015) report on the presence of isolated findings of *T. longirostris* from several collection spots (two of them were recovered from the seabed) of provisionally Vallesian age within the Kassandra sand deposits, considering that they originate from the Antonios Formation of Western Chalkidiki and date to the late Miocene. This Formation is biostratigraphically dated from the early/middle Miocene boundary (close to MN4/5) until the late Miocene (pre-middle Turolian but possibly Vallesian) (Syrides 1990; Koufos 2013; Lazaridis et al. 2017).

Anancinae Hay, 1922
***Anancus* Aymard in Dorlhac, 1855**

Type Species *Mastodon arvernensis* Croizet and Jobert, 1828.

Other Included Species *A. capensis* Sanders, 2007; *A kenyensis* (MacInnes, 1942); *A. lehmanni* Gaziry, 1997; *A. osiris* Arambourg, 1945; *A. perimensis* (Falconer and Cautley, 1847); *A. petrocchii* Coppens, 1965; *A. sinensis* (Hopwood, 1935); *A. sivalensis* (Cautley, 1836); *A. ultimus* Sanders, 2011.

Distribution Late Miocene–Early Pleistocene of Europe, Africa, and Asia.

Comments Anancine gomphotheres, represented by the single genus *Anancus*, have tetralophodont (to pentalophodont) intermediate molars, whose main morphological feature is the dislocation of the pretrite and posttrite half-loph(id)s and the resultant alternate arrangement of the successive loph(id)s (anancoidy). In particu-

lar, in upper molars, the pretrite half-lophs are mesially offset, whereas in lower molars the pretrite half-lophids are distally dislocated, establishing thus an alternate contact of the successive loph(id)s (Tassy 1986). Other anancine characters include the high and short cranium with domed and elevated vault, the enlarged tympanic bullae, the brevirostrine mandible without tusks, the straight upper tusks (*Anancus* means "without a bend"; although slightly curved upper tusks exist) lacking enamel bands, and the absence of premolars, except in *A. kenyensis* (Tassy 1986; Hautier et al. 2009). The earliest occurrences of *Anancus* are traced during the Turolian (late Miocene). The genus flourished in the Old World during the Pliocene (in Europe commonly co-occurring with the zygolophodont *Mammut borsoni*) and survived until the Early Pleistocene (co-occurring also with *Mammuthus*), being the last gomphothere of the Old World.

Anancus lehmanni Gaziry, 1997

Nomenclatural and Taxonomical History Anancine gomphotheres from the late Miocene of Europe were recognized as *Mastodon* cf. *longirostris* (Schlosser 1907), subsequently to transitional forms between *Mastodon longirostris* and *Mastodon arvernensis* (e.g., Schlesinger 1917; Zapfe 1957) and later on to *Anancus* sp. (Tassy 1986; Markov 2008b). Gaziry (1997) studied the elephantimorphs from Dorn-Dürkheim 1 (Germany) and described four taxa: *Tetralophodon longirostris*, *Anancus arvernensis turoliensis*, *Stegotetrabelodon lehmanni*, and *Stegolophodon caementifer*, the second one a new subspecies and the latter two new species. However, apart from the material referred by Gaziry to "*A. a. turoliensis*," the holotype of "*S. lehmanni*" and other specimens attributed to this species are also included in *Anancus*, as well as specimens of *T. longirostris* (Konidaris and Roussiakis 2019). The species name *lehmanni* has nomenclatural priority over the subspecies name *turoliensis* due to its original higher taxonomic ranking (see also discussion in Markov 2008b). Konidaris and Roussiakis (2019) revised the known anancine specimens from the late Miocene of Europe (see below) and attributed them to *Anancus lehmanni*.

Type Material SMF-DD 3151(holotype), right M3 (Gaziry 1997: pl. 3, fig. 3).

Type Locality Dorn-Dürkheim-1, Germany, Turolian.

Distribution Late Miocene (middle Turolian, MN12) of Greece (Chomateri), and from numerous localities from the late Miocene (middle–late Turolian, MN12–13) of Germany, Austria, Slovakia, Hungary, Spain, Romania, North Macedonia, Bulgaria, Northern Caucasus, and Turkey.

Remarks The late Miocene anancines from Europe are well distinguished from the roughly contemporaneous, but more derived, *A. kenyensis*, and the Plio–Pleistocene *A. arvernensis*, as well as from other anancines, in the morphology of the mandible (longer symphysis, condyle only slightly higher than the coronoid

process), the cranium (straight and parallel premaxillary tusk alveoli, more anterior location of the orbit), the upper tusks (downturned, running almost parallel), and the primitive molar features on the cheek teeth (weak anancoidy, simple occlusal morphology, thick and unfolded to coarsely folded enamel on the molars) (Konidaris and Roussiakis 2019). The combination of the above traits is unique among anancines and permits the distinction at the species level, the proper name of which is *Anancus lehmanni* [see discussions in Markov (2008b) and Konidaris and Roussiakis (2019)]. Previously known only from the Pliocene and the Pleistocene of Greece, *Anancus* was recently reported for the first time from the late Miocene of Greece in Chomateri (Fig. 12a), marking its earliest occurrence in the Greek fossil record (Konidaris 2013; Konidaris and Koufos 2013a, b; Konidaris and Roussiakis 2017, 2019). The appearance of *Anancus* in Europe at the second half of the Turolian (~7.2 Ma) coincides with a faunal turnover in both the eastern and western sector of the European Mediterranean region and, in the Southern Balkans in particular, with the decline of the "Pikermian" large mammal fauna (Kostopoulos 2009; Böhme et al. 2017).

Anancus arvernensis (Croizet and Jobert, 1828)

Nomenclatural and Taxonomical History Croizet and Jobert (1828) erected *Mastodon arvernensis* based on juvenile dental specimens from Perrier in Puy-de-Dôme (Auvergne-Rhône-Alpes, France). In 1855 Aymard coined the genus *Anancus* and the species *A. macroplus*, which was slightly later synonymized with *Mastodon*
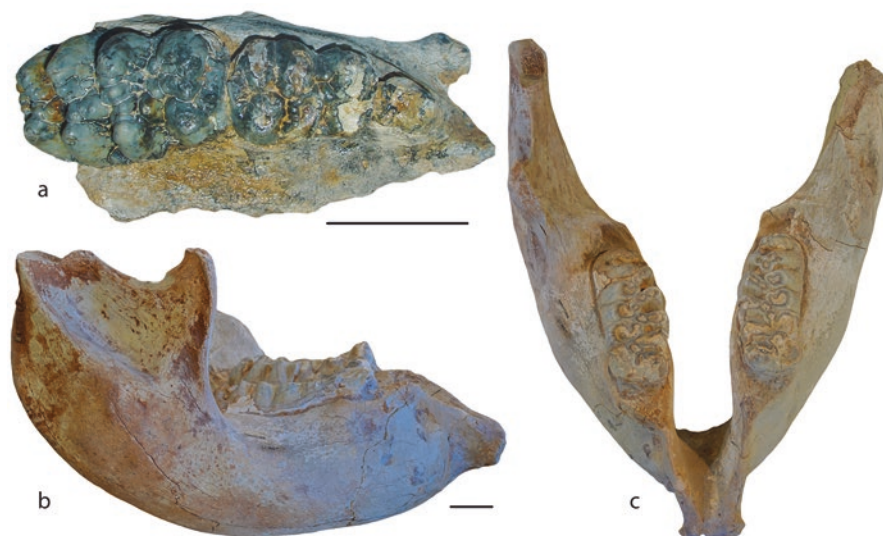

Fig. 12 (**a**), Right maxilla fragment with DP2–DP4 (AMPG-13Π/1972) of *Anancus lehmanni* from the late Miocene (Turolian) of Chomateri (copyright G. Konidaris); (**b–c**), mandible with the m3s (AMPG-1918) of *Anancus arvernensis* from the late Pliocene of Sesklon in b dorsal view and c right lateral view (copyright A. Athanassiou). Scale bars equal 5 cm

arvernensis (Lartet 1859), although the new combination was not utilized. Osborn (1936) recognized the binomen *Anancus arvernensis*. Meanwhile, Schlesinger (1917, 1922) attributed material from Austria and Hungary to *Mastodon* (*Dibunodon*) *arvernense*, a subgenus which is though a junior synonym of *Anancus* (Matsumoto 1927; Gaziry 1976).

Type Material MNHN-A.C. 1830 (lectotype), right maxilla fragment with DP2–DP3 (Croizet and Jobert 1828: pl. 2, fig. 7).

Type Locality Perrier-les-Étouaires, France, late Pliocene, late Ruscinian, MN16.

Distribution Several Pliocene–Early Pleistocene localities of Greece, (e.g., Milia, Gephyra, Sesklon, Vatera, Apolakkia, Nigrita) and in the Pliocene–Early Pleistocene (Ruscinian–middle Villafranchian, MN14–MNQ17) of Europe.

Remarks This species represents the Pliocene–Pleistocene representative of the European anancines and the last gomphothere to have survived in Europe. The richest material originates from Dorkovo (early Pliocene; Bulgaria), but important material is known also from Chilhac (France) and Valdarno (Italy) (Weithofer 1890; Boeuf 1992; Metz-Muller 2000; Rook et al. 2013). The research of Metz-Muller (2000) proved the high intraspecific variability (including the complexity of the cheek teeth and the occasional occurrence of pentalophodont m2) and included the biometrical study of the mandibles resulting in the definition of dental ages; moreover, the study showed that *A. arvernensis* presents a tendency towards shortening of the molars, increase of the hypsodonty, and simplification of the crown.

In Greece, although several *A. arvernensis* specimens are known, most of them are isolated dental findings with uncertain stratigraphic position. However, important and stratified material is known from Sesklon (including a partial cranium, a mandible and an upper tusk, Fig. 12b–c; Symeonidis and Tataris 1983; Athsanassiou 2016, 2018), Nigrita (a partial cranium with the upper tusks and the molars; Athanassiou 2017), Apolakkia (a partial cranium with the upper tusks and the molars; Theodorou et al. 2000), Milia (mandible and teeth; Tsoukala and Mol 2016), Gephyra (mandibles and postcranials; Crégut-Bonnoure and Tsoukala 2017), Kalliphytos (mandible; Athanassiou 2016), and Vatera (teeth; de Vos et al. 2002).

Stegodontidae Osborn, 1918
Stegodon **Falconer and Cautley, 1847**

Type Species *Mastodon elephantoides* Clift, 1828.

Other Included Species See Saegusa et al. (2005) and Aiba et al. (2010) for a complete list.

Distribution Late Miocene–Late Pleistocene of Asia, Africa, and Europe.

Fig. 13 Right m3 fragment (SIA 22) of *Stegodon* sp. possibly from the wider area of Siatista (Kozani), without information on the exact locality; (**a**), occlusal view; (**b**), lingual view (photo Hans Wildschut, Dick Mol). Scale bar equals 5 cm

Comments The genus *Stegodon* includes the stegodontids, which are characterized and differentiated from the more archaic *Stegolophodon* by their intermediate molars with five or more loph(id)s, third molars with no distinct central conule, absence of lower tusks, and two lophids above the mesial root of the lower third molar (Saegusa et al. 2005).

Stegodon sp.

Remarks A fragment of a third molar of *Stegodon* sp. (Fig. 13) from an unknown locality (and therefore no information about geological age), but possibly from the wider area of Siatista (Kozani), constitutes the first evidence of the presence of stegodontids in Europe, extending their previously known geographical distribution (Mol et al. 2010).

6 Concluding Remarks

Proboscideans are common in the Neogene faunas of Greece with relatively abundant material, and they are present in most of the Neogene fossiliferous sites, both in today's continental and insular Greece. They have been the largest terrestrial mammals in the Neogene faunas of the country, dominating the ecosystems of that time. Recent investigations on the Miocene and Pliocene proboscideans, including the revision and study of old collections, and the study of new specimens from excavations carried out in Greece during the last years, have resulted in the update of their taxonomy and biostratigraphy. Based on our current knowledge, we can reach several conclusions.

During the early Miocene, the only proboscidean that is known in Greece is the deinothere *Prodeinotherium cuvieri*, documented at Gavathas (Lesvos Island), where the find-bearing locality is dated as older than 18.4 Ma (late MN3). The Gavathas deinothere marks the first appearance of deinotheres in Europe and documents their penetration into the continent as part of the complex "Proboscidean

Datum Event," after the establishment of the so-called *Gomphotherium* landbridge in the middle Burdigalian (~19.0–18.0 Ma, early MN3).

In the middle Miocene, the deinothere *Prodeinotherium bavaricum* and the trilophodont choerolophodontid *Choerolophodon chioticus* are recognized in Thymiana (Chios Island), dated to ~15.5 Ma (MN5). *Choerolophodon chioticus* is the most primitive choerolophodontid in Europe and marks their first penetration into the continent, being part of the third European phase of the "Proboscidean Datum Event" (Tassy 1990). This phase is probably part of the first middle Miocene migrational event that took place in the late Orleanian (17.0–15.0 Ma, MN5), involving also the arrival in Europe of the amebelodontid *Protanancus* (Rögl 1999; Koufos et al. 2005; Markov and Vergiev 2010).

During the late Miocene, proboscideans are more diverse and well documented in the Greek fossil record due to a high number of fossiliferous localities; however, *Choerolophodon* is in most of the localities the dominant proboscidean in terms of abundance. In the early Vallesian (MN9), *Choerolophodon anatolicus* is identified in Pentalophos-1 (Axios valley). During the late Vallesian (MN 10), the deinothere *Deinotherium giganteum* and the primitive morph of *Choerolophodon pentelici* co-existed in Ravin de la Pluie (Axios valley). In the early Turolian (MN11) appeared the zygodont *Mammut* sp. (*M. obliquelophus*?), which co-existed with the advanced morph of *C. pentelici* in Ravin des Zouaves-5 (Axios valley). In the middle Turolian *C. pentelici*, the tetralophodont amebelodontid *Konobelodon atticus*, *Mammut* sp. (*M. obliquelophus*?), and the huge-sized deinothere *D. proavum* are recorded, the co-occurrence of which is documented in Pikermi. These four species are recognized also in the Mytilini Formation of Samos Island. During the middle Turolian, but postdating the classical Pikermi, appeared the tetralophodont gomphothere *Anancus lehmanni*, the most primitive anancine of Europe. In the late Turolian (MN13) are traced the last occurrences of *C. pentelici*, present with certainty in the Dytiko localities (Axios valley) and perhaps in Maramena.

During the Pliocene, *Anancus arvernensis* and *Mammut borsoni* are recognized. The fossiliferous localities of this period are few and the lack of stratigraphic information for several findings makes the determination of their first appearances problematic. However, *M. borsoni* survived until the end of the Pliocene (MN16) and *A. arvernensis* until the beginning of the Early Pleistocene (MNQ17). The co-occurrence of these species is documented in Milia (early late Pliocene, MN16a). Finally, the first recorded occurrence of *Stegodon* in Greece represents also the first evidence of the presence of stegodontids in Europe.

Appendix

List of Greek localities containing Neogene and Early Pleistocene proboscidean fossils. Type localities are marked with bold. Locality numbers refer to the collection numbers of the PaleoBiology Database (PBDB)

Localities[PBDB No]	Age (MN; GPTS in Ma)	Taxon
Vatera F[183341]	Early Pleistocene (MNQ17)	*Anancus* cf. *arvernensis*[1]
Vatera H[183343]	Early Pleistocene (MNQ17)	*Anancus arvernensis*[1]
Chorigos	Pliocene–Early Pleistocene	*Mammut borsoni*[2]
Neapolis-Grevena basin	Pliocene–Early Pleistocene	*Mammut borsoni*[3]
Sani[202529]	Pliocene–Early Pleistocene	*Anancus arvernensis*[4]
Axios valley ("Dormislou", perhaps close to Gephyra)	Pliocene–Early Pleistocene	*Anancus arvernensis*[5]
Kalliphytos[202532]	Pliocene–Early Pleistocene	*Anancus arvernensis*[6]
Klima	Pliocene–Early Pleistocene	*Anancus arvernensis*[7]
Antimachia[207130]	Pliocene–Early Pleistocene	*Anancus arvernensis*[8]
R. Almyri	Pliocene–Early Pleistocene	*Anancus arvernensis*[9]
Kardamaena[204662]	Pliocene–Early Pleistocene	*Anancus arvernensis*[10]
Pylos	Pliocene–Early Pleistocene	*Anancus arvernensis*[11]
Skoura	Pliocene–Early Pleistocene	*Anancus arvernensis*[12]
Spaides (Eleonas)	Pliocene–Early Pleistocene	*Anancus arvernensis*[13,14]
Nigrita[202533]	Pliocene–Early Pleistocene	*Anancus arvernensis*[15]
Chilia Dendra, Koufalia	Pliocene–Early Pleistocene	*Anancus arvernensis*[b]
Gephyra-1[182685]	Late Pliocene (MN16)	*Anancus arvernensis*[16]

Localities[PBDB No]	Age (MN; GPTS in Ma)	Taxon
Sesklon[34614]	Late Pliocene (MN16)	*Anancus arvernensis*[6,17–18]
Milia-1[187636]	Late Pliocene (MN 16a)	*Mammut borsoni*[19–20]
Milia-2[185862]	Late Pliocene (MN 16a)	*Mammut borsoni*[20], *Anancus arvernensis*[20]
Milia-3[195291]	Late Pliocene (MN 16a)	*Mammut borsoni*[20]
Milia-4[182686]	Late Pliocene (MN 16a)	*Mammut borsoni*[20]
Milia-5[185859]	Late Pliocene (MN 16a)	*Mammut borsoni*[20], *Anancus arvernensis*[20]
Milia-6[195292]	Late Pliocene (MN 16a)	*Mammut borsoni*[20]
Milia-7[195294]	Late Pliocene (MN 16a)	*Mammut borsoni*[20]
Milia-8[195295]	Late Pliocene (MN 16a)	*Mammut borsoni*[20], *Anancus arvernensis*[20]
Milia-9[195296]	Late Pliocene (MN 16a)	*Mammut borsoni*[20]
Milia-10[185860]	Late Pliocene (MN 16a)	*Mammut borsoni*[20]
Milia-11[195299]	Late Pliocene (MN 16a)	*Mammut borsoni*[20]
Milia[202530]	Late Pliocene	*Anancus arvernensis*[4,a]
Apolakkia I[184242]	Pliocene	*Anancus arvernensis*[14]
Apolakkia II[202499]	Pliocene	Proboscidea indet.[14]
Agia Triada[202531]	Pliocene	*Anancus arvernensis*[4]
Angelochori, Angelon beach	Pliocene	*Anancus arvernensis*[c]
Maramena[32189]	Miocene/Pliocene (MN13/14)	*Choerolophodon pentelici*[21]
Dikaia[210641]	Late Miocene	*Choerolophodon pentelici*[22]
Pyrgos Vassilissis[195555]	Late Miocene	*Choerolophodon pentelici*[23]
Sani[202528]	Late Miocene	*Choerolophodon pentelici*[4]
Servia[202257]	Late Miocene	*Choerolophodon pentelici*[24], *Deinotherium* sp.[24]
Fourka[202330]	Late Miocene	*Tetralophodon longirostris*[25]
Chelona beach[202500]	Late Miocene	*Tetralophodon longirostris*[25]
seabed of Kryopigi[202500]	Late Miocene	*Tetralophodon longirostris*[25]
Neokaisareia[206458]	Turolian	*Mammut* sp. (*M. obliquelophus*?)[26]
Palaio Keramidi	Turolian	*Mammut* sp. (*M. obliquelophus*?)[26]
Dytiko 2[32375]	Late Turolian (MN13)	*Choerolophodon pentelici*[27]
Dytiko 3[32376]	Late Turolian (MN13)	*Choerolophodon pentelici*[27]
Kryopigi[157582]	Late Miocene (MN12–13)	*Choerolophodon pentelici*[28]

Localities[PBDB No]	Age (MN; GPTS in Ma)	Taxon
Mytilinii 1A-Samos[202215]	Middle Turolian (MN12; ~7.1)	*Mammut* sp. (*M. obliquelophus*?)[29–30]
Mytilinii 1B-Samos[202216]	Middle Turolian (MN12; ~7.1)	*Choerolophodon pentelici*[27,29,30]
Andriano-Samos	Middle Turolian (MN12; ~7.1)	*Choerolophodon pentelici*[30,32], *Deinotherium proavum*[30,32]
Chomateri[195562]	Middle Turolian (MN12; ~7.16)	*Anancus lehmanni*[33–34]
Perivolaki[194879]	Middle Turolian (MN12; 7.3–7.1)	*Deinotherium proavum*[33,35]
Pikermi[182754]	**Middle Turolian (MN12; ~7.3)**	***Choerolophodon pentelici*[27,30,33,36–38]**, ***Deinotherium proavum*[33,36–37,39–44]**, ***Mammut* sp. (*M. obliquelophus*?)[33,36–38]**, ***Konobelodon atticus*[33,36–38,40,45]**
Pikermi Valley-1[202630]	Middle Turolian (MN12)	*Mammut* sp. (*M. obliquelophus*?)[46]
Pikermi Valley-3[202631]	Middle Turolian (MN12)	*Deinotherium proavum*[44]
Halmyropotamos[202213]	?middle Turolian (?MN12)	*Deinotherium proavum*[44,47], *Mammut* sp. (*M. obliquelophus*?)[33,48]
Prochoma-1[202222]	Middle Turolian (MN12)	*Choerolophodon pentelici*[31,33]
Vathylakkos-2[202703]	Middle Turolian (MN12)	*Choerolophodon pentelici*[31,33]
Kerassia-1	?middle Turolian (?MN 12)	*Choerolophodon*? sp.[49]
Kerassia-4[195435]	?middle Turolian (?MN 12)	*Konobelodon atticus*[45,49]
Kerassia-6[195437]	?middle Turolian (?MN 12)	*Choerolophodon* sp.[49]
Kerassia[195431]	?middle Turolian (?MN 12)	*Deinotherium* sp.[50]
Ravin des Zouaves 5[195489]	Early Turolian (MN11; ~8.2)	*Mammut* sp. (*M. obliquelophus*?)[30,33,51], *Choerolophodon pentelici*[30,33,51]
Maronia, Crete[202722]	Turolian (MN11–13)	*Deinotherium proavum*[52]
Gela, Crete[202723]	Turolian (MN11–13)	*Deinotherium proavum*[53–54]
Zakros, Crete	Turolian (MN11–13)	*Deinotherium proavum*[54–55]
Samos Island, NHMW collection[182751] MGL collection[202120] HGI collection HLMD collection[202724] SMF collection[202725]	Turolian (MN11–13)	*Choerolophodon pentelici*[29–33,56–58], *Konobelodon atticus*[30,32,33,45,58], *Deinotherium proavum*[30,32,33]
Nikiti-2[73869]	Early Turolian (MN11; 8.7–8.2)	*Choerolophodon pentelici*[30,31,33,59]

Localities[PBDB No]	Age (MN; GPTS in Ma)	Taxon
Ravin X[182745]	?early Turolian (?MN11)	*Choerolophodon pentelici*[30–31]
Platania, Drama[182682]	Late Vallesian/early Turolian (MN10/ MN11)	*Konobelodon* cf. *atticus*[26]
Ravin de la Pluie[191070]	Late Vallesian (MN10; ~9.3)	*Deinotherium giganteum*[30,33], *Choerolophodon pentelici*[30–31,33]
Xirochori 1[195490]	Late Vallesian (MN10; ~9.6)	*Choerolophodon pentelici*[30–31,33]
Ravin des Zouaves 1[182746]	Late Vallesian (MN10)	*Choerolophodon pentelici*[30–31,33]
Agia Paraskevi, Kassandra[202726]	Late Miocene	*Deinotherium giganteum*[60]
Pentalophos 1[202119]	Early Vallesian (MN9)	*Choerolophodon anatolicus*[30–31,33]
Thymiana[182752]	**Middle Miocene (MN5; >15.5)**	***Choerolophodon chioticus*[27,61–62]**, *Prodeinotherium bavaricum*[61]
Psara Island	?middle Miocene	*Prodeinotherium bavaricum*[63]
Gavathas, Lesvos Island[195540]	Early Miocene (MN3; >18.4)	*Prodeinotherium cuvieri*[64,a]
Thermopigi[73553]	Turolian (MN11–13)	*Deinotherium* sp.[26], Elephantimorpha indet.[26]
Nikiti-1[202729]	Late Vallesian (MN10)	Proboscidea indet.[59]
Antonios[73861]	Early/middle Miocene (MN4/5)	Proboscidea indet.[65]
Central Macedonia	?	*Deinotherium giganteum*[66]
Vathylakkos area	?	*Mammut borsoni*[11]
possibly from the wider area of Siatista (Kozani)[202732]	?	*Stegodon* sp.[67]

[a]This study

[b]A right hemimandible fragment with the m3 (partially broken), stored at the Ephorate of Palaeoanthropology and Speleology, Office of Northern Greece (Thessaloniki) (pers. comm. Athanassiou 2019)

[C]A small fragment of a molar (LGPUT-AAT 17) and a medial condyle of a right femur (LGPUT-AAT 16) were collected (surface findings/unknown precise stratigraphic position) from an area near the fossil findspot of Angelochori, Angelon beach (Thessaloniki), for which Tsoukala (2018) proposed a correlation to the late Pliocene (MN 16)

[1]de Vos et al. 2002, [2]Dermitzakis et al. 1982, [3]Brunn 1956, [4]Koufos 1977, [5]Sakellariou-Mane 1972, [6]Athanassiou 2016, [7]Steensma 1988, [8]Forsyth Major 1887, [9]Desio 1931, [10]Charrier and Giglio 1969, [11]Mitzopoulos 1967, [12]Georgalas 1941, [13]Gidarakos 1938, [14]Theodorou et al. 2000, [15]Athanassiou 2017, [16]Crégut-Bonnoure and Tsoukala 2017, [17]Symeonidis and Tataris 1983, [18]Athanassiou 2018, [19]Tsoukala 2000, [20]Tsoukala and Mol 2016, [21]Schmidt-Kittler et al. 1995, [22]Tsoukala et al. 2007, [23]Freyberg 1951, [24]Paraskevaidis 1977, [25]Lazaridis and Tsoukala 2014b, [26]Konidaris and Tsoukala 2020, [27]Konidaris et al. 2016, [28]Lazaridis and Tsoukala 2014a, [29]Konidaris and Koufos 2009, [30]Konidaris and Koufos 2013a, [31]Konidaris et al. 2016, [32]Konidaris and Koufos 2019, [33]Konidaris 2013; [34]Konidaris and Roussiakis 2019, [35]Koufos 2006, [36]Gaudry 1862, [37]Gaudry 1867; [38]Tassy 1985, [39]Wagner 1848, [40]Wagner 1857, [41]Weinsheimer 1883, [42]Dietrich 1916, [43]Weithofer 1888, [44]Konidaris et al. 2017, [45]Konidaris et al. 2014, [46]Roussiakis et al. 2014, [47]Melentis 1969, [48]Melentis 1967, [49]Theodorou et al. 2003, [50]van der Made and Moyà-Solà 1989, [51]Koufos 1980, [52]Athanassiou 2004, [53]Poulakakis et al. 2005, [54]Iliopoulos et al. 2014, [55]Fassoulas and Iliopoulos 2011, [56]Schlesinger 1917, [57]Schlesinger 1922, [58]Lehmann 1950, [59]Konidaris and Koufos 2016, [60]Tsoukala and Melentis 1994, [61]Paraskevaidis 1940, [62]Tobien 1980, [63]Besenecker and Symeonidis 1974, [64]Koufos et al. 2003, [65]Koufos and Syrides 1997, [66]Symeonidis 1969, [67]Mol et al. 2010

References

Aiba H, Baba K, Matsukawa M (2010) A new species of *Stegodon* (Mammalia, Proboscidea) from the Kazusa Group (lower Pleistocene), Hachioji City, Tokyo, Japan and its evolutionary morphodynamics. Palaeontology 53:471–490

Aiglstorfer M, Göhlich UB, Böhme M, Gross M (2014) A partial skeleton of *Deinotherium* (Proboscidea, Mammalia) from the late Middle Miocene Gratkorn locality (Austria). Palaeobiodivers Palaeoenviron 94:49–70

Andrews CW (1911) On a new species of *Dinotherium* (*Dinotherium hobleyi*) from British East Africa. Proc Zool Soc London 81:943–945

Antoine PO, Welcomme JL, Marivaux L, Baloch I, Benammi M, Tassy P (2003) First record of Paleogene Elephantoidea (Mammalia, Proboscidea) from the Bugti Hills of Pakistan. J Vertebr Paleontol 23:977–980

Arambourg C (1934) Le *Dinotherium* des gisements de l'Omo. C R Soc Géol Fr 1934:86–87

Arambourg C (1945) *Anancus osiris*, un mastodonte nouveau du Pliocène inférieur d'Egypte. Bull Soc Géol Fr 15:479–495

Arambourg C, Piveteau J (1929) Les Vertébrés du Pontien de Salonique. Ann Paléontol 18:59–138

Athanassiou A (2004) On a *Deinotherium* (Proboscidea) finding in the Neogene of Crete. Carnets Géol 2004(05):1–7

Athanassiou A (2016) Craniomandibular remains of *Anancus arvernensis* (Proboscidea, Mammalia) from Greece: The samples from Kallíphytos (E. Macedonia) and Sésklo (Thessaly). Quat Int 406:25–34

Athanassiou A (2017) A cranial specimen of *Anancus arvernensis* from Nigríta, Northern Greece. 7th International Conference on Mammoths and their Relatives, Taichung

Athanassiou A (2018) A Villafranchian *Hipparion*-bearing mammal fauna from Sésklo (E. Thessaly, Greece): implications for the question of *Hipparion–Equus* sympatry in Europe. Quaternary 1:1–24

Athanassiou A (this volume) The fossil record of non-endemic elephants and mammoths (Mammalia: Proboscidea: Elephantidae) in Greece. In: Vlachos E (ed) The fossil vertebrates of Greece vol. 1 – basal vertebrates, amphibians, reptiles, afrotherians, glires, and primates. Springer, Cham

Barbour EH (1927) Preliminary notice of a new proboscidean *Amebelodon fricki*, gen. et sp. nov. Bull Nebr State Museum 13:131–134

Barbour EH (1929) *Torynobelodon loomisi*, gen. et sp. nov. Bull Nebr State Museum 16:147–153

Barbour EH, Hibbard CW (1941) A shovel-tusked mastodon, *Amebelodon fricki*, from Kansas. Bull Univ Nebr State Museum 2:37–46

Bergounioux FM, Crouzel F (1960) *Tetralophodon curvirostris* n. sp. (Mamm., Proboscidea) aus dem Unterpliozän (Pontien) von Esselborn (Rheinhessen). Jahresber Mitt Oberrhein Geol Ver 42:119–121

Bergounioux FM, Crouzel F (1962) Les Déinothéridés d'Europe. Ann Paléontol 48:1–56

Besenecker H, Symeonidis NK (1974) Der erste Säugetierfund aus dem Neogen der griechischen Insel Psara (Ostägäis). Ann Géol Pays Hellén 26:109–117

Blumenbach JF (1799) Handbuch der Naturgeschichte, 6th edn. Dieterich, Göttingen

Boeuf O (1992) *Anancus arvernensis chilhiacensis* nov. subsp. (Proboscidea, Mammalia), un Mastodonte du Plio-Pléistocène de Haute-Loire, France. Geobios 14:179–188

Böhme M, Aiglstorfer M, Uhl D, Kullmer O (2012) The antiquity of the Rhine River: stratigraphic coverage of the *Dinotheriensande* (Eppelsheim Formation) of the Mainz Basin (Germany). PLoS One 7:e36817

Böhme M, Spassov N, Ebner M, Geraads D, Hristova L, Kirscher U, Kötter S, Linnemann U, Prieto J, Roussiakis S, Theodorou G, Uhlig G, Winklhofer M (2017) Messinian age and savannah environment of the possible hominin *Graecopithecus* from Europe. PLoS One 12:e0177347

Bonaparte CL (1845) Catalogo Metodico dei Mammiferi Europei. Luigi di Giacomo Pirola, Milan

Borson E (1823) Note sur des dents du grand mastodonte trouvées en Piémont et sur des machoires et dents fossiles prises dans la mine de houille de Cadibona proche Savone. Mem Reale Acad Sci Torino 27:31–42

Brunn JH (1956) Contribution à l'étude géologique du Pinde septentrional et d'une partie de la Macédoine occidentale. Ann Géol Pays Hellén 7:1–358

Cautley PT (1836) Note on the teeth of the mastodon à dents etroites of the Siwálik Hills. J Asiat Soc Bengal 5:294–296

Charrier G, Giglio A (1969) Primi risultati di una campagna di rilevamento geologico nell'isola di Coo (Sporadi meridionali – Mare Egeo). Boll Assoc Min Subalp 6:482–516

Chow MC, Chang YP (1974) Chinese fossil elephantoids (in Chinese). Science Press, Beijing

Clift W (1828) On the fossil remains of two new species of *Mastodon*, and of other vertebrated animals, found on the left bank of the Irawadi. Trans Geol Soc Lond 2:369–375

Codrea V (1994) A priority issue: *Deinotherium proavum* Eichwald or *Deinotherium gigantissimum* Ştefănescu? In: Nicorici E (ed) The Miocene from the Transylvanian Basin-Romania, Cluj-Napoca, pp 105–110

Cooper LN, Seiffert ER, Clementz M, Madar SI, Bajpai S, Hussain ST, Thewissen JGM (2014) Anthracobunids from the Middle Eocene of India and Pakistan are stem perissodactyls. PLoS One 9:e109232

Coppens Y (1965) Les proboscidiens du Tchad. In: Actes du Vᵉ Congrés Panafricain de Préhistoire et de l'Étude du Quaternaire, Santa Cruz de Tenerife, pp 331–387

Crégut-Bonnoure E, Tsoukala E (2017) The Pliocene Artiodactyla and Proboscidea (Mammalia) from Gephyra (lower Axios valley, Macedonia, Greece). Discovery of a new boselaphine. Quat Int 445:200–214

Croizet JB, Jobert ACG (1828) Recherches sur les ossemens fossiles du département du Puy-de-Dôme. Principaux Libraries, Paris

de Bonis L, Brunet M, Heintz E, Sen S (1992) La province greco-irano-afghane et la réparition des faunes mammaliennes au Miocène supérieur. Paleontol i Evol 24–25:103–112

de Vos J, van der Made J, Athanassiou A, Lyras G, Sondaar PY, Dermitzakis MD (2002) Preliminary note on the Late Pliocene fauna from Vatera (Lesvos, Greece). Ann Géol Pays Hellén 39:37–70

Dermitzakis MD, Symeonidis NK, De Boer LEM, Sondaar PY (1982) The evolution of the elephants (in Greek). Edit Lab Geol Palaeont, Univ Athens

Desio A (1931) Le isole Italiane dell'Egeo. Mem Descrittive Carta Geol Ital 24:1–534

Dietrich WO (1916) Über die Hand und den Fuss von *Dinotherium*. Zeitschr D Geol Ges 68:44–53

Dooley ACJ, Scott E, Green J, Springer KB, Dooley BS, Smith GJ (2019) *Mammut pacificus* sp. nov., a newly recognized species of mastodon from the Pleistocene of western North America. Peer J 7:e6614

Dorlhac MJ (1855) Notice géologique sur le cratère de Coupet et sur son gisement de gemmes et d'ossements fossiles. Ann Soc Agric Sci Arts Commer Puy 19:497–517

Éhik J (1930) *Prodinotherium hungaricum* n. g., sp., with an appendix by Szalay, T.: on the geological occurrence of *Prodinotheirum hungaricum* ÉHIK. Geol Hung, Ser Palaeontol 6:1–24

Eichwald E (1831) Zoologia specialis quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universum, et Poloniae in specie. Josephi Zawadzki, Vilnae

Eichwald E (1835) De pecorum et pachydermorum reliquiis fossilibus in Lithuania, Volhynia et Podolia repertis. Nova Acta Acad Caesareae Leopoldino-Carolinae Ger Nat Curiosorum 17:677–780

Falconer H (1845) Description of some fossil remains of *Dinotherium*, Giraffe, and other Mammalia from the gulf of Cambay, western Coast of India. Q J Geol Soc Lond 1:356–372

Falconer H (1857) On the species of mastodon and elephant occurring in the fossil state in Great Britain. Part I. *Mastodon*. Q J Geol Soc Lond 13:307–360

Falconer H (1868) Description of some fossil remains of *Dinotherium*, Giraffe, and other Mammalia, from Perim Island, Gulf of Cambay, western coast of India. In: Murchison C (ed) Palaeontological memoirs and notes of the late Hugh Falconer, A.M., M.D, London, pp 391–411

Falconer H, Cautley PT (1847) Fauna antiqua sivalensis, being the fossil zoology of the Sewalik Hills, in the North of India. Smith, Elder and Co., London

Fassoulas C, Iliopoulos G (2011) The excavations of *Deinotherium giganteum* from Siteia: life and environment in Crete during the Miocene. In: Proceedings of the 10th international cretological congress, Chania, pp 11–25

Ferretti MP, Rook L, Torre D (2003) *Stegotetrabelodon* (Proboscidea, Elephantidae) from the late Miocene of southern Italy. J Vertebr Paleontol 23:659–666

Forsyth Major CJ (1887) Faune mammalogische delle isole di Cos et di Samos. Atti Soc Tosc Sci Nat 5:272–275

Forsyth Major CJ (1888) Sur un gisement d'ossements fossiles dans l'île de Samos, contemporains de l'âge de Pikermi. C R Hebd Séances Acad Sci 107:1178–1181

Forsyth Major CJ (1894) Le gisement ossifère de Mytilinii et catalogue d'ossements fossiles recueillis à Mitylini, île de Samos, et déposés au Collège Galliard à Lausanne. Georges Bridel and Cie, Lausanne

Freyberg BV (1951) Die Pikermifauna von Tour la Reine. Ann Géol Pays Hellén 3:7–10

Gaudry A (1862) Animaux fossiles et géologie de l'Attique. Savy, Paris

Gaudry A (1867) Animaux fossiles et géologie de l'Attique. Atlas, Savy, Paris

Gaudry A, Lartet E (1856) Résultats des recherches paléontologiques entreprises dans l'Attique sous les auspices de l'Académie. C R Acad Sci Paris 43:271–274

Gaziry AW (1976) Jungtertiäre Mastodonten aus Anatolien (Türkei). Geol Jb 22:3–143

Gaziry AW (1987a) New mammals from the Jabal Zaltan site, Libya. Senckenb Lethaea 68:69–89

Gaziry AW (1987b) Remains of Proboscidea from the early Pliocene of Sahabi, Libya. In: Boaz NT, El-Arnauti A, Gaziry AW, Heinzelin JD, Boaz DD (eds) Neogene paleontology and geology of Sahabi. A. R. Liss, New York, pp 183–203

Gaziry AW (1997) Die Mastodonten (Proboscidea, Mammalia) aus Dorn-Dürkheim 1 (Rheinhessen). Cour Forsch-Inst Senck 197:73–115

Georgalas CG (1941) Über das Vorkommen von *Anancus* (*Mastodon*) *arvernensis* Croiz. und Job. in der Umgebung von Skoura (SÖ von Sparta). Prakt Akad Ath 16:94–100

Gheerbrant E (2009) Paleocene emergence of elephant relatives and the rapid radiation of African ungulates. PNAS 106:10717–10721

Gheerbrant E, Tassy P (2009) L'origine et l'évolution des éléphants. C R Palevol 8:281–294

Gheerbrant E, Sudre J, Cappetta H (1996) A Palaeocene proboscidean from Morocco. Nature 383:68–70

Gheerbrant E, Sudre J, Cappetta H, Iarochéne M, Amaghzaz M, Bouya B (2002) A new large mammal from the Ypresian of Morocco: evidence of surprising diversity of early proboscideans. Acta Palaeontol Pol 47:493–506

Gheerbrant E, Sudre J, Tassy P, Amaghzaz M, Bouya B, Iarochène M (2005) Nouvelles données sur *Phosphatherium escuilliei* (Mammalia, Proboscidea) de l'Éocène inférieur du Maroc, apports à la phylogénie des Proboscidea et des ongulés lophodontes. Geodiversitas 27:239–333

Gheerbrant E, Schmitt A, Kocsis L (2018) Early African fossils elucidate the origin of embrithopod mammals. Curr Biol 28:2167–2173

Gidarakos D (1938) Trouvailles paléontologiques des mammifères en Béotie. Prakt Akad Ath 13:418–422

Ginsburg L, Chevrier F (2001) Les Dinothères du bassin de la Loire et l'évolution du genre *Deinotherium* en France. Symbioses 5:9–24

Gräf IE (1957) Die Prinzipien der Artbestimmung bei *Dinotherium*. Palaeontographica 108:131–185

Gregory JT (1945) An *Amebelodon* jaw from the Texas Panhandle. Univ Texas Publ 4401:477–484

Harris JM (1973) *Prodeinotherium* from Gebel Zelten, Libya. Bull Brit Mus (Nat Hist) (Geol) 23:285–348

Hautier L, Mackaye HT, Lihoreau F, Tassy P, Vignaud P, Brunet M (2009) New material of *Anancus kenyensis* (Proboscidea, Mammalia) from Toros-Menalla (Late Miocene, Chad): contribution to the systematics of African anancines. J Afr Earth Sci 53:171–176

Hay OP (1922) Further observations on some extinct elephants. Proc Biol Soc Wash 35:97–101

Hays I (1834) Descriptions of the specimens of inferior maxillary bones of mastodons in the cabinet of the American Philosophical Society, with remarks on the genus *Tetracaulodon* (Godman), etc. Trans Am Philos Soc 4:317–339

Hopwood AT (1935) Fossil Proboscidea from China. Palæont Sin 9:1–108

Huttunen K (2002) Systematics and taxonomy of the European Deinotheriidae (Proboscidea, Mammalia). Ann Naturhist Mus Wien 103(A):237–250

Huttunen K (2004) On a *Prodeinotherium bavaricum* (Proboscidea, Mammalia) skeleton from Franzensbad, Czech Republic. Ann Nat Mus Wien 105(A):333–361

Huttunen K, Göhlich UB (2002) A partial skeleton of *Prodeinotherium bavaricum* (Proboscidea, Mammalia) from the Middle Miocene of Unterzolling (Upper Freshwater Molasse, Germany). Geobios 35:489–514

Iliopoulos G, Fassoulas C, Tzortzi M (2014) An almost complete skeleton of a large *Deinotherium* (Proboscidea, Mammalia) from the Late Miocene of Aghia Photia, Siteia (Crete Island, Greece). In: Kostopoulos DS, Vlachos E, Tsoukala E (eds) 6th International Conference on Mammoths and their Relatives, Grevena-Siatista. Sci Annals, School Geol, Aristotle Univ Thessaloniki, Greece, sp vol 102: 72–73

Illiger C (1811) Prodromus systematis mammalium et avium additis terminis zoographicis utri-usque classis. C. Salfield, Berlin

Jourdan M (1861) Des terrains sidérolitiques. C R Hebd Séances Acad Sci 53:1009–1014

Kaup JJ (1829) *Deinotherium giganteum.* Eine Gattung der Vorwelt aus der Ordnung der Pachydermen. Isis 22:401–404

Kaup JJ (1832a) Description d'ossemens fossiles de mammifères inconnus jusqu'à présent, qui se trouvent au Muséum grand-ducal de Darmstadt. J.G. Heyer, Darmstadt

Kaup J (1832b) Ueber zwei Fragmente eines Unterkiefers von *Mastodon angustidens* Cuv., nach welchen diese Art in die Gattung Tetracaulodon Godmann gehört. Isis 25:628–631

Kaup JJ (1835) Description d'ossemens fossiles de mammifères inconnus jusqu'à-présent qui se trouvent au Muséum grand-ducal de Darmstadt. J.P. Diehl, Darmstadt

Kerr R (1792) The animal kingdom, or zoological system, of the celebrated Sir Charles Linnaeus, Edinburgh

Klähn H (1922) Die badischen Mastodonten und ihre süddeutschen Verwandten. Borntraeger, Berlin

Konidaris GE (2013) Palaeontological and biostratigraphical study of the Neogene Proboscidea from Greece. Ph.D. thesis, Sci Annals, School Geol, Aristotle Univ Thessaloniki, Greece 153, 1–326

Konidaris GE, Koufos GD (2009) The late Miocene mammal faunas of the Mytilinii Basin, Samos Island, Greece: new collection. 8. Proboscidea. In: Koufos GD, Nagel D (eds) The late Miocene Mammal Faunas of Samos, vol 31. Beit Paläontol Wien, pp 139–155

Konidaris GE, Koufos GD (2013a) Late Miocene Proboscidea (Mammalia) from Macedonia and Samos Island, Greece: preliminary results. Paläont Z 87:121–140

Konidaris GE, Koufos GD (2013b) The late Miocene proboscideans of Greece: taxonomy, bio-chronology, palaeoecology. 14th Congress of the Regional Committee on Mediterranean Stratigraphy (RCMNS), Istanbul

Konidaris GE, Koufos GD (2016) Proboscidea. In: Koufos GD, Kostopoulos DS (eds) Paleontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). Geobios 49:37–44

Konidaris GE, Koufos GD (2019) Late Miocene proboscideans from Samos Island (Greece) revis-ited: new specimens from old collections. Paläont Z 93:115–134

Konidaris GE, Roussiakis SJ (2017) *Anancus* (Proboscidea, Mammalia) from Chomateri – the first record of the genus in the late Miocene of Greece. 15th Congress of the Regional Committee on Mediterranean Neogene Stratigraphy (RCMNS), Athens

Konidaris GE, Roussiakis SJ (2019) The first record of *Anancus* (Mammalia, Proboscidea) in the late Miocene of Greece and reappraisal of the primitive anancines from Europe. J Vertebr Palaeontol:e1534118

Konidaris GE, Tsoukala E (2020) Proboscideans from the upper Miocene localities of Thermopigi, Neokaisareia and Platania (Northern Greece). Ann Paléontol 106:102380

Konidaris GE, Roussiakis SJ, Theodorou GE, Koufos GD (2014) The Eurasian occurrence of the shovel-tusker *Konobelodon* (Mammalia, Proboscidea) as illuminated by its presence in the late Miocene of Pikermi (Greece). J Vertebr Paleontol 34:1437–1453

Konidaris GE, Koufos GD, Kostopoulos DS, Merceron G (2016) Taxonomy, biostratigraphy and palaeoecology of *Choerolophodon* (Proboscidea, Mammalia) in the Miocene of SE Europe-SW Asia: implications for phylogeny and biogeography. J Syst Palaeontol 14:1–27

Konidaris GE, Roussiakis SJ, Athanassiou A, Theodorou GE (2017) The huge-sized deinothere *Deinotherium proavum* (Proboscidea, Mammalia) from the Late Miocene localities Pikermi and Halmyropotamos (Greece). Quat Int 430:5–21

Kostopoulos DS (2009) The Pikermian Event: temporal and spatial resolution of the Turolian large mammal fauna in SE Europe. Palaeogeogr Palaeoclimatol Palaeoecol 274:82–95

Koufos GD (1977) New finds of mastodonts from Macedonia (Greece). Sci Ann Fac Phys Mathem Univ Thessaloniki 17:97–115

Koufos GD (1980) Palaeontological and stratigraphical study of the continental Neogene deposits of Axios Basin. Ph.D. thesis, Sci Annals, Fac Phys & Mathem, Univ Thessaloniki, Greece 19:1–322

Koufos GD (2006) The Neogene mammal localities of Greece: Faunas, chronology and biostratigraphy. Hellenic J Geosci 41:183–214

Koufos GD (2013) Neogene mammal biostratigraphy and chronology of Greece. In: Wang X, Flynn LJ, Fortelius M (eds) Fossil mammals of Asia. Neogene biostratigraphy and chronology. Columbia University Press, New York, pp 596–621

Koufos GD, Kostopoulos DS (eds) (2016) Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). Geobios 49(1–2):1–154

Koufos GD, Nagel D (eds) (2009) The Late Miocene mammal faunas of Samos, vol 31. Beit Paläontol Wien

Koufos GD, Syrides GE (1997) A new Early/Middle Miocene mammal locality from Macedonia, Greece. C R Acad Sci Paris 325:511–516

Koufos GD, Zouros N, Mourouzidou O (2003) *Prodeinotherium bavaricum* (Proboscidea, Mammalia) from Lesvos island, Greece; the appearance of deinotheres in the eastern Mediterranean. Geobios 36:305–315

Koufos GD, Kostopoulos DS, Vlachou TD (2005) Neogene/Quaternary mammalian migrations in Eastern Mediterranean. Belgian J Zool 135:181–190

Kovachev D, Nikolov I (2006) *Deinotherium thraceiensis* sp. nov. from the Miocene near Ezerovo, Plovdiv District. Geol Balc 35:5–40

Kubiak H (1972) The skull of *Mammut praetypicum* (Proboscidea, Mammalia) from the collection of the Jagiellonian University in Cracow. Poland Acta Zool Cracoviensia 17:305–324

Lambert WD (1990) Rediagnosis of the genus *Amebelodon* (Mammalia, Proboscidea, Gomphotheriidae), with a new subgenus and species, *Amebelodon* (*Konobelodon*) *britti*. J Paleontol 64:1032–1040

Lambert WD, Shoshani J (1998) Proboscidea. In: Janis CM, Scott KM, Jacobs LL (eds) Evolution of tertiary mammals of North America. Cambridge University Press, Cambridge, pp 606–621

Lartet E (1859) Sur la dentition des proboscidiens fossiles (*Dinotherium*, Mastodontes et Éléphants) et sur la distribution géographique et stratigraphique de leurs débris en Europe. Bull Soc Géol Fr 16:469–515

Lazaridis G (2015) Study of the Late Miocene vertebrate locality of Kryopigi and other localities of Kassandra Peninsula, Chalkidiki (Greece). Systematics, taphonomy, paleoecology, biochronology. Ph.D. thesis, Sci Annals, School Geol, Aristotle Univ Thessaloniki, Greece 174, 1–355

Lazaridis G, Tsoukala E (2014a) *Choerolophodon pentelici* (Gaudry and Lartet, 1856) from the Turolian locality of Kryopigi (Kassandra, Chalkidiki, Greece). In: Kostopoulos DS, Vlachos E, Tsoukala E (eds) 6th international conference on mammoths and their relatives, Grevena-Siatista. Sci Annals, School Geol, Aristotle Univ Thessaloniki, Greece, sp vol 102:100

Lazaridis G, Tsoukala E (2014b) *Tetralophodon longirostris* (Kaup, 1832) from Late Miocene of the Kassandra peninsula (Chalkidiki, Greece). In: Kostopoulos DS, Vlachos E, Tsoukala E (eds) 6th international conference on mammoths and their relatives, Grevena-Siatista. Sci Annals, School Geol, Aristotle Univ Thessaloniki, Greece, sp vol 102:101

Lazaridis G, Kostopoulos DS, Lyras G, Roussiakis S (2017) A new Late Miocene ovibovine-like bovid (Bovidae, Mammalia) from the Kassandra Peninsula (Chalkidiki, Northern Greece) and implications to the phylogeography of the group. Paläontol Z 91:427–437

Lehmann U (1950) Über Mastodontenreste in der Bayerischen Staatssammlung in München. Palaeontogr Abt A 99:121–228

Lydekker R (1884) Additional Siwalik Perissodactyla and Proboscidea Memoirs of the Geological Survey of India. Palaeontol Indica 10:1–34

MacInnes DG (1942) Miocene and Post-Miocene Proboscidea from East Africa. Trans Zool Soc Lond 25:33–106

Maglio VJ (1974) A new proboscidean from the late Miocene of Kenya. Palaeontology 17:699–705

Markov GN (2008a) Fossil proboscideans (Mammalia) from the vicinities of Varna: a rare indication of middle Miocene vertebrate fauna in Bulgaria. Hist Nat Bulg 19:137–152

Markov GN (2008b) The Turolian proboscideans (Mammalia) of Europe: preliminary observations. Hist Nat Bulg 19:153–178

Markov GN, Vergiev S (2010) First report of cf. *Protanancus* (Mammalia, Proboscidea, Amebelodontidae) from Europe. Geodiversitas 32:493–500

Matsumoto H (1927) On two new mastodonts and an archetypal stegodont of Japan. Sci Rep Tohoku Imperial Univ 10:1–11

Mayet L (1908) Étude des mammifères miocènes des Sables de l'Orléanais et des Faluns de la Touraine. Ann Univ Lyon 24:1–336

Mazo AV, Montoya P (2003) Proboscidea (Mammalia) from the Upper Miocene of Crevillente (Alicante, Spain). Scr Geol 126:79–109

Mebrate A (1987) The long-jawed gomphotheres. Ph.D. thesis, University of Kansas

Melentis JK (1967) Die Pikermi-Fauna von Halmyropotamos (Euböa, Griechenland), 1. Teil: Odontologie und Kraniologie. Ann Géol Pays Hellén 19:283–411

Melentis JK (1969) Die Pikermi-Fauna von Halmyropotamos (Euböa, Griechenland), 2. Teil: Osteologie. Ann Géol Pays Hellén 28:217–306

Metz-Muller F (2000) La population d'*Anancus arvernensis* (Proboscidea, Mammalia) du Pliocène de Dorkovo (Bulgarie); étude des modalités évolutives d'*Anancus arvernensis* et phylogénie du genre *Anancus*. Ph.D. thesis, Muséum National d'Histoire Naturelle

Mitzopoulos MK (1967) *Zygolophodon borsoni* und *Anancus (Bunolophodon) arvernensis* aus dem Oberpliozän von Griechenland. Ann Géol Pays Hellén 18:436–446

Mol D, Tsoukala E, Batsi A (2010) A *Stegodon* from the area of Siatista (Kozani, Macedonia, Greece), the first evidence of the presence of *Stegodon* in Europe. In: 5th International conference on mammoths and their relatives Le Puy-en-Velay. Quaternaire, sp vol 102:85–87

Mothé D, Avilla LS, Asevedo L, Borges-Silva L, Rosas M, Labarca-Encina R, Souberlich R, Soibelzon E, Roman-Carrion JL, Ríos SD, Rincon AD, de Oliveira GC, Lopes RP (2017) Sixty years after 'The mastodonts of Brazil': The state of the art of South American proboscideans (Proboscidea, Gomphotheriidae). Quat Int 443:52–64

Mucha BB (1980) A new species of yoke-toothed mastodont from the Pliocene of Southwest USSR. In: Negadaev-Nikonov KN (ed) Quaternary and Neogene faunas and floras of Moldavskaya SSR. Shtiintsa, Kishinev, pp 19–26

Osborn HF (1918) A long-jawed mastodon skeleton from South Dakota and phylogeny of the Proboscidea. Bull Geol Soc Am Bull 29:133–137

Osborn HF (1921) First appearance of the true mastodon in America. Am Mus Novit 10:1–6

Osborn HF (1926) Additional new genera and species of the mastodontoid Proboscidea. Am Mus Novit 238:1–16

Osborn HF (1936) Proboscidea. A monograph of the discovery, evolution, migration and extinction of the mastodonts and elephants of the world, Volume I: Moeritherioidea, Deinotherioidea, Mastodontoidea. American Museum Press, New York

Ozansoy F (1965) Étude des gisements continentaux et des mammifères du Cénozoïque de Turquie. Mem Soc Géol Fr 102:1–92

Paraskevaidis I (1940) Eine obermiozäne Fauna von Chios. N Jb Min Geol Paläont 83:363–442

Paraskevaidis I (1977) Säugetierreste aus Griechenland. Proceedings of the 6th Colloquium on the Geology of the Aegean Region 3:1143–1154

Pickford M (2001) Afrochoerodon nov. gen. *kisumuensis* (MacInnes) (Proboscidea, Mammalia) from Cheparawa, Middle Miocene, Kenya. Ann Paléontol 87:99–113

Pickford M, Pourabrishami Z (2013) Deciphering Dinotheriensande deinotheriid diversity. Palaeobiodivers Palaeoenviron 93:121–150

Pilgrim GE (1913) The correlation of the Siwaliks with mammal horizons of Europe. Rec Geol Surv India 43:264–326

Pohlig H (1988) Dentition und Kraniologie des *Elephas antiquus* Falc. mit Beiträgen über *Elephas primigenius* Blum. und *Elephas meridionalis* Nesti. Nova Acta Ksl Leop-Carol Deutsch Akad Naturf 53:1–280

Poulakakis N, Lymberakis P, Fassoulas C (2005) *Deinotherium giganteum* (Proboscidea, Deinotheriidae) from the late Miocene of Crete. J Vertebr Paleontol 25:732–736

Qiu ZX, Wang BJ, Li H, Deng T, Sun Y (2007) First discovery of deinothere in China. Vertebr Palas 45:261–277

Rögl F (1999) Circum-Mediterranean Miocene paleogeography. In: Rössner GE, Heissig K (eds) The Miocene land mammals of Europe. Verlag Dr. Friedrich Pfeil, München, pp 39–48

Rook L, Croitor R, Delfino M, Ferretti MP, Gallai G, Pavia M (2013) The Upper Valdarno Plio-Pleistocene vertebrate record: an historical overview, with notes on palaeobiology and stratigraphic significance of some important taxa. Ital J Geosci 132:104–125

Roussiakis S, Athanassiou A, Michailidis D, Mitsopoulou V, Solomos C, Theodorou G (2014) Remarks on new proboscidean remains from the classical Late Miocene locality of Pikermi and their associated fauna. In: Kostopoulos DS, Vlachos E, Tsoukala E (eds) 6th International Conference on Mammoths and their Relatives. Grevena-Siatista. Sci Annals, School Geol, Aristotle Univ Thessaloniki, Greece, sp vol 102:171–172

Saegusa H, Thasod Y, Ratanasthien B (2005) Notes on Asian stegodontids. Quat Int 126–128:31–48

Sakellariou-Mane H (1972) Presence d'*Anancus arvernensis* dans les couches supérieures du Pliocène de la Valée du Vardar. Folia Biochim Biol Graeca 9:31–36

Sanders WJ (2003) Proboscidea. In: Fortelius M, Kappelman J, Sen S, Bernor RL (eds) Geology and paleontology of the Miocene Sinap formation. Turkey. Columbia University Press, New York, pp 202–219

Sanders WJ (2007) Taxonomic review of fossil Proboscidea (Mammalia) from Langebaanweg, South Africa. Trans Royal Soc S Afr 62:1–16

Sanders WJ (2008) Review of fossil Proboscidea from the Late Miocene-Early Pliocene site of As Sahabi, Libya. In: Boaz NT, El-Arnauti A, Pavlakis P, Salem MJ (eds) Circum-Mediterranean geology and biotic evolution during the Neogene period: the perspective from Libya. University of Garyounis, Benghazi, pp 241–256

Sanders WJ (2011) Proboscidea. In: Harisson T (ed) Paleontology and geology of laetoli: human evolution in context. Volume 2: fossil hominins and the associated fauna, Vertebrate paleobiology and paleoanthropology. Springer, pp 233–262

Sanders WJ (2018) Horizontal tooth displacement and premolar occurrence in elephants and other elephantiform proboscideans. Hist Biol 30:137–156

Sanders WJ, Gheerbrant E, Harris JM, Saegusa H, Delmer C (2010) Proboscidea. In: Werdelin L, Sanders WJ (eds) Cenozoic mammals of Africa. University of California Press, Berkeley, pp 161–251

Saunders J (1996) North American Mammutidae. In: Shoshani J, Tassy P (eds) The probosci-
    dea: evolution and palaeoecology of elephants and their relatives. Oxford University Press,
    New York, pp 271–279

Schlesinger G (1917) Die Mastodonten des K. K. Naturhistorischen Hofmuseums. Denkschr K K
    Nat Hofmus 1:1–230

Schlesinger G (1922) Die Mastodonten der Budapester. Sammlungen Geol Hung 2:1–284

Schlosser M (1907) Ueber Säugetiere und Süsswassergastropoden aus Pliocänablagerungen
    Spaniens und über die natürliche Grenze von Miocän und Pliocän. N Jb Min Geol Paläont 2:1–41

Schmidt-Kittler N, de Bruijn H, Doukas C (1995) 1. General introduction. In: Schmidt-Kittler
    N (ed) The vertebrate locality of Maramena (Macedonia, Greece) at the Turolian-Ruscinian
    boundary (Neogene), vol 28. Münchner Geowiss Abh, München, pp 9–18

Seiffert ER, Nasir S, Al-Harthy A, Groenke J, Kraatz B, Stevens N, Al-Sayigh A (2012) Diversity
    in the later Paleogene proboscidean radiation: a small barytheriid from the Oligocene of Dhofar
    Governorate, Sultanate of Oman. Naturwiss 99:133–141

Shoshani J (1996) Para- or monophyly of the gomphotheres and their position within Proboscidea.
    In: Shoshani J, Tassy P (eds) The Proboscidea: evolution and palaeoecology of elephants and
    their relatives. Oxford University Press, New York, pp 149–177

Shoshani J (1998) Understanding proboscidean evolution: a formidable task. Trends Ecol Evol
    13:480–487

Shoshani J (2002) Proboscidea (Elephants). eLS. Wiley

Shoshani J, Tassy P (1996a) Summary, conclusions, and a glimpse into the future. In: Shoshani J,
    Tassy P (eds) The proboscidea: evolution and palaeoecology of elephants and their relatives.
    Oxford University Press, New York, pp 335–348

Shoshani J, Tassy P (eds) (1996b) The proboscidea: evolution and palaeoecology of elephants and
    their relatives. Oxford University Press, New York

Shoshani J, Tassy P (2005) Advances in proboscidean taxonomy and classification, anatomy and
    physiology, and ecology and behavior. Quat Int 126–128:5–20

Shoshani J, Golenberg EM, Yang H (1998) Elephantidae phylogeny: morphological versus molec-
    ular results. Acta Theriologica 5:89–122

Shoshani J, Walter RC, Abraha M, Berhe S, Tassy P, Sanders WJ, Marchant GH, Libsekal Y,
    Ghirmai T, Zinner D (2006) A proboscidean from the late Oligocene of Eritrea, a "missing
    link" between early Elephantiformes and Elephantimorpha, and biogeographic implications.
    Proc Natl Acad Sci 103:17296–17301

Steensma KJ (1988) Plio-/Pleistozäne Großsäugetiere (Mammalia) aus dem Beckem von Kastoria/
    Grevena, südlich von Neapolis - NW-Griechenland. Ph.D. thesis, Technische Universität
    Clausthal

Stefanescu G (1892) On the existence of the *Dinotherium* in Roumania. Bull Geol Soc Am 3:81–83

Symeonidis NK, Tataris A (1983) The first results of the geological and palaeontological study of
    the Sesklo basin and its broader environment (Eastern Thessaly, Greece) (in Greek). Ann Géol
    Pays Hellén 31:146–190

Syrides GE (1990) Lithostratigraphic, biostratigraphic and palaeogeographic study of the
    Neogene-Quaternary sedimentary deposits of Chalkidiki peninsula, Macedonia, Greece (in
    Greek). Ph.D. thesis, Sci Annals, School Geol, Aristotle Univ Thessaloniki, Greece 1:1–243

Tarabukin BA (1974) New data on the systematics, phylogeny and ecology of Suborder
    Deinotherioidea Osborn (1921). In: Mammals of the late Cenozoic from Southwestern USSR,
    Kishinev, pp 77–90

Tassy P (1985) La place des mastodontes Miocènes de l'Ancien Monde dans la phylogénie
    des Proboscidea (Mammalia): Hypothèses et conjectures. Ph.D. thesis, Université Pierre et
    Marie Curie

Tassy P (1986) Nouveaux Elephantoidea (Mammalia) dans le Miocène du Kenya. CNRS, Paris

Tassy P (1990) The "Proboscidean Datum Event": how many proboscideans and how many
    events? In: Linsday EH, Mein P, Fahlbusch V (eds) European Neogene mammal chronology.
    Plenum Press, New York, pp 237–252

Tassy P (1994) Origin and differentiation of the Elephantiformes (Mammalia, Proboscidea). Verh Nat Ver Hamb 34:73–94

Tassy P (1996a) Who is who among the Proboscidea? In: Shoshani J, Tassy P (eds) The Proboscidea: evolution and palaeoecology of elephants and their relatives. Oxford University Press, New York, pp 39–48

Tassy P (1996b) The earliest gomphotheres. In: Shoshani J, Tassy P (eds) The Proboscidea: evolution and palaeoecology of elephants and their relatives. Oxford University Press, New York, pp 89–91

Tassy P (1999) Miocene Elephantids (Mammalia) from the Emirate of Abu Dhabi, United Arab Emirates: palaeobiogeographic implications. In: Whybrow PJ, Hill A (eds) Fossil vertebrates of Arabia. Yale University Press, New Haven/London, pp 209–233

Tassy P (2005) Proboscideans (Mammalia) from the late Miocene of Akkaşdağı, Turkey. In: Sen S (ed) Geology, mammals and environments at Akkaşdağı, late Miocene of Central Anatolia, vol 27. Geodiversitas, Paris, pp 707–714

Tassy P (2016) Proboscidea. In: Sen S (ed) Late Miocene mammal locality of Küçükçekmece, European Turkey, vol 38. Geodiversitas, Paris, pp 261–271

Tassy P (2018) Remarks on the cranium of *Eozygodon morotoensis* (Proboscidea, Mammalia) from the early Miocene of Africa, and the question of the monophyly of Elephantimorpha. Rev Paléobiol 37:593–607

Tassy P, Sen S, Jaeger JJ, Mazin JM, Dalfes N (1989) Une sous-espèce nouvelle de *Choerolophodon pentelici* (Proboscidea, Mammalia) à Esme Akçaköy, Miocène supérieur d'Anatolie occidentale. C R Acad Sci Paris 309:2143–2146

Theodorou G, Spjeldnaes N, Hanken NM, Lauritzen SE, Velitzelos E, Athanassiou A, Roussiakis S (2000) Description and taphonomic investigations of Neogene Proboscidea from Rhodos, Greece. Ann Géol Pays Hellén 38:133–156

Theodorou G, Athanassiou A, Roussiakis S, Iliopoulos G (2003) Preliminary remarks on the Late Miocene herbivores of Kerassiá (Northern Euboea, Greece). In: Reumer JWF, Wessels W (eds) Distribution and migration of Tertiary Mammals in Eurasia. A volume in honour of Hans de Bruijn, vol 10. Deinsea, Rotterdam, pp 519–530

Theodorou GE, Roussiakis SJ, Athanassiou A, Filippidi A (2010) Mammalian remains from a new site near the classical locality of Pikermi (Attica, Greece). In: Christofides G, Kantiranis N, Kostopoulos DS, Chatzipetros AA (eds) 19th CBGA Congress, Thessaloniki. Sci Annals, School Geol, Aristotle Univ Thessaloniki, Greece sp vol 99:109–119

Tobien H (1973) On the evolution of mastodonts (Proboscidea, Mammalia). Part I: The bunodont trilophodont groups. Notizbl hess Landesamt Bodenforsch 101:202–276

Tobien H (1978) On the evolution of mastodonts (Proboscidea, Mammalia). Part 2: The bunodont tetralophodont groups. Geol Jb Hessen 106:159–208

Tobien H (1980) A note on the skull and mandible of a new choerolophodont mastodont (Proboscidea, Mammalia) from the middle Miocene of Chios (Aegean Sea, Greece). In: Jacobs LL (ed) Aspects of vertebrate history: essays in honor of Edwin Harris Colbert. Museum of Northern Arizona Press, Flagstaff, pp 299–307

Tobien H (1996) Evolution of zygodons with emphasis on dentition. In: Shoshani J, Tassy P (eds) The Proboscidea: evolution and palaeoecology of elephants and their relatives. Oxford University Press, New York, pp 76–85

Tsoukala E (2000) Remains of a Pliocene *Mammut borsoni* (Hays, 1834) (Proboscidea, Mammalia), from Milia (Grevena, W. Macedonia, Greece). Ann Paléontol 86:165–191

Tsoukala E (2018) Rhinocerotidae from the Late Miocene and Late Pliocene of Macedonia, Greece. A revision of the Neogene-Quaternary Rhinocerotidae of Greece. Rev Paléobiol 37:609–630

Tsoukala ES, Melentis JK (1994) *Deinotherium giganteum* Kaup (Proboscidea) from Kassandra peninsula (Chalkidiki, Macedonia, Greece). Geobios 27:633–640

Tsoukala E, Mol D (2016) The Proboscidea of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). Quat Int 406:4–24

Tsoukala E, Vaxevanopoulos M, Lazaridis G (2007) Neogene mammalian remains from Dikaia (Evros, Thrace, Greece). The Archaeological Work in Macedonia and Thrace 2005, 19:1–11

Vacek M (1877) Über österreichische Mastodonten und ihre Beziehungen zu den Mastodon-Arten Europas. Abh Kais-Königlichen geol Reichenstalt 7:1–45

van der Maarel FH (1932) Contributions to the knowledge of the fossil mammalian fauna of Java. Wetenschappelijke Mededelingen Dienst van den Mijnbouw in Nederlandsch-Indië 15:1–208

van der Made J, Moyà-Solà S (1989) European Suinae (Artiodactyla) from the Late Miocene onwards. Boll Soc Paleontol Ital 28:329–339

von Koenigswald W, Göhlich UB (2019) Biogeography of Mammutidae (Proboscidea) or What's your name again? *Mammut*?, 90th Annual Meeting of the Paläontologische Gesellschaft. Staatliche Naturwissenschaftliche Sammlungen Bayerns - Bayerische Staatssammlung für Paläontologie und Geologie, Munich, p 83

von Meyer H (1831) Mittheilung an geheimen Rath von Leonhard. Jb Min Geogn Geol Petrefaktenkunde 2:296–297

von Meyer H (1833) Das *Dinotherium bavaricum*, mit Rückshicht auf die riesenmäßige fossile Thiergattung der Dinotherien überhaupt, und auf die Struktur der Mahlzähne in den Tapiren. Verh Kais Leopoldinisch-Carolinischen Akad Naturforsch 16:487–516

Vörös I (1989) *Prodeinotherium petenyii* sp. n. from the Lower Miocene at Putnok (North Hungary). Fragm Min Palaeont 14:101–110

Wagner A (1848) Urweltliche Säugthier-Ueberreste aus Griechenland. Abh bayerisch Akad Wiss 5:335–378

Wagner A (1857) Neue Beiträge zur Kenntnis der fossilen Säugthier-Ueberreste von Pikermi. Abh bayerisch Akad Wiss 8:109–158

Wang SQ, Deng T (2011) The first *Choerolophodon* (Proboscidea, Gomphotheriidae) skull from China Science. China Earth Sci 54:1326–1337

Wang SQ, Shi QQ, He W, Chen SQ, Yang XW (2016) A new species of the tetralophodont amebelodontine *Konobelodon* Lambert, 1990 (Proboscidea, Mammalia) from the Late Miocene of China. Geodiversitas 38:65–97

Wang SQ, Deng T, Ye J, He W, Chen SQ (2017a) Morphological and ecological diversity of Amebelodontidae (Proboscidea, Mammalia) revealed by a Miocene fossil accumulation of an upper-tuskless proboscidean. J Syst Palaeontol 15:601–615

Wang SQ, Saegusa H, Duangkrayom J, He W, Chen SQ (2017b) A new species of *Tetralophodon* from the Linxia Basin and the biostratigraphic significance of tetralophodont gomphotheres from the Upper Miocene of Northern China. Palaeoworld 26:703–717

Weinsheimer O (1883) Über *Dinotherium giganteum* Kaup. Palaeontol Abh 1:207–281

Weithofer KA (1888) Beiträge zur Kenntnis der Fauna von Pikermi bei Athen. Beitr Paläontol Österr-Ung 6:225–292

Weithofer KA (1890) Die fossilen Proboscidier des Arnothales in Toskana. Beit Palaeontol Oesterr – Ungarns und des Orients 8:107–240

Zapfe H (1957) Ein bedeutender *Mastodon*-Fund aus dem Unterpliozän von Niederösterreich. N Jb Geol Palaeont Abh 104:382–406