

The Fossil Record of Continental Elephants and Mammoths (Mammalia: Proboscidea: Elephantidae) in Greece



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1 Introduction

The family Elephantidae Gray, 1821, is the evolutionary most derived clade of the order Proboscidea. It comprises very large-sized proboscidean mammals that share in common a suite of morphologic characters, such as the anteroposteriorly shortened skull with pneumatized cranial bones; the long, columnar extremities; and the multiplication of dental cusps, resulting in a lamellar molar structure. Quite like the other derived proboscidean families (see Konidaris and Tsoukala [this volume](#)), the Elephantidae also have long tusks, horizontal replacement of the cheek teeth, and a long trunk.

As it is the case with most proboscidean families, the Elephantidae emerged in Africa. This happened in the late Miocene (about 9–7 Ma), during the last major radiation event of the African Proboscidea (Maglio 1973; Todd and Roth 1996; Sanders et al. 2010). Starting in the late Pliocene, members of the family migrated repeatedly out of the continent and dispersed rapidly across Eurasia. During the Early Pleistocene, they colonised North America, but failed to disperse to South America, where the already established—though evolutionary more basal—gomphotheriids continued to thrive. As a consequence of the family's late migration out of Africa, the Elephantidae of Eurasia and America were already highly derived forms within proboscideans. They maintained their nearly ubiquitous presence in the Northern Hemisphere as essential members of the megaherbivore faunas until the latest Pleistocene–early Holocene, when they succumbed widely to the extensive end-Pleistocene megafaunal extinction. At present, the family's geographic

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distribution, taxonomic diversity, and populations are extremely reduced, primarily because of habitat loss due to the expansion of human activities. The present populations are restricted in patchy regions of sub-Saharan Africa and SE Asia and are classified to the African genus *Loxodonta* Cuvier, 1825—with two species, *L. africana* (Blumenbach, 1797) and *L. cyclotis* (Matschie, 1900)—and the Asian *Elephas* Linnaeus, 1758, with one species, *E. maximus* Linnaeus, 1758.

Except for the extant *Elephas*, Eurasia has accommodated three additional elephantid genera during the late Neogene and Quaternary: *Stegotrabelodon* Petrocchi, 1941; *Mammuthus* Brookes, 1828; and *Palaeoloxodon* Matsumoto, 1924. The last two have an important fossil record in the whole continent, as well as in the territory of Greece in particular. *Stegotrabelodon* is a less derived taxon, documented in just a few upper Miocene–lower Pliocene localities of Eurasia (Tassy 1999; Ferretti et al. 2017), and it is not considered here, because it is as yet unknown in the fossil record of Greece. Another fossil group not addressed in the present review is the dwarf insular elephant forms, evolved after successful colonisation of remote islands. These are presented by Lyras et al. (volume 2).

Methods Upper and lower molars are abbreviated as M and m respectively; deciduous molars as D/d (e.g., M2, m3, D4, etc.). The measurements and indices were taken and calculated according to Maglio (1973). In particular, the lamellar frequency of molars is calculated as the number of lamellae per 10 cm of molar length, and the hypsodonty index as the percentage of molar height with respect to molar width. All measurements include cement. The length is measured perpendicular to the average direction of the lamellae. The geochronologic and stratigraphic framework follows Pillans and Gibbard (2012). Geochronologic ages are given, where available, in thousand or million years before present, abbreviated as ‘ka’ or ‘Ma’, respectively. ‘MIS’ stands for ‘Marine Isotope Stage’, ‘MNQ’ for ‘Mammal Neogene and Quaternary Zones’ (Guérin 1990), and ‘ICZN’ for ‘International Code of Zoological Nomenclature’. Transliterated local geographic names are typed accented when necessary, in order to help with their correct pronunciation.

2 Phylogenetic Relationships and Taxonomy

Traditionally, the phylogenetic roots of Elephantidae were usually placed among the Stegodontidae Osborn, 1918, close to a form morphologically similar to the genera *Stegodon* or *Stegolophodon* (Osborn 1936; Aguirre 1969). Indeed, both families exhibit similar specialisations, such as a fore-and-aft shearing movement of the jaws during mastication and the dense packing of transverse ridges in molars, and they have been placed together in the past as subfamilies within Elephantidae (e.g., Kalb and Mebrate 1993; Kalb and Froehlich 1995). More recent studies have shown, however, that these characters are rather convergent and do not indicate a phylogenetic relationship. Moreover, the stegodonts were already advanced enough to be considered as ancestors of the elephants (Maglio 1973; Tassy 1996; Todd and Roth

1996). Instead, the ancestry of the Elephantidae (and the Stegodontidae as well) is currently traced to the late Neogene tetralophodont gomphotheres of Africa, i.e., those members of Gomphotheriidae with four lophs/lophids in the intermediate molars (D4–M2 and d4–m2) (see, e.g., Maglio 1973; Tassy 1996). Advanced gomphotheriids already showed trends towards cranial rostrocaudal shortening, that characterises the Elephantidae, while the highly derived elephant molar morphology resulted from the rearrangement of the main and accessory cusps in order to form transverse enamel ridges.

This particular lamellar molar structure, i.e., the merging of the lingual and buccal cusps into a mesiodistally compressed plate (lamella), is the synapomorphy that unites the Elephantidae. Several successive plates (at least six in m3/M3), joined to each other with cement, form the elephantid molar (Kalb and Mebrate 1993; Todd and Roth 1996). With advancing dental wear, this structure forms transverse enamel loops on the occlusal surface. The family is further subdivided in two subfamilies, Stegotetabelodontinae Aguirre, 1969, and Elephantinae Gray, 1821, which appear to be phylogenetically sister taxa (Kalb and Mebrate 1993; Kalb and Froehlich 1995; Tassy and Debruyne 2001), although a direct ancestor–descendant relationship between them has been also proposed in the past (e.g., Maglio 1973; Coppens et al. 1978). The Stegotetabelodontinae are monotypic and include only the genus *Stegotetabelodon* Petrocchi, 1941, which still retains several gomphothere-like characters, such as the long mandibular symphysis bearing a pair of long tusks, the presence of premolars, the presence of a well-developed median sulcus between the lingual and buccal cusps/cuspids (in unworn or little worn molars only), and the occurrence of central conules in the molars (Maglio 1973; Coppens et al. 1978; Sanders et al. 2010). The Elephantinae include all the other genera of the family, namely, *Stegodibelodon* Coppens, 1972; *Primelephas* Maglio, 1970; *Mammuthus* Brookes, 1828; *Elephas* Linnaeus, 1758; *Palaeoloxodon* Matsumoto, 1924; and *Loxodonta* Cuvier, 1825. Collectively, they are characterised by a tuskless mandible with shortened symphysis, true lamellar structure of the molars (totally obliterated median sulcus), and at least seven lamellae in M3/m3 (Kalb and Mebrate 1993; Todd and Roth 1996; Sanders et al. 2010). *Stegodibelodon* and *Primelephas* are the most primitive genera, featuring brachyodont molars with few lamellae. Both are monotypic and differ from *Stegotetabelodon* in the absence of lower tusks and the more apparent lamellar structure of the molars. Because of its plesiomorphic morphology, *Stegodibelodon* has previously been placed by certain authors in the Stegotetabelodontinae (for a comprehensive review of the various proposed taxonomic schemes, see Kalb and Mebrate 1993). *Mammuthus*, *Elephas*, *Palaeoloxodon*, and *Loxodonta* constitute the most derived genera of the Elephantidae (note, however, that *Palaeoloxodon* has been often considered until recently as a subgenus of *Elephas*; e.g., Palombo and Ferretti 2005). *Mammuthus*, *Elephas*, and *Loxodonta* emerged in Africa as archaic forms during the late Miocene–early Pliocene and followed similar evolutionary trends across their distinct clades, which mainly involve shortening of the skull and mandible, increasing number of dental lamellae, and increasing hypsodonty (Maglio 1973; Todd and Roth 1996; Sanders et al. 2010). *Palaeoloxodon* is most typically known from the Middle–Late Pleistocene of

Eurasia, but the immediate ancestry of the Eurasian species can be traced to *P. recki* (Dietrich, 1916) from the Plio-Pleistocene of East Africa (Maglio 1973; Beden 1983; Saegusa and Gilbert 2008). *Loxodonta* remained an exclusively African taxon from its first appearance until today. On the contrary, *Mammuthus*, *Elephas*, and *Palaeoloxodon* migrated out of their continent of origin through at least three migration events during the late Pliocene–Early Pleistocene (Maglio 1973).

The phylogenetic relationships among the derived Elephantidae remain as yet not fully resolved, despite the numerous classifications published after Osborn's (1936, 1942) monumental opus (for an overview, see Tassy 1990; Tassy and Shoshani 1996). Morphology-based phylogenies usually place *Elephas* (including *Palaeoloxodon*) close to *Mammuthus* and consider *Loxodonta* as a sister taxon of the former two (Beden 1979; Tassy 1990, 1996; Shoshani 1996; Shoshani et al. 1998, 2007; Shoshani and Tassy 2005; Sanders et al. 2010). However, different phylogenetic trees, also deriving from morphological data, exist as well. Maglio (1973, figs 13, 15) considered that these three genera derived as independent lineages from *Primelephas*. Todd (2010), based on cranial and dental morphology, found that *Loxodonta* and *Elephas* (including *Palaeoloxodon*) derived from *Primelephas*, while the *Mammuthus* lineage was traced back to *Stegotetrabelodon*. Phylogenetic studies involving molecular data still support the traditional *Elephas*–*Mammuthus* clustering (e.g., Yang et al. 1996; Ozawa et al. 1997). Nevertheless, a *Mammuthus*–*Loxodonta* clade has been also indicated as most probable as well (Hagelberg et al. 1994; Thomas et al. 2000). Recently, Meyer et al. (2017) and Palkopoulou et al. (2018) clustered *Elephas* with *Mammuthus*, and *Palaeoloxodon* with *Loxodonta*, and noted that *Palaeoloxodon*'s genome has also an *Elephas* and a *Mammuthus* component, illustrating a quite complicated picture of elephantid phylogeny and interrelationships.

3 Historical Overview and Distribution

Fossil remains of elephants were known in Greece since the Antiquity, but they were not recognised as such. Instead, they were thought of as bones of mythical, huge-sized anthropomorphic creatures, such as Giants or Cyclopes. Pausanias, a Greek geographer of the second century AD, mentioned the presence of huge bones in the Megalopolis area (central Peloponnese), which he attributed to fallen Giants, after a fierce battle between them and the Gods. According to a well-known ancient myth, the battle had taken place in this area. The Megalopolis Basin is presently well known as a rich area in fossil mammal sites. Interestingly, the oldest known scientific account to me on fossil elephantids from Greece (Roth 1854) explicitly mentions the presence of numerous elephant remains in this basin, while Kandeloros (1898, p. 8) and Bürchner (1903) recorded information made available to them by local people, according to which huge bones were unearthed in the area in the late 1830s and the 1850s. A few years later, Mitzopoulos et al. (1862) reported very briefly on the excavation of an elephant molar in August 1861 at an undefined

findspot near the village Leontári, within the same basin. Later on, the exposure of rich fossil accumulations in the same region due to erosion was the occasion for extensive excavations by Prof. Theodor Skuphos (also transliterated as Skouphos or Skoufos; University of Athens) at two sites, Íssoma and Kalývia Karyón (Bürchner 1903; Skuphos 1905). According to Bürchner (1903), among the finds were numerous elephant fossils, including an allegedly complete skeleton with skull (Fig. 1).

Since the first fossil discoveries in Megalopolis Basin, proboscidean fossils have been recovered in numerous other localities from Greece (see Figs. 2, 3 and Appendix), being one of the richest and widely distributed vertebrate groups in the country. Other early references to elephant fossils were similarly very brief and anecdotal, usually providing neither a description, nor any photograph of the finds, and are not mentioned here (see Appendix for a more complete list). During the 1950s and later, there was a marked increase in the vertebrate palaeontological research within the Greek territory, resulting in new occurrences of both mammoths and elephants. Psarianos and Thenius (1954) were the first authors to describe an elephantid fossil from Greece in detail: they studied a lower third molar referred to *Elephas (Archidiskodon) meridionalis* (= *Mammuthus meridionalis*) from Giáltra, Aedipsós region, N. Euboea, a single find collected from a conglomerate layer within a lignite sequence. Four years later, one of these authors (Psarianos 1958) reported on isolated molars from W. Macedonia (localities Tsotyli and Polylakkos) and E. Macedonia (Phlíppi) and attributed them to species of the *Mammuthus*



Fig. 1 A partial skull with tusk(s) referred to *Palaeoloxodon antiquus*, in right lateral view, during the excavation of Prof. Th. Skuphos (University of Athens) in Megalopolis Basin, 1902 (photograph by Th. Skuphos). This is quite possibly the skull from the area of the village Íssoma, mentioned by Bürchner (1903), which is considered lost

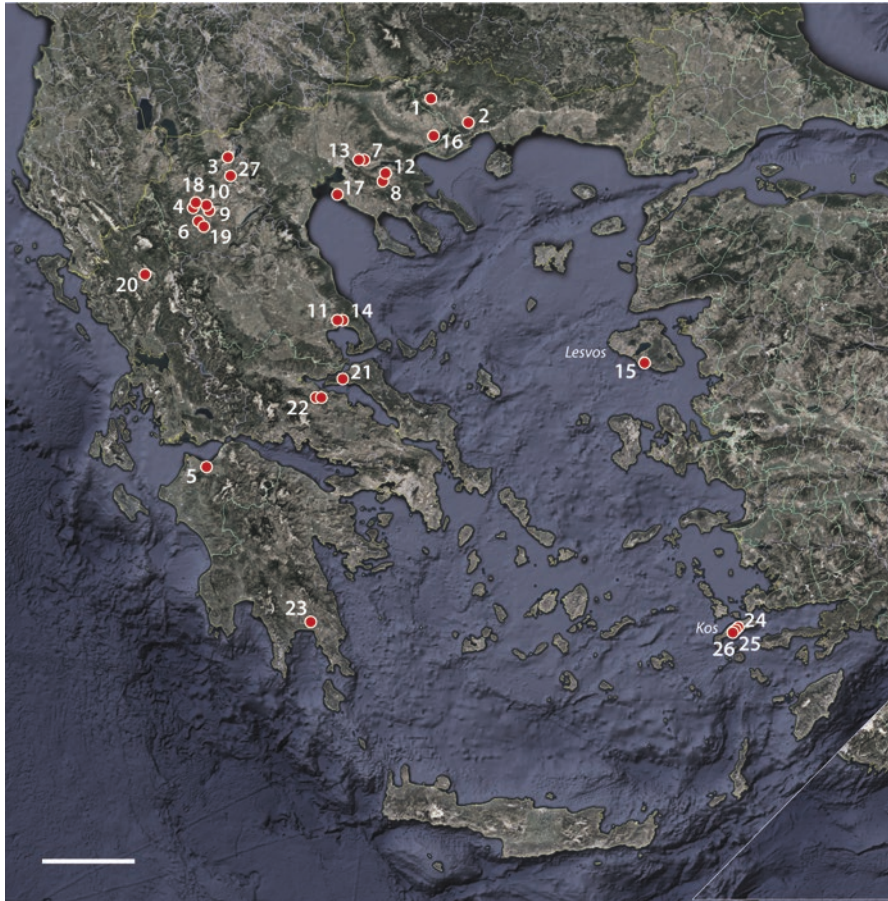


Fig. 2 Map of Greece showing the geographic distribution of localities with continental elephants referred to the genus *Mammuthus* (including a possible occurrence marked with question mark). Geographically adjacent localities are grouped together under the same numbered bullet: **1**, Angítis; **2**, Phílippi; **3**, Sotíras; **4**, Tsoytíli; **5**, Loussiká; **6**, Polýlakkos, Peponiá; **7**, Apolloniá; **8**, Kalamotó localities; **9**, Kapetánios; **10**, Libákos; **11**, Sesklo; **12**, Tsiótra Vryssi; **13**, Gerakarou; **14**, Halykés(?); **15**, Vaterá localities; **16**, Symbolí; **17**, Epanomí; **18**, Kípi; **19**, Q-Profil; **20**, Ioánnina (exact location unknown); **21**, Giáltra; **22**, Reghínio, Zéli; **23**, Vlachiótis; **24**, Antimáchia; **25**, Kardámaena; **26**, Almyrí; **27**, Kardiá. 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

lineage (*Archidiskodon meridionalis*, *A. cf. meridionalis* and *Mammonteus trogontherii*, respectively). There is no further faunal, geographic, or geologic information about the localities. According to Koulidou (2013), one of the *M. meridionalis* molars actually belongs to *M. rumanus*, due to its very low lamellar frequency. Shortly later, Melentis (1960) published another isolated find, a lower third molar, from an unknown locality in the Ioánnina region, Epirus, which he determined

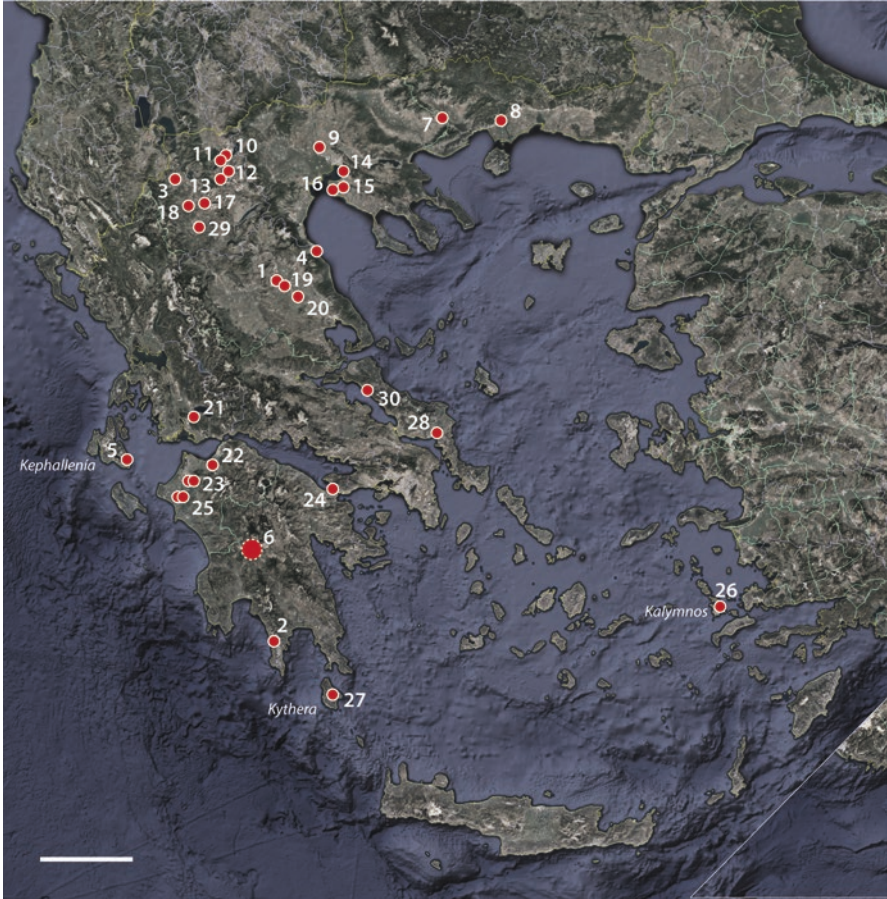


Fig. 3 Map of Greece showing the geographic distribution of localities with continental elephants referred to the genus *Palaeoloxodon* (including certain insecure occurrences marked with question mark). Geographically adjacent localities are grouped together under the same numbered bullet: **1**, Peniós Valley; **2**, Kalamákia Cave; **3**, Tsákoní(?); **4**, Peniós estuary; **5**, Póros; **6**, various localities in Megalópolis Basin (Kyparíssia, Marathousa, Íssoma, Íssoma KYT, Kalývia Karyón, Léfkro, Leontári); **7**, Symbolí; **8**, Xeriás; **9**, Ravin de l'éléphant(?); **10**, Pétres, Sotíras; **11**, Amýntaio, Philótas; **12**, Lágoúra(?); **13**, Ptolemaís; **14**, Allatíni(?); **15**, Trílophos(?); **16**, Epanomí(?); **17**, Kalonéri; **18**, Tsotýli; **19**, Terpsithéa; **20**, Néa Léfkí, Chálki; **21**, Trichonía; **22**, Pátras; **23**, Nissí, Sími; **24**, Canal of Corinth; **25**, Roupáki, Ano Olga(?); **26**, Kálymnos; **27**, Kýthera; **28**, Alivéri; **29**, Ambéllia (Grevená); **30**, Límni(?). 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

taxonomically down to the subspecies level: *Elephas (Archidiskodon) meridionalis archaicus* Depéret and Mayet, 1923. The find exhibits indeed all the characters of *M. meridionalis* and can be attributed to this species, though a subspecific classification is not justified according to the current taxonomic practice.

The following year, Melentis initiated a series of publications on the rich fossil material excavated by Skuphos in 1902 in the Megalopolis Basin, of which the elephantid remains constituted a significant component (Melentis 1961, 1963; Fig. 4). Note, however, that the skull mentioned by Bürchner (1903) and photographed by Skuphos (Fig. 1) is not included in the sample studied by Melentis, presumably because meanwhile it had been severely damaged or destroyed. Its whereabouts is currently unknown. Melentis (1961, 1963) described the material in every possible detail and concluded to an extreme taxonomic diversity of elephant species within the uppermost part of the basin's sedimentary sequence (Íssoma section; Melentis 1961, p. 242), recognizing no less than six taxa: *Palaeoloxodon antiquus antiquus*, *P. antiquus italicus*, *P. melitensis*, *Archidiskodon meridionalis meridionalis*, *A. meridionalis cromerensis*, and *Mammonteus primigenius primigenius*. Thus, the sequence was considered by the author as spanning the entire Pleistocene. More recently, it has been documented that the Megalopolis Basin



Fig. 4 Craniodental specimens from the Megalopolis Basin, referred to *Palaeoloxodon antiquus*. Both were published by Melentis (1961), who reported that they come from the locality Íssoma (Skuphos excavations, 1902). (a) A maxillary part with both M3s (MEG 1960/70), occlusal view. The rostral end is at the bottom of the figure. (b) A right m3 (MEG 1960/77), occlusal view. (c) The same specimen in lingual view. Note the characteristic for this species narrow crowns, with plicate enamel that forms median sinuses, and the 'dot-dash-dot' wear pattern in incipiently worn lamellae. Both specimens, as well as their original photographs used here, belong to the collections of the Museum of Paleontology and Geology, University of Athens. Scale bar equals 10 cm

lignite sequence (Marathousa member) was deposited during the Middle Pleistocene (e.g., van Vugt et al. 2000; Tourloukis et al. 2018). The Íssoma section extends (at least mainly) in a detrital sequence that overlies unconformably the Marathousa member and could be of late Middle–Late Pleistocene age. Consequently, Melentis’ elephantid taxa list has to be revised. Indeed, a re-examination of the available material (including unpublished samples stored in the Museum of Paleontology and Geology, University of Athens) shows that the dental specimens referred by Melentis (1961) to *A. meridionalis* are very similar to those he referred to *P. antiquus*, being hypsodont molars with narrow crowns and *P. antiquus*-type wear patterns (see Fig. 4 for a representative sample), as well as tusks that exhibit weak bent and torsion, and well obtuse Schreger angles in their dentine (see Fig. 5 for an example of

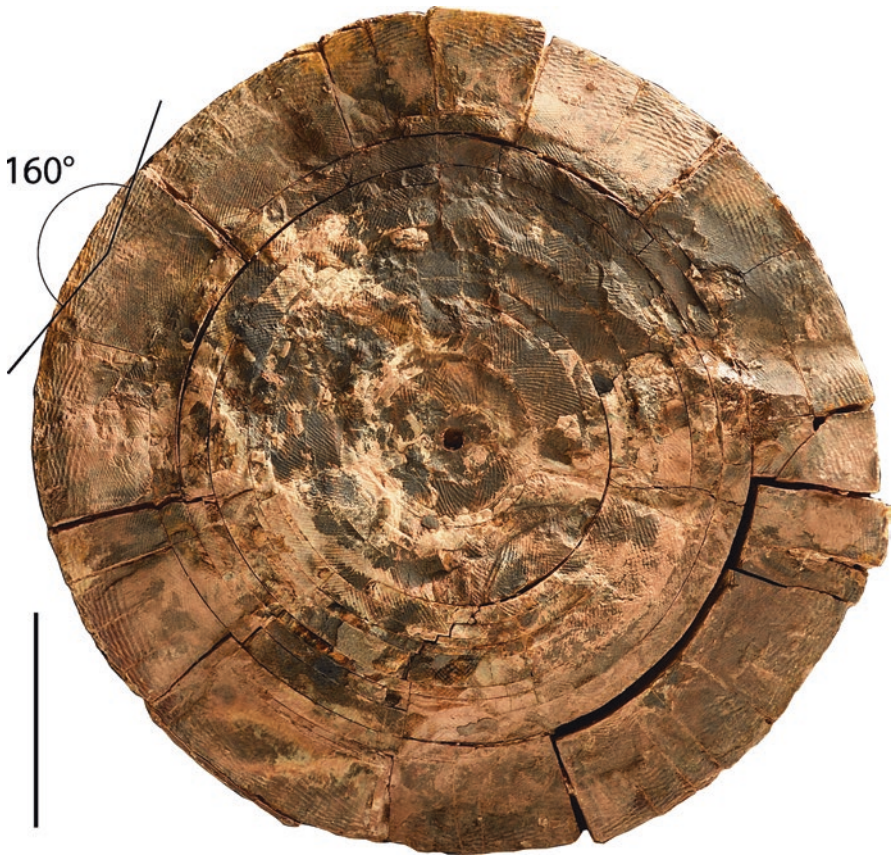


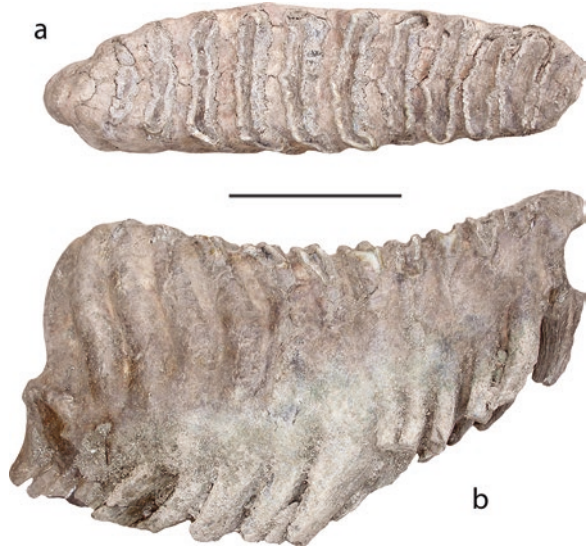
Fig. 5 Natural cross section of a *Palaeoloxodon antiquus* tusk, exhibiting obtuse Schreger angles near its periphery, which distinguish this species from those of the genus *Mammuthus* (see, e.g., Palombo and Villa 2001). This specimen—a 1.8 m-long tusk part—was excavated in September 2011 at Íssoma KYT (Megalopolis Basin, Peloponnese) and is kept in the collections of the Ephorate of Palaeoanthropology–Speleology (Ministry of Culture and Sports, Athens). Graphical scale equals 3 cm

a recently excavated specimen from the Íssoma area). They are morphologically very similar to *P. antiquus*, and they should be assigned to this species. Moreover, the sympatric occurrence of a dwarf species ('*P. melitensis*') among normal-sized elephants is ecologically impossible: dwarf elephant populations occurred only in isolated insular environments, characterised by greatly impoverished endemic faunas. The two dental specimens assigned to this species are better referred to a juvenile individual of *P. antiquus*. These inconsistencies in Melentis' taxonomy were first pointed out by Sondaar and Boekschoten (1967, pp. 562–563), who argued that only *P. antiquus* and *M. primigenius* existed in the Megalopolis Basin. Later research has further shown that the woolly mammoth molar described by Melentis (1961) actually belongs to a sample from the locality Telichka (Kiev, Ukraine), which was acquired by the Natural History Museum of the University of Athens in 1904, and was apparently mixed with the similarly coloured Megalopolis material excavated 2 years before, despite the clear labelling on the Telichka material (Lyras 2007; Iliopoulos et al. 2010). Indeed, recent research at several sites within the Megalopolis Basin never yielded any other elephantid species except for *P. antiquus*, which is currently the only proboscidean known to have existed in the area (Athanassiou 2018; Konidaris et al. 2018). A few proboscidean dental fragments (one of a molar and three of tusks) from undefined sites within the Megalopolis Basin published by Sickenberg (1976) as *Mammuthus (Archidiscodon) meridionalis*, based on the molar fragment morphology, are not in fact inconsistent with an attribution to *P. antiquus*, because of their incomplete preservation. The sample is actually not determinable further than the family level. The same is true for the postcranial finds from the basin referred to various species (Melentis 1963; Sickenberg 1976), since, contrary to what has been stated in older publications (see, e.g., Andrews and Forster Cooper 1928; Melentis 1963), there are no reliable criteria to distinguish between *Palaeoloxodon* and *Mammuthus* postcrania (Lister and Stuart 2010).

Melentis carried out excavations in the Megalopolis Basin as well, yielding most importantly a nice, partially preserved skull, which he assigned to *P. antiquus germanicus* (Stefanescu, 1924) (Melentis 1965). The specimen's morphology (two-bulged parieto-occipital crest, long and narrow hypsodont M3s) is consistent with an attribution to the straight-tusked elephant (Fig. 12a).

During the 1960s, numerous other papers were published describing or reporting on isolated elephantid dental specimens throughout the territory of Greece (Marinos 1964; Mitzopoulos 1964, 1967; Boessneck in Milójević et al. 1965; Astre 1966; Faugères 1966; Melentis 1966a, b; Schneider 1968; Symeonidis 1970). Most important of these studies is the one dealing with the *Palaeoloxodon* sample found in the Peniós River banks, west of Lárissa (Boessneck in Milójević et al. 1965), which is associated with Palaeolithic artefacts. The area continues to yield Late Pleistocene fossils when the river water level is low (Athanassiou 2001, 2011; Fig. 6). Three dental specimens from the Peniós River estuary, situated about 50 km NE of Lárissa, are referred by Paraskevaidis (1977) to three distinct species, but they are all referable to *Palaeoloxodon* as well. Unpublished proboscidean samples from the area of Lárissa, which quite probably belong to elephantid species, include a 2.6 m-long and 14 cm in diameter tusk found close to the village Mesorráchi in 1907 (reported

Fig. 6 Lower right third molar, referred to *Palaeoloxodon antiquus*, from Peniós River valley, west of the city of Lárisa (Late Pleistocene). The figured specimen belongs to a sample collected by the author in August 2007, during a dry period that resulted in exposure of large areas of the riverbed, due to very low water level. (a) occlusal view, (b) buccal view. Graphical scale equals 10 cm



anonymously in the local newspaper ‘Mikrá’, number 305, June 6, 1907), as well as bone and/or tusk fragments from Megálo Monastíri (findspot 50 in Runnels and van Andel 1993).

The presence of the straight-tusked elephant (*P. antiquus*) is also recorded at Vathýlakkos (Axiós Valley, Central Macedonia) (de Bonis et al. 1973), in an area well known for its late Miocene mammal faunas. The elephant-bearing site—accordingly named ‘Ravin de l’éléphant’—has yielded a single elephant find: an unworn m3. Recently, the specimen was described by Koulidou (2013) as *M. cf. primigenius*. However, its low number of lamellae for a woolly mammoth (17), as well as its long and narrow shape, makes the original attribution to *P. antiquus* more probable, despite the specimen’s high lamellar frequency. Nevertheless, it remains taxonomically enigmatic, requiring certainly a more thorough study.

Another very interesting locality is Pétres (W. Macedonia), where a skull of *Palaeoloxodon antiquus* was found, but never excavated (Velitzelos and Schneider 1973). The authors removed and studied the molars only, while the rest apparently was left in situ and possibly eroded soon thereafter. In the same paper, three other molars from the nearby locality of Sotíras are presented, referred to *M. trogontherii* and *A. meridionalis*, although they exhibit typical *Palaeoloxodon* morphology (see also Tsoukala et al. 2011). Judging from the published material, it seems that both *P. antiquus* and *M. trogontherii* were present at Sotíras (see also Marinos 1964; Tsoukala et al. 2011; Koulidou 2013). New material from this locality was recently published by Tsoukala et al. (2011) (*P. antiquus*) and Koulidou (2013) (*M. trogontherii*).

Poulianos and Poulianos (1980) presented a nearly complete elephant skeleton they excavated in a sand pit near Perdíkka (Ptolemaís, W. Macedonia) in 1977 (Fig. 7). The authors emphasised the presence of lithic artefacts associated with the



Fig. 7 The almost complete skeleton of *Palaeoloxodon antiquus* from Perdíkfas, W. Macedonia, exhibited in situ (photograph taken on October 20, 1999). The partially preserved skull is to the left. Note the minimal dispersion of the skeletal elements and the anatomical association among most of them. An extraordinary feature of the find is the total lack of the autopodia. This skeleton was excavated in 1977 by A. Poulianos (Poulianos and Poulianos 1980) and described briefly by N. Poulianos (1986)

elephant, and since they referred the find to the species *Archidiskodon meridionalis*, they argued for evidence of hunting in a quite early time period. A few years later, the second author revised the specimen's taxonomic attribution and referred it to *Elephas (Palaeoloxodon)* aff. *antiquus*, though he insisted on an age of about 2.0–2.5 Ma (Poulianos 1986). Nevertheless, the Perdíkfas elephant has clear dental characters of *Palaeoloxodon antiquus* (narrow crowns, plicate enamel, presence of a median sinus in enamel loops), and it should be referred to as such (see also Tsoukala et al. 2011). Its age is Middle–Late Pleistocene. Elephantid fossils continue to emerge in the sand pits of the area, but are usually fragmentary.

In 1981, Koufos described a small fossil fauna of Late Pleistocene age from Angítis river valley, Sérres (E. Macedonia). The fauna is of a cold-steppe character and includes two partially preserved dental specimens referred to *Mammuthus* cf. *primigenius*. Excavations carried out later (1992–1999) by the Ministry of Culture yielded some more mammoth material in a horse-dominated faunal assemblage (Trantalidou 2013). In the same decade of 1980s, two other studies dealt with fossil elephantids. Symeonidis and Theodorou (1986) described a partly preserved upper molar and tusk parts from a locality near Vlachióti (Laconia, SE Peloponnese) and referred it to *Archidiskodon meridionalis*. A few years later, Steensma (1988) studied the mammal fossils from five sites along the Haliákmon valley, in the region of Neápolis (Kozáni, W. Macedonia), which were collected in the late 1970s during

fieldwork by the Technical University of Clausthal (Germany). Elephantidae were identified on dental and osteological specimens in four of the studied sites, Libákos, Kapetánios, Polyíakkos, and Q-Profil, and referred to *Archidiskodon meridionalis* (tentatively in the last two localities). Based on their faunal content, Steensma (1988) places the localities in the Lower Pleistocene (see also Fig. 13). In the same year, Koufos and Pavlides (1988) reported the discovery of a partial elephantine mandible at Sotíras (W. Macedonia), which they preliminarily referred to *Archidiskodon cf. meridionalis*. The same specimen was later described by Koulidou (2013) as *M. trogontherii*.

A prominent elephantid find published during the next decade is a partial skeleton from the locality Ambéllia, in the town of Grevená (W. Macedonia) (Tsoukala and Lister 1998). The find, its skull and dentition, in particular, show typical characters of *P. antiquus*, such as divergent tusk alveoli, narrow molars with thick, plicate enamel, etc. (Tsoukala and Lister 1998). An interesting point of this study is the dating of the find in a glacial period (MIS 6) of the late Middle Pleistocene, when this species was not present in northern European regions. This indicates that the southern European regions acted as refugia for temperate-climate species, which later recolonised the North during interglacials. Other contemporary studies include Athanassiou (1998), who identified the species *M. meridionalis* at Sésklo (Magnesia, Thessaly) and Elephantidae indet. at the closely situated Halykés, and Tsoukala (1999), who documented the presence of Elephantidae indet. in the cave of Apídima C (Mani, S. Peloponnese). Regarding the sample from Sésklo, it should be noted that a tusk referred by Athanassiou (1998) to *M. meridionalis*, belongs most probably to the gomphothere *Anancus arvernensis* (see Athanassiou 2016). The presence of the southern mammoth at Sésklo is inferred from two carpal bones, which are too large to be assigned to *Anancus*, but it is not well supported on this scarce available material. The presence of *Mammuthus* at Sésklo should be regarded as tentative.

During the 1990s, elephant dental remains were also excavated at Nissí, Símiiza and Roupáki areas, all closely situated in the Peniós River basin (Elis region, NW Peloponnese). At Nissí, a tusk excavated by the Museum of Paleontology and Geology, University of Athens, remains unpublished, but its physical characters show that it belongs to *P. antiquus* (see also Agiadi and Theodorou 2005). A very similar tusk was found at Símiiza during road construction works (Dermitzakis pers. com.), as yet also unpublished. The same species was documented at Roupáki, based on a tusk, tusk fragments, and two very large M3s, all deriving from an illegal excavation and probably belonging to the same individual (Athanassiou 2000). Proboscidean remains indicated by Dermitzakis and Theodorou on a map (in Dermitzakis et al. 1982, fig. 64) from the nearby locality of Ano Olga may also belong to *P. antiquus*, as does the rest of the proboscidean samples from the region of Elis, but the whereabouts of the corresponding sample is unknown.

In a brief review of the Pliocene–Early Pleistocene Proboscidea of Greece, Athanassiou and Kostopoulos (2001) described elephantid specimens from the Lower Pleistocene localities of Gerakaróú and Apollonía (Central Macedonia), which they tentatively referred to *Mammuthus meridionalis*. New material published quite recently from the latter locality corroborated that insecure attribution

(Konidaris et al. 2020). During the following years scanty elephantid material was published from Vaterá (Lesbos Island) as *M. cf. meridionalis* and from Tsákoni (Kastoriá, W. Macedonia) as cf. *Elephas antiquus* (de Vos et al. 2002; Athanassiou 2004, respectively). Other localities, which are rather poor in elephantid material, are Kalamotó with *M. meridionalis* (Tsoukala and Chatzopoulou 2005), Reghínio (Athanassiou 2006a), Kípi (in the area of Neápolis, W. Macedonia; Athanassiou 2006b, fig. 6, 7; Harvati et al. 2008), and Epanomí with *M. cf. meridionalis* (Athanassiou and Kostopoulos 2010). An additional locality in the area of Neápolis, Trapezítsa, has yielded numerous tusk fragments exhibiting acute Schreger angles that could be assigned to *Mammuthus*. However, the original position of most identifiable fragments close to the tusk axis makes this feature atypical, and the finds are better referred to Elephantidae indet. Harvati et al. (2008) mentioned the presence of *Elephas antiquus* at Lágoura close to Néo Kostarázi (W. Macedonia), based on a lamella fragment. Although the morphology of the lamella is consistent with *P. antiquus*, an attribution to an early *Mammuthus* such as *M. meridionalis* cannot be excluded, so the find is referred here to Elephantidae indet. as well. The site has also yielded long bones, most notably a distal humerus and a radius.

Similarly taxonomically problematic is a partial left lower molar found in 2015 at Zéli (Central Greece,). The specimen (Fig. 8) preserves just four lamellae that belong quite probably to its distal part. Its maximal width is 91 mm (measured mesially) and its height about 125 mm (measured in the second preserved lamella). A hypsodonty index of 137 is calculated for the preserved part. The mean lamellar frequency is calculated as 5.2 lamellae per 10 cm, ranging between 4.5 and 5.8 from the base to the top of the crown. All lamellae are completely unworn, except for the

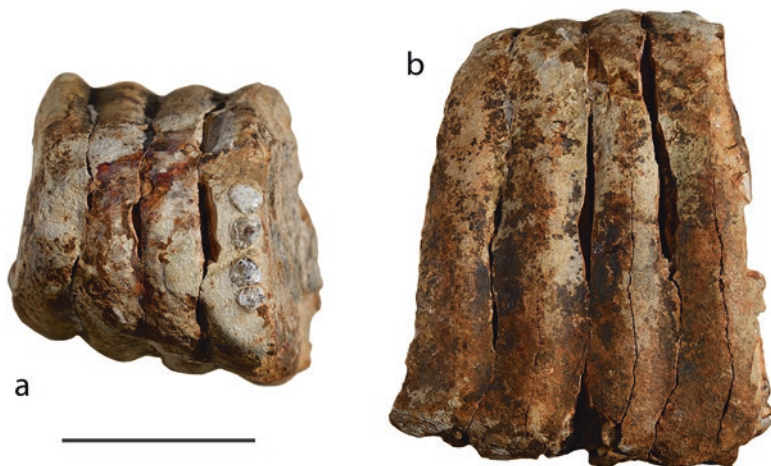


Fig. 8 A partial left lower molar referred to *Mammuthus* sp. from Zéli, Central Greece. (a) Occlusal view, (b) lingual view (the mesial end is on the right). Graphical scale equals 5 cm. The specimen is kept in the Ephorate of Palaeoanthropology–Speleology (Ministry of Culture and Sports, Athens)



Fig. 9 A part of the *Mammuthus trogontherii* skeleton from the lower Middle Pleistocene of Loussiká, NW Peloponnese (Athanasioiu 2012): scapulae and ribs in situ during the excavation carried out by the Ephorate of Palaeoanthropology–Speleology, May 2003. The hammer is used for scale (length: 30 cm). The skeleton is currently curated at the Archaeological Museum of Patras

mesialmost one, which shows signs of incipient wear. More specifically, its occlusal surface has four transversely (linguobuccally) arranged enamel islets of quasi-circular shape. The specimen's metrical characters (proportions and lamellar frequency), as well as the wear pattern observable on the mesialmost lamella, are consistent with an attribution to an early species of *Mammuthus*, like *M. meridionalis*. However, its incomplete preservation does not allow for a taxonomic attribution further than the genus level.

Masseti (2006) figured a partial lower molar of *P. antiquus*, still attached to a mandibular fragment, allegedly coming from Kálymnos Island. The specimen is kept in the Archaeological Museum of Kálymnos, together with some additional elephant and hippopotamus specimens, possibly from the same locality(ies) on the island. Kálymnos was connected to the mainland during most of the Pleistocene, having, as a result, a fossil fauna of continental, non-endemic character.

In the recent years, of particular interest is a partial skeleton of a mammoth, excavated in 2001 and 2003 near Loussiká (NW Peloponnese) by the Ministry of Culture (Fig. 9). The find was referred to the Middle Pleistocene steppe mammoth, *M. trogontherii*, as evidenced from its cranial and dental morphology (Athanasioiu 2012), though it had been previously preliminarily assigned to *Elephas antiquus* (Doukas and Athanasioiu 2003; Athanasioiu 2010). This wrong taxonomic identification has been also cited by Tsoukala et al. (2011). The latter authors, in their review of the occurrences of *P. antiquus* in Greece, described additionally new material of this species from the localities Kalonéri, Xeriás, Terpsithéa, Néa Léfki,

Fig. 10 A left upper third molar from Symbolí (Sérres, E. Macedonia), the holotype of the subspecies *Archidiskodon meridionalis proarchaicus* Melentis, 1966. Occlusal view. The mesial end is at the top. Note the wide crown, with thick lamellae and enamel. The specimen is referred here to *Mammuthus meridionalis*. It belongs to the collections of the Museum of Paleontology and Geology, University of Athens. Original photograph courtesy of the same museum. Scale bar equals 10 cm



and Sotíras (already mentioned above in this section). The Kalonéri (Kozáni, W. Macedonia, located very close to Libákos and Kípi) specimen is a damaged skull, preserving the premaxillaries and both tusks. Xeriás (Kavála, E. Macedonia) yielded only fragmentary material. In Terpsithéa and Néa Léfkí, both very close to the city of Lárisa (Thessaly), a fragmentary mandible and tusk parts (respectively) have been recovered from the terrace deposits of the river Peniós. A young-adult mandible from Sotíras with m1s and m2s is an important find, enriching the *P. antiquus* sample that was already known from this locality (Velitzelos and Schneider 1973).

Koulidou (2013) reviewed the museum collections (Geology–Paleontology Museum, Aristotle University of Thessaloniki) of Plio-Pleistocene Proboscidea from Northern Greece and concluded that *P. antiquus* occurs at Tsotyli and Sotíras, *M. meridionalis* at Tsotyli and Phlíppi, *M. trogontherii* at Sotíras, Phlíppi and possibly (cf.) at Tsotyli, and *M. cf. primigenius* at Phlíppi and Vathýlakkos (site ‘Ravin de l’éléphant’, based on a m3 originally referred to *P. antiquus* by de Bonis et al. 1973). She also documented the presence of *M. rumanus* at Tsotyli and possibly (cf.) at Kardiá, for the first time in Greece. The Tsotyli specimen was described soon after in detail by Kostopoulos and Koulidou (2015), who, although recognised its morphologic affinities with dental specimens referred to *M. rumanus*, refrained from assigning it to a species.

Two other important finds published recently are two partial skeletons of *Palaeoloxodon antiquus*, discovered in W. Macedonia and in Peloponnese, respectively. The former was unearthed in 2005 during mining works in Amýntaio Lignite Mine and was described in detail by Kevrekidis and Mol (2016). The latter was



Fig. 11 The Marathousa 1 skeleton of a male *Palaeoloxodon antiquus* (Megalopolis Basin, central Peloponnese; view to the East) during an early excavation stage (November 3, 2014), when several skeletal elements were still buried. The skeleton was found scattered mainly in a ENE–WSW direction, but generally well preserved. The plaster jacket at the eastern end of the excavation covers the skull (figured after its preparation in Fig. 12b). The find was published preliminarily by Konidaris et al. (2018)

located in 2013 during archaeological prospecting in Marathoussa Lignite Mine, Megalopolis Basin, and was excavated during the years 2013–2019 (Konidaris et al. 2018; Panagopoulou et al. 2018; Figs. 11 and 12b). A significant feature of the Marathousa skeleton is that it is associated with lithic artefacts and bears cut marks, documenting butchering activities by humans on the elephant corpse (Konidaris et al. 2018; Panagopoulou et al. 2018). At about the same time, the Megalopolis

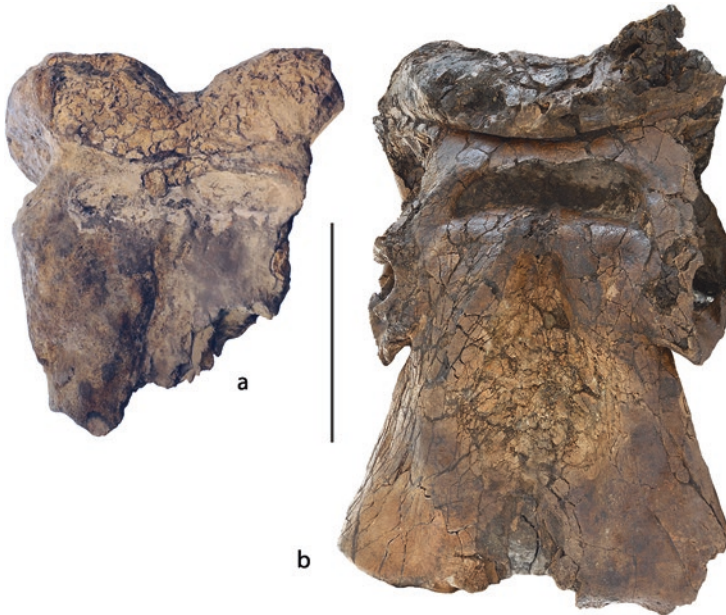


Fig. 12 Cranial specimens of *Palaeoloxodon* from Greek localities. (a) Partial skull from Léfketro, Megalopolis Basin, in frontal view, published by Melentis (1965) (Museum of Paleontology and Geology, National and Kapodistrian University of Athens), (b) the complete skull of the Marathousa I skeleton, Megalopolis Basin, in frontal view (Ephorate of Palaeoanthropology–Speleology, currently under study; see also Konidaris et al. 2018). Scale bar equals 50 cm

Basin yielded additional fossil samples: in September 2011 a tusk and a scapula, possibly associated with a lithic artefact, were found during the construction of an electricity distribution centre, not far from the village Íssoma (locality ‘Íssoma KYT’). A few days later, two more tusk parts were found in the same locality, 200 m to the North of the previous finds, but both were reduced to small fragments, presumably because of long aerial exposure before burial. Íssoma KYT yielded some more tusk parts in October of the same year. The following year, 2012, a team of the University of Athens excavated a ravine at Íssoma (which is allegedly one of the spots exploited by Skuphos during his 1902 expedition) and unearthed a few mammal fossils, most notably a complete elephant tusk (Theodorou 2014). All these recent finds in the broader area of Íssoma (localities ‘Íssoma’ and ‘Íssoma KYT’) are referred to *P. antiquus*, based on the tusk morphology (weak curve and torsion) and the obtuse Schreger angles observed in the fragment cross sections.

A recent (2015) discovery of an elephant maxilla on the island of Kephallenía led Theodorou et al. (2018) to erect a new species, *Elephas (Palaeoloxodon) cephalonicus*, accepting that the find belonged to an endemic, incipiently dwarfing population. Following Athanassiou et al. (2019), *P. cephalonicus* is considered here as a junior synonym of *P. antiquus*, because it does not differ diagnostically from the mainland *Palaeoloxodon* of Greece (see Sect. [Invalid Taxa](#)).

4 Systematic Paleontology

This section considers only non-endemic, normal-sized elephants, excluding the several species of insular dwarfs, which have been described from the islands of Greece and presented separately (Lyras et al. [volume 2](#)).

Valid Taxa

Elephantidae Gray, 1821

Type Genus *Elephas* Linnaeus, 1758.

***Mammuthus* Brookes, 1828**

Type Species *Elephas primigenius* Blumenbach, 1799.

Included Taxa The genus is known with four continental species in Greece, *M. ex gr. rumanus*, *M. meridionalis*, *M. trogontherii*, and *M. cf. primigenius*.

Remarks *Mammuthus* is an elephantid genus that reached Eurasia during the late Pliocene (at about 3.5 Ma, or somewhat later), after having evolved in Africa. The oldest representatives of the genus in Eurasia are, though, quite primitive, featuring brachyodont or barely hypsodont molars that consist of just a few lamellae. Yet, during the Pleistocene the mammoth lineage underwent impressive evolutionary modifications in response to the recession of the forests and the expansion of open environments. These included primarily a great increase in hypsodonty, multiplication of the molar lamellae, and increase of their frequency, thinning of the enamel, and rostrocaudal shortening and dorsoventral deepening of the skull and the mandible. These morphological changes had been traditionally considered as a prime example of gradual, orthogenetic evolution, a conclusion biased by the fact that practically only the European fossil samples were well known. In a Eurasian-wide perspective, Lister et al. (2005) illustrated a quite different evolutionary setting, according to which long periods of stasis, corresponding to the biochronological ranges of species, were interrupted by introductions of new morphotypes, apparently originating in NE Asia and spreading to the west possibly by means of genetic input to geographically adjacent populations.

Mammuthus exhibit a unique suite of morphological characters that include a single-domed skull, subparallel tusk alveoli, curved and twisted tusks, and broad molars with usually weakly plicate enamel. Early and Middle Pleistocene species evolved very large body sizes, but a considerable gradual body size reduction is observed from the late Middle Pleistocene onwards. The Eurasian species currently classified in this genus are the following (from the oldest to most recent), *M. rumanus*, *M. meridionalis*, *M. trogontherii*, and *M. primigenius*, the first being by far the

least well known and taxonomically documented, due to its scarcity. All were originally placed in *Elephas*, considered in a much wider sense, usually equivalent to the current subfamily Elephantinae. Other taxonomic names have been applied to members of this clade as well, usually in order to split it in taxa of genus or subgenus rank, such as *Archidiskodon* Pohlig, 1888, *Parelephas* Osborn, 1924, and *Mammonteus* Osborn, 1924. Maglio (1973) showed the phylogenetic continuity of the relevant species and adopted their classification under a single genus, *Mammuthus*. The same opinion had been expressed before in Simpson's classification of mammals (Simpson 1945), while Osborn (1942), though splitting the lineage into three genera, recognised their close relationship and placed them together in a single subfamily, Mammontinae Osborn, 1921. The classification of these species under the genus *Mammuthus* is followed today by the majority of authors, except for most Eastern European ones, who generally prefer to classify the late Pliocene–Early Pleistocene mammoth species to *Archidiskodon* (with *Elephas meridionalis* as the type species).

The species of the mammoth lineage shared the continent with other proboscideans, such as the mammutid *Mammuth borsoni* during the late Pliocene, the gomphotheriid *Anancus arvernensis* during the late Pliocene and the Early Pleistocene, and the elephantid *Palaeoloxodon antiquus* during the Middle and the Late Pleistocene.

***Mammuthus ex gr. rumanus* (Stefanescu, 1924)**

Nomenclatural and Taxonomical History The species was erected by its author, without any description, as a primitive ‘mutation’ of *Elephas antiquus* (i.e., a subspecies in the current taxonomic practice). Stefanescu (1924) referred to an older publication (Athanasiu 1915) for a description of the type specimen (a partial m3 from Tulucești, Romania), where it was assigned to *Elephas cf. meridionalis*. More recently, Radulescu and Samson (1995) described a molar from Cernătești, Romania, as *M. rumanus*. The late Pliocene and earliest Pleistocene elephantid material from Europe consists of scarce dental samples, which, due to their plesiomorphic characters, are difficult to assign to a genus. They were habitually referred to the Asian species *Elephas planifrons* Falconer and Cautley, 1846 (e.g., Depéret and Mayet 1923; Osborn 1942, p. 969; Maglio 1973), to *Archidiskodon gromovi* Garutt and Alexeeva, 1964 (e.g., Azzaroli 1977), or considered primitive forms of *M. meridionalis*. In addition, Maschenko (2010) coined *Archidiskodon garutti* for a small Early Pleistocene dental sample from the Stavropol region, Russia (its provenance locality is disputed), which, however, except for its more pronounced brachyodonty, does not seem to differentiate significantly from *M. rumanus* on the basis of the author's metrical and morphological data (see also Baygusheva et al. 2011).

Type Material Stefanescu (1924) apparently considered as the holotype a partially preserved lower third molar (m3) figured by Athanasiu (1915, pl. XVII, fig. 4) and referred to as *Elephas cf. meridionalis* by the same author. Fairly recently, Lister and van Essen (2003) proposed as a neotype the complete upper third molar from

Cernătești (Romania), because of the false assumption that the holotype had been lost (Lister et al. 2005).

Type Locality Upper Pliocene of Tuluțești (Galați region, Romania), biochronologically dated to the zone MN16a. Regional stratigraphic correlations and palaeomagnetic data place this locality to the middle Gauss (Kaena event, about 3.0–3.1 Ma) (Radulescu et al. 2003).

Distribution Primitive elephantine dental specimens attributable or similar to *M. rumanus* have been described (apart from the two Romanian localities mentioned above) from Bossilkovtsi (Bulgaria; Markov and Spassov 2003), the Stavropol area (SW Russia, Maschenko 2010), Kale Tepe-3 (Turkey; Albayrak 2017; though morphologically closer to *Elephas*, according to the author), Bethlehem and Erq el Ahmar (Israel; Markov 2012; Rabinovich and Lister 2017; Rabinovich et al. 2019), and two localities in Shanxi (NE China; Wei et al. 2006). Lister and van Essen (2003) also referred to this species the samples from Montopoli and Laiatico (Italy) and Red Crag (England), but this opinion was moderated as provisional shortly later (Lister et al. 2005). Obada (2010) added another Romanian locality to the species' distribution, Orodelu (Dolj, S. Romania), but considered the Cernătești specimen as a new distinct species (*Archidiskodon stefanescui*). An m3 from Podari (Dolj, S. Romania), described by the same author as *Loxodonta* sp., may also be attributable to *M. rumanus*, on the basis of the morphologic and metrical characters presented by Obada (2010).

In Greece, mammoth finds with archaic dental characters are known from Tsotyli (two specimens) and Kardiá (one specimen) in W. Macedonia (Koulidou 2013). Their stratigraphic origin is unknown, because they derive from old incidental collections, not systematic excavations. Koulidou (2013) referred them to *M. rumanus*. One of the Tsotyli specimens had been already published by Psarianos (1958) as *Archidiskodon* cf. *meridionalis*. The second specimen from the same locality is the most important of them and has been re-described in detail by Kostopoulos and Koulidou (2015). It is a part of a maxilla, bearing two rather brachyodont molars (M2 and M3) that consist of very few lamellae. Kostopoulos and Koulidou (2015) do not assign it to a species, due to our incomplete knowledge of the early mammoth morphology and variation. Here, however, it is included provisionally to *M. ex gr. rumanus*, together with the other two primitive elephantid finds from Greece, for the sake of simplicity, until more material becomes available.

Taxonomic Remarks The species *M. rumanus* was reviewed and described in detail by Lister and van Essen (2003), who essentially resurrected it internationally after many years of local use (e.g., Radulescu and Samson 1995) and expanded its distribution out of Eastern Europe. The authors pointed out that this species is distinctly different from *M. meridionalis*, in contrast with other names proposed for primitive mammoths, such as *M. gromovi*, whose type material is similar to the typical *M. meridionalis* (at least dentally), thus not separable from it at the species level.

Moreover, in African localities there is evidence for populations very similar to *M. rumanus*, which may indicate that this species had a transcontinental distribution, and was involved in the mammoths' migration out of Africa (Markov 2012). Certain authors, however, prefer to classify *rumanus* as a basal subspecies of '*Archidiskodon meridionalis*', immediately preceding *gromovi* in the biostratigraphic subspecies succession of this species (e.g., Vislobokova 2005; Baygusheva and Titov 2012). The name is used here as *M. ex gr. rumanus* to include the primitive elephantid finds from Greece and similar samples from the wider European region, pending the availability of more material and a systematic revision of this group. Currently, the scarcity of well-dated dental finds and the lack of cranial material make even a generic attribution insecure in most cases, while the true metrical and morphological variation within the species is incompletely known. *Mammuthus rumanus* is characterised dentally by a low number of lamellae (8–10 in M3/m3) and low lamellar frequency (3–5 lamellae per 10 cm of molar length), while their hypsodonty index is comparable to the minimum values calculated for *M. meridionalis* (Lister and van Essen 2003; Lister et al. 2005). Occlusally, the enamel loops often form prominent, distally directed median folds, a feature homologous to the gomphothere central conules, which is reduced in later mammoth species.

Mammuthus meridionalis (Nesti, 1825)

Nomenclatural and Taxonomical History This species was defined by Nesti (1825) on an Early Pleistocene elephantine sample collected in the region of Upper Valdarno, N. Italy. Part of this material had been previously referred to the Asian elephant, *Elephas maximus*, and to the woolly mammoth, *M. primigenius* (see a historical account in Palombo and Ferretti 2005). Because of the species' long biostratigraphic range, numerous subspecies (usually chrono-subspecies) have been named to account for different evolutionary levels. Common names found in the literature are *M. m. gromovi* (Garutt and Alexeeva, 1964), *M. m. meridionalis*, *M. m. vestinus* (Azzaroli, 1972), *M. m. tamanensis* (Dubrovo, 1963), and *M. m. depereti* Coppens and Beden, 1982 (roughly from the stratigraphically oldest to more recent ones). Subspecies names that have been used to identify Greek fossils include *M. m. meridionalis*, *M. m. cromerensis* Depéret and Mayet, 1923, *M. m. archaicus* Depéret and Mayet, 1923, *M. m. proarchaicus* Melentis, 1966, and *M. m. vestinus* (Azzaroli, 1972) (Melentis 1960, 1961, 1966a; Mitzopoulos 1967; Konidaris et al. 2020).

Type Material No holotype was designated by Nesti (1825), who, however, figured two skulls and several limb bones in his study. One of these skulls (IGF-1054; Palaeontological Museum of Florence, Italy) was later designated as the lectotype by Depéret and Mayet (1923). The type locality has yielded until today a rich hypodigm that includes skeletons, several skulls and mandibles, and hundreds of molars and postcranial elements (Palombo and Ferretti 2005).

Type Locality Lower Pleistocene fluvio-lacustrine deposits of the Montevarchi group, Upper Valdarno, Italy. This sequence includes the Matassino (older) and the Tasso (newer) faunas, and it is dated to the time interval 2.0–1.77 Ma (Palombo and Ferretti 2005).

Distribution The species is quite common, known from hundreds of localities widespread across Eurasia, except for its northernmost regions. It is also tentatively reported from Northern Africa (Maglio 1973; Sanders et al. 2010). Its presence in North America, assumed in the past by some authors (e.g., Osborn 1942; Maglio 1973), is not supported by recent research (Lister and Sher 2015). Geochronologically, it appeared at about the beginning of the Pleistocene (2.6 Ma) and persisted till the early part of the Middle Pleistocene (possibly as late as 0.6 Ma) (Lister et al. 2005). In Greece, the species occurs usually as single dental finds currently in more than 20 localities (see Appendix) situated throughout the country. Most of them are not datable further than a general placing in the Lower Pleistocene.

Taxonomic Remarks This is the oldest well-known species of the genus. It is of large body size, with moderately rostro-caudally shortened skull and mandible. The skull has a concave forehead in lateral view and forms dorsally a single dome due to the dorsal expansion of the parietal and occipital bones. With regard to more advanced species of the genus, the mandibular symphysis is long. The tusks are robust, curved, and twisted, and the molars are wide, weakly to moderately hypsodont (hypsodonty index: 99–146 in M3s, 110–143 in m3s; Lister and Stuart 2010), with thick lamellae and moderately thick enamel. The third molars (M3/m3) consist of 12–14 lamellae (in rare cases 11 or 15; Lister et al. 2005).

The species exhibited a gradual evolution during its long history mainly towards a higher cranial dome, higher lamellae number, increased hypsodonty, and thinner enamel. This guided certain authors to assign the known samples to distinct evolutionary stages. Depéret and Mayet (1923) distinguished four ‘mutations’ (archaic, typical, Saint-Prestien, and *cromerensis*), the last of which is presently referable to *M. trogontherii*, at least partly. Maglio (1973) designated three evolutionary stages, ‘Laiatico’, ‘Montevarchi’, and ‘Bacton’ (from less to more derived), the second of which is the one observed in the material of the type locality. The Laiatico stage samples have been later related to *Archidiskodon gromovi* (see Azzaroli 1977) and to *M. rumanus* (see Lister and van Essen 2003; Lister et al. 2005). However, the scarce available material of these archaic mammoth forms is still inadequate for an unambiguous species-level taxonomy (Palombo and Ferretti 2005). The Bacton stage includes the most advanced samples of the species that reached the highest lamellae number and hypsodonty and corresponds roughly to the local subspecies *M. m. vestinus*, *M. m. depereti*, and *M. m. tamanensis* mentioned above.

The Greek fossil record of *M. meridionalis* remains still rather poor. Despite this fact, certain isolated dental specimens were determined taxonomically down to the subspecies level, without considering the wide morphological variability of mammoth molar characters, which are also wear dependent (see, e.g., Lister and Sher 2015). This taxonomic practice, followed during the 1960s, is certainly not

appropriate, and the subspecific part of the name should be dropped. The molars studied by Melentis (1960, 1966a) form an example (Fig. 10; see also above). Moreover, in some cases, the samples are referable to *Palaeoloxodon antiquus* (see below in this section), not to a mammoth. The case of the Megalopolis sample (Melentis 1961) has been already mentioned above. Another example are the two molars from Néa Kómi or Perdíkkas (exact locality data are not given), which were referred to *Archidiskodon meridionalis archaicus* by Mitzopoulos (1964, 1967): the high and narrow crowns, as well as the occlusal wear pattern point to the straight-tusked elephant, which is frequently found in the area, and not to an archaic mammoth. The same is quite probably true for a molar from Chálki referred by Schneider (1968) to *Elephas (Archidiskodon) meridionalis cf. cromerensis* (see also Athanassiou 2002). A taxonomic determination at the subspecies level has been published again very recently (*M. m. vestinus* from Apollonia; Konidaris et al. 2020), but this time it was employed to classify a richer sample, which is clearly evolutionary more advanced than the typical samples of the species.

***Mammuthus trogontherii* (Pohlig, 1885)**

Nomenclatural and Taxonomical History The recognition of this taxon was the result of an extensive study on the Pleistocene elephants of Europe elaborated by Pohlig (1888, 1891). However, a short description of the species as an intermediate form between *M. meridionalis* and *M. primigenius*, accompanied by a statement of the name *Elephas trogontherii*, is to be found in a letter of the author referring to this study, which was published in 1885. The use of this name is widespread since then. Maglio (1973) preferred to use an older name, *M. armeniacus* (Falconer, 1857), which he considered as a senior synonym of *M. trogontherii*. This opinion was not followed by most later authors, however, because *M. armeniacus* is insufficiently documented on the basis of poor material from a difficult to relocate and undated type locality (Adam 1988; Lister 1996). The use of the name *M. trogontherii* is currently ubiquitous. Other junior synonyms of *M. trogontherii* include *Elephas intermedius* Jourdan, 1891; *Elephas nestii* Pohlig, 1891; and *Elephas wuesti* Pavlow, 1910.

Type Material No type material was designated by the species author, so that the total molar sample from Süßenborn (Thuringia, Germany), described in detail by Pohlig (1888), can be considered as syntypes. Later, Osborn (1942) chose an upper and a lower third molar out of the type series as a lectotype, despite the fact that the two specimens, though belonging to the same fossil collection, do not necessarily belong to the same individual. To correct for this error, Kahlke (1990) fixed one of Osborn's specimens (the upper third molar) as the lectotype, based on the same choice made by Dubrovo in a series of papers (e.g., Dubrovo 1965), who, however, repeatedly referred to the molar as a lower third one. The type locality has yielded more than a thousand molars of this species (Guenther 1969), which constitute a very good statistical sample to characterise the species dentally.

Type Locality Fluvial sediments of Süßenborn, upper terrace system of the river Ilm (Thuringia, central Germany), dated to early Middle Pleistocene (about 600 ka) (Lister and Sher 2001).

Distribution This species is common, known from many localities across Eurasia. In Europe it is first recorded at about 1.0 Ma, initially coexisting in certain parts of the continent with *M. meridionalis* (see Lister et al. 2005) and becomes a common faunal element after about 0.8 Ma. However, fossils with *M. trogontherii* morphology are already known from much older, Lower Pleistocene deposits in N. China, dated at 1.66 Ma (Wei and Lister 2005), and in E. Siberia at about 1.2 Ma (Lister and Sher 2001), suggesting that E. Asia was the centre of evolution and dispersion of this species. *M. trogontherii* persisted in Europe until about 200 ka, but, again, Chinese finds postdate the species' last occurrence in Europe, surviving until the latest Pleistocene (Wei et al. 2010).

Taxonomic Remarks Morphologically intermediate between *M. meridionalis* and *M. primigenius*, *M. trogontherii* features, with respect to older mammoth forms, a rostro-caudally shorter and higher skull, a deeper mandible with shorter symphysis, and more advanced molars, with more lamellae, thinner enamel and distinctly increased hypsodonty. Some early finds from Europe exhibit a less derived, mosaic dental morphology, characterised by advanced hypsodonty, but rather low lamellar count (15–17), or vice versa, high lamellar count, but moderate hypsodonty (Lister et al. 2005; Lister and Stuart 2010). Typical *M. trogontherii* have a lamellar number of 17–22 and a hypsodonty index of 153–206 in M3 and 141–177 in m3 (Lister and Stuart 2010). *M. trogontherii* has been credited the title of the largest-bodied elephantid (possibly also proboscidean), with exceptionally large males estimated to weigh more than 20,000 kg (Christiansen 2004). However, the species underwent a progressive body size reduction during the Middle Pleistocene, with later and smaller forms often referred to the subspecies *M. trogontherii chosaricus* Dubrovo, 1966 (in some cases elevated to the species level), approaching the morphology of *M. primigenius*. Due to the complexity of the *M. trogontherii*–*M. primigenius* transition, this taxon (in subspecies or species rank) is rarely used in systematics anymore (see Lister 1996).

The species' fossil record in Greece is limited (see Appendix), as it is not so common in southern latitudes. Psarianos (1958) and Marinou (1964) mention its presence in Macedonia (localities Sotíras, W. Macedonia, and Philippi, E. Macedonia) on the basis of three isolated molars. Later, Velitzelos and Schneider (1973) described two additional molars from Sotíras as *M. trogontherii*, but one of them (in their figs. 6 and 7) is better attributed to *P. antiquus*, which is also present in the site. More recently, Koulidou (2013), in a comprehensive study of the available proboscidean material from Northern Greece, described dental specimens referable to this species from the localities Tsotyli, Sotíras, and Philippi.

An exceptional find, compared to the generally poor samples of the species throughout the country, is a partial skeleton excavated in 2001 and 2003 at Loussiká, NW Peloponnese (Athanasidou 2012; Fig. 9). The recovered anatomical parts

include the skull and mandible, part of the axial skeleton, and many limb bones that document a large 45-year-old male individual, estimated to have stood about 3.5–3.8 m high and have weighed 8 tons (Athanassiou 2012; Larramendi 2016). The Loussiká mammoth is also important in a European perspective, due to the rarity of skeletons of this species, and its location, which is comprised among the southernmost recorded.

***Mammuthus cf. primigenius* (Blumenbach, 1799)**

Nomenclatural and Taxonomical History The woolly mammoth was one of the first fossil proboscidean species to be recorded in the scientific literature. Thanks to its abundant remnants discovered throughout the Northern Hemisphere, which include not only fossil skeletal elements but also well-preserved carcasses with soft tissues often found in the permafrost of the northernmost territories, *M. primigenius* is likewise one of the best-known extinct animals. Quite like most derived Proboscidea, this species was initially classified in the genus *Elephas*. Osborn (1942) used the name *Mammonteus* Osborn, 1924, but Maglio (1973) restored *Mammuthus* as the valid genus name according to the rules of zoological nomenclature. Many woolly mammoth fossils discovered during the nineteenth and early twentieth centuries were given a plethora of different names of species or subspecies rank, most of which were not accompanied by a diagnosis or even a description and were soon forgotten (Garutt 1964; see also the synonymy list in Maglio 1973, p. 60).

Type Material The species' original publication did not include a description, nor a designation of type material. Osborn (1942, p. 1122) selected as lectotypes two molars from Blumenbach's personal collection, deriving from Germany and Siberia, respectively. Gromova argued in 1965 (cited in Garutt et al. 1990) that only one of these specimens, the molar from Siberia, should be designated as the lectotype of the species. Maglio (1973, p. 60) shared the same opinion. However, the Blumenbach's collection seems to have been lost or destroyed during World War II. To address these problems, Garutt et al. (1990) proposed to designate an adult nearly complete male skeleton discovered in 1948 on the Taimyr Peninsula, N. Siberia, as the neotype of the species.

Type Locality Uppermost Pleistocene of Taimyr Peninsula, N. Siberia (place of origin of the species' neotype; Garutt et al. 1990).

Distribution As in the case of its immediate ancestor, *M. primigenius* was first emerged in the E. Asia and subsequently dispersed west to the rest of the Eurasia, and east to N. America through Beringia. In Europe, it is first recorded at about 200 ka (Lister et al. 2005) and became widespread, particularly in periods of cold climate. By the end of the Pleistocene the species populations started to recede to the North, probably because of the climate warming and expansion of forests, combined with hunting pressure by humans. The last *M. primigenius* finds from the European North have been ^{14}C dated to the Younger Dryas / Holocene boundary,

about 11.4–11.8 ka (Ukkonen et al. 2011). The species' palaeogeographic range continued to shrink rapidly, until its ultimate extinction at about 3.7 ka on Wrangel Island, NE Siberia (Stuart et al. 2002).

Since this is a cold-adapted species, it is very rare in Greece, limited geographically to the country's northern part, and quite possibly also geochronologically to periods of cold climate. It has been tentatively identified (as *M. cf. primigenius*) on dental and osteological material in Angítis (E. Macedonia), dated to the Late Pleistocene (34–28 ka) (Koufos 1981; Trantalidou 2013) and Phílippi (E. Macedonia) on a molar fragment (Koulidou 2013). A third potential locality, according to Koulidou (2013), is Ravin de l'éléphant (Vathýlakkos, Central Macedonia), based on a molar with enigmatic morphology originally assigned to *P. antiquus* (de Bonis et al. 1973; see also below).

Taxonomic Remarks *Mammuthus primigenius* represents the last stage in mammoth evolution in Eurasia, a species adapted to life in cold and dry steppe–tundra habitats. Compared to its ancestral species *M. trogontherii*, it is characterised by a reduction in body size and the evolution of more advanced molars, with more lamellae and thinner enamel. Typical *M. primigenius* have third molars with 23–28 lamellae, though specimens with fewer lamellae (as few as twenty) have been recorded in Europe (Lister and Sher 2001; Lister and Stuart 2010). The hypsodonty index does not seem to have changed, with the range of 160–209 calculated for the rich Upper Pleistocene locality Předmostí (Czechia) (Lister and Sher 2001; Lister and Stuart 2010).

Several fossils from Greece have been referred to *M. primigenius*, but their identity is often doubtful. The dental specimen allegedly from Megalopolis Basin (Melentis 1961) clearly belongs to a woolly mammoth, but comes in fact from a Ukrainian locality (see Sect. 3). A molar from the Peniós estuary (Thessaly) (Paraskevaidis 1977, pl. 3, fig. 3) seems to have thick lamellae and enamel (the author did not provide a scale bar or measurements, while the whereabouts of the specimen is unknown). It is rather attributable to a less advanced mammoth species, or more probably to *P. antiquus*, which is common at several sites along the Peniós valley. Angítis (E. Macedonia) is the only site where the species seems to have been more frequent, though more diagnostic material is needed for a secure species-level determination (Koufos 1981; Trantalidou 2013). Recently, Koulidou (2013) referred to the woolly mammoth a third molar from Ravin de l'éléphant (Vathýlakkos, Central Macedonia), reported as *P. antiquus italicus* by de Bonis et al. (1973). The specimen consists of only 17 lamellae according to Koulidou (2013), a feature which differentiates it strongly from the *M. primigenius* hypodigm. Its completely unworn occlusal surface hampers its taxonomic identification. Its long and narrow crown may indicate an affinity to *P. antiquus* (in accordance to the original assignment by de Bonis et al. 1973), but the lamellar frequency is quite high (about 9 based on Koulidou's figures), consistent with the morphology of an advanced mammoth. The Vathýlakkos find is referred here to cf. *P. antiquus*, until more data become available. A partial molar from Phílippi referred by the same author (Koulidou 2013) to *M. cf. primigenius* is rather too incompletely preserved to be

identified at the species level, though, also in this case, it is characterised by very high lamellar frequency, as in *M. primigenius*.

***Palaeoloxodon* Matsumoto, 1924**

Type Species *Elephas namadicus naumanni* Makiyama, 1924 (raised to the species level since the early 1970s).

Included Taxa The genus is known with a single species in continental Greece, *P. antiquus*.

Remarks Although *Palaeoloxodon* is a genus mainly occurring and studied in Europe and E. Asia, it is of African origin, just as the other elephantine genera (Osborn 1942; Aguirre 1969; Maglio 1973; Saegusa and Gilbert 2008). It is known to have existed in E. Africa at least since the early Pliocene with the species *P. ekoensis* (Maglio, 1970) and *P. recki* (Dietrich, 1916), which already exhibited the apomorphic characters of the genus, though in more ancestral states (Maglio 1973). *Palaeoloxodon* probably migrated to Eurasia during the terminal Early Pleistocene, at about 1.0 Ma (Saegusa and Gilbert 2008) and enjoyed a wide dispersal in the continent in habitats of temperate climate. *Palaeoloxodon* never migrated to America, quite probably because of the cold and arid steppe environment of NE Asia and Beringia, which was hostile to the populations of this genus. In Eurasia it became extinct during the last glacial period of the Late Pleistocene (Stuart 2005; Saegusa and Gilbert 2008).

Palaeoloxodon are readily distinguished from the mammoths on cranial characters, while there are also distinctive dental features. The skull is very large, high and rostro-caudally short, with a double-domed vertex dorsally and concave frontoparietal surface. The tusk alveoli are divergent (at least in advanced species) not closely positioned like *Mammuthus*. The tusks are weakly curved and twisted, in contrast to the spirally twisted and more curved tusks of *Mammuthus*. The molars exhibit low hypsodonty and low lamellae number in early forms, but have more lamellae and become very hypsodont in Pleistocene species. However, *Palaeoloxodon* never reached the level of lamellar multiplication observed in advanced mammoths. Moreover, *Palaeoloxodon* is characterised by the presence of a 'loxodont sinus', a thickening of the lamellae in their central area, observed as a large median fold on the occlusal surface, a persisting plesiomorphic feature not retained in advanced *Mammuthus*.

***Palaeoloxodon antiquus* (Falconer and Cautley, 1847)**

Nomenclatural and Taxonomical History This very common European elephant species was initially published as *Elephas antiquus* Falconer and Cautley, 1847, together with a very similar Asian species, *E. namadicus* Falconer and Cautley, 1847. Matsumoto (1924) introduced a new name for the Japanese samples, *Palaeoloxodon*, and placed it in subgeneric rank under the genus *Loxodonta*. Later in the same year, Osborn (1924) coined the genus names *Sivalikia* for the Asian samples and *Pilgrimia* for the Mediterranean dwarf forms and the African species

E. recki. The same author soon created a new genus for the European species, *Hesperoloxodon* Osborn, 1931, based on a skull from Italy. Finally, Osborn (1942, p. 1179) accepted the synonymy of *Sivalikia* and *Pilgrimia* with *Palaeoloxodon*, but retained *Hesperoloxodon* for the European non-insular samples. Aguirre (1969) considerably reduced Osborn's taxonomic splitting, using *Palaeoloxodon* as a genus name for all African and Eurasian species of the relevant morphology (*recki*, *namadicus*, *antiquus*, *falconeri*, etc.). Maglio (1973) synonymised *Palaeoloxodon* with *Elephas*, and *antiquus* with *namadicus*, basing his arguments on cranial morphology and accepting a certain degree of intraspecific variation. However, these suggestions were generally not followed by later authors, who continued to use both *Palaeoloxodon* (in genus or subgenus rank under *Elephas*) and *antiquus*, pending a large-scale revision of the *namadicus*–*antiquus* group. In the recent literature, *Palaeoloxodon* is consistently employed in genus rank (following Inuzuka and Takahashi 2004, Shoshani et al. 2007 and Todd 2010), and *antiquus* continues to be used exclusively for the European and Middle East populations.

Type Material The species is defined on a partially preserved mandibular part bearing the m2, which was designated as the lectotype by Osborn (1942, p. 1218).

Type Locality The type locality is unknown, but Palombo and Ferretti (2005) cited a personal communication with P. Davies and A. Lister, according to which the lectotype probably comes from the upper Middle Pleistocene deposits at Grays, a site in the terrace system of the river Thames (England).

Distribution *Palaeoloxodon antiquus* is by far the most common elephantine species in Southern Europe, expanding its range to the North during periods of warmer climate. The species occurs in hundreds of localities throughout Europe, particularly in Italy, Germany, and France (see, e.g., Palombo et al. 2010, fig. 6). In Greece, it is quite widespread geographically, occurring in numerous localities, from Western and Central Macedonia in the North to Southern Peloponnese and Kýthera Island in the South and from Kephallenía Island in the West to Kálymnos Island in the East. Yet unpublished material includes tusks from Alivéri (Euboea) and Nissí (NW Peloponnese) (Museum of Paleontology and Geology, National and Kapodistrian University of Athens). The former was believed to belong to *M. meridionalis* (see Doukas and Athanassiou 2003), but has clear *P. antiquus* morphology. A left m3 from Philótas (NW Macedonia), curated in the Petralona Museum (Chalidikí) may also belong to this species.

Palaeoloxodon antiquus first appeared in Europe just before the beginning of the Middle Pleistocene, at about 0.9–0.8 Ma and became extinct in Northern Europe at the end of the Last Interglacial (Eemian), as its range contracted to the South following the retreat of the temperate vegetation to the same direction (Stuart 2005)—note, nevertheless, that *P. antiquus* molars from the Netherlands have been dated to as late as 32.5 ka (Bosscha Erdbrink et al. 2001; Mol et al. 2007). Southern Europe acted as a refugium for temperate-adapted floras and faunas during the glacial periods of the Pleistocene, and this was also the case during the Last Glacial, allowing

for a later extinction date in this region. On the Italian Peninsula, this species continued to constitute a common element of the Late Pleistocene faunas and became extinct sometime during the MIS 3 (about 60–27 ka) (Palombo and Ferretti 2005). On the Iberian Peninsula, *P. antiquus* is reported to have persisted until about 33 ka (Sousa and Figueiredo 2001), while a more recent date of 23.5 ka appears to be controversial (Stuart 2005).

The Greek fossil record of *P. antiquus* is in most cases not dated using physical methods (either directly on the elephant fossils, or on associated samples). Only three samples have been dated so far. The geochronologically oldest dated find is the skeleton from Marathousa 1 (Megalopolis Basin; Fig. 11), which yielded an age estimation of 0.50–0.42 Ma (MIS 12), resulting from combining palaeomagnetic, radiometric, and optical methods (Blackwell et al. 2018; Jacobs et al. 2018; Tourloukis et al. 2018). A more recent elephant skeleton from Ambéllia, Grevená, was dated to MIS 6 (165–170 ± 25 ka) using the Electron Spin Resonance method (Bassiakos in Tsoukala and Lister 1998). Last, a maxilla from Póros, Kephallenía Island, was dated by Theodorou et al. (2018) at 104.2 ± 18.5 ka, using Infrared Optically Stimulated Luminescence Dating of feldspar. An additional locality is dated indirectly. This is Peniós Valley, located west of the city of Lárissa (Thessaly), where the fossils are found in the river's lower terrace. The age of these deposits has been estimated to 45–30 ka, based on ¹⁴C dating of freshwater molluscs and U/Th dating of pedogenic carbonates from several sites in the river banks (Demitrack 1986), while Runnels and van Andel (1993) extended this range back to 60–30 ka, based on archaeological correlations. This is the most recent date obtained for *P. antiquus* samples in Greece (Athanassiou 2011).

Taxonomic Remarks *Palaeoloxodon antiquus* is a very large-bodied elephant with largest male individuals estimated to have stood 4 m high at the shoulders (Larramendi et al. 2017). It is characterised by a massive rostrocaudally compressed skull, with a two-bulged vertex. Dorsally the skull often forms a strong parieto-occipital crest that folds rostrally over the frontal surface and overhangs the external nares. Another prominent feature of this species is the long and fan-shaped premaxillaries, which widen distally in accord to the strongly divergent tusks (see, e.g., Fig. 12b). The mandible is deep, to accommodate the hypsodont molars, and has a short symphysis. The tusks are weakly curved and exhibit only slight torsion. Their dentine structure is manifested in cross sections as curved Schreger lines that form obtuse angles near the tusk periphery (Palombo and Villa 2001; see also Fig. 5). The molars are narrow and hypsodont, with coarsely folded, rather thick enamel that forms a 'loxodont sinus', i.e., a central thickening of the lamellae expressed on the occlusal surface as a median widening of the enamel loops. Incipiently worn lamellae usually present a 'dot-dash-dot' wear pattern, i.e., a central wide elliptical enamel loop, and two smaller of more circular shape on the lingual and buccal side. The third molars (M3/m3) normally have 12–18 plates (Maglio 1973) but may reach 20 in exceptional cases (Palombo and Ferretti 2005). The lamellar frequency ranges between 4.4 and 7.7 lamellae per 10 cm of molar length (Maglio 1973), usually about 5–6.

The question on the taxonomic relationship between the European *P. antiquus* and the Asian *P. namadicus* remains still open, because of the need for a wide-scale revision of the available cranial material. Maglio (1973) considered the two species as synonyms, with *P. namadicus* having priority, based on the absence of dental differences and the considerable variability observed in the Indian cranial samples, which incorporate the morphologies found in Europe. Indeed, the characteristic development of a parieto-occipital crest observed in Indian samples (the so-called ‘*namadicus* morph’ of Saegusa and Gilbert 2008) is also found in Italy (e.g., in Pian dell’Olmo, La Polledrara di Cecanibbio, and Pignataro Interamna; Maccagno 1962; Palombo and Ferretti 2005; Anzidei et al. 2012). Skulls with a weak parieto-occipital crest (the so-called ‘Stuttgart morph’ of Saegusa and Gilbert 2008) are more common in Germany (e.g., in Steinheim an der Murr and Neumark-Nord; Osborn 1942, p. 1254; Palombo et al. 2010), but this morphology is also present in India (Saegusa and Gilbert 2008). Saegusa and Gilbert (2008) considered three alternative hypotheses to explain the occurrence of both these morphologies: (a) they reflect pronounced intraspecific variation; (b) they represent two distinct taxa, of which the more advanced (*namadicus* morph) replaced the ancestral one; and (c) they represent two distinct taxa occurring contemporaneously. The authors considered option (a) as the least plausible and discussed the other two. In the case of option (b), they place the taxonomic replacement sometime during, or slightly before, MIS 9.

Concerning the Greek samples, the morphology of the parietofrontal region is observable in two skulls, one from Léfkro (Melentis 1965) and one from Marathousa 1 (Konidaris et al. 2018). Both bear prominent parieto-occipital crests (Fig. 12) that bend rostrally over the nasal opening. The skull from Léfkro (Fig. 12a) seems to have had a somewhat stronger crest that bends down closer to the nares (*contra* Melentis 1965, who stated that there is no such crest). A more accurate assessment is not possible, however, because the region is partially eroded before burial and partially damaged, possibly during excavation or preparation. Nevertheless, none of the Megalopolis Basin skulls exhibits the extreme infolding of the crest observed in the specimens from Godávári, India (Osborn 1942, p. 1250) and La Polledrara di Cecanibbio, Italy (Palombo and Ferretti 2005; Anzidei et al. 2012; but see also Larramendi et al. 2020 for a re-evaluation of the condition seen in this skull). Léfkro and Marathousa 1 are geographically adjacent, the former being located about 8 km SSE of the latter. Their exact relative stratigraphic position is unknown, but both derive from organic-rich lacustrine sediments of the Marathousa Member of the Choremi Formation within the Megalopolis Basin (Vinken 1965; Tourloukis et al. 2018) and are expected to have a similar geological age. The development of the parieto-occipital crest in other skulls from Greek localities, like those from Grevená (Tsoukala and Lister 1998) and Amýntaio (Kevrekidis and Mol 2016) is unknown because the relevant cranial part is not preserved. The Perdíkka elephant skull apparently preserves this region, but it is not observable, since the skull remains in situ lying on its frontal plane (Fig. 7).

The Greek fossil record sheds some light to the problem of the relationship between the ‘*namadicus*’ and the ‘Stuttgart’ morphs. The early presence of ‘*namadicus* morph’ skulls in Greece (Marathousa 1 is dated to MIS 12; Blackwell et al. 2018; Jacobs et al. 2018; Tourloukis et al. 2018), with respect to the more recent dating of ‘Stuttgart morph’ specimens from Germany (MIS 11 or 9 in Steinheim, van Asperen 2013; MIS 7 in Neumark-Nord, Palombo et al. 2010), is not consistent with the hypothesis (b) of Saegusa and Gilbert (2008), according to which the ‘*namadicus* morph’ succeeded the ‘Stuttgart morph’ during MIS 9. Thus, the two morphologies are not evolutionarily related and must be referred either to different conspecific populations or to different species [hypotheses (a) and (c), respectively, in Saegusa and Gilbert 2008]. According to an additional option, favoured here, the two morphs and their intermediate stages might be an effect of intra-population variation, occurring mainly as a result of sexual dimorphism and ontogeny. If the parieto-occipital crest primarily functioned as a muscle insertion area, then its development might reflect the relative size of the tusks, which is expected to vary significantly among male, female, young, and old individuals. Quite recently, Larramendi et al. (2020) revisited the issue, examining the development of the parieto-occipital crest in cranial specimens from Africa, Asia, and Europe, and concluded that, indeed, the European samples cannot be divided into two species based on this feature. Evaluating a wider range of cranial and postcranial characters, they retained, though, the specific distinction between the European and the S. Asian straight-tusked elephants (*P. antiquus* and *P. namadicus*, respectively).

Unavailable Taxa

***Elephas gortynius* Skuphos, *Elephas antiquus* var. *gortyniensis* Depéret, 1913, and *Elephas minor* Skuphos**

These three species-group names appear in the literature, being attributed directly or indirectly to Th. Skuphos, and referring to the elephant fossils he excavated in 1902 in the Megalopolis Basin (see Sect. 3). In particular, Büchner (1903) and Georgalas (1929) mentioned *E. gortynius* as a species-rank name coined and used in lectures by Skuphos. According to these authors, the name *gortynius* referred to an allegedly complete skeleton from the area of Íssoma, which is not available presently, at least as a whole. The find was not described, except for a vague mentioning of its large size. Georgalas (1929) added *E. minor* as well, but in its Greek version, not latinised. According to him, the name *minor* was based on a very small molar (not described), which apparently belongs to a juvenile individual. Both names are considered herein as *nomina nuda*. This is because, to my knowledge, none of them has been ever published by Skuphos in any form of scientific or popular publication (that is why their authorships lack a publication year), and consequently they do not

fulfil the criteria of availability (Art. 11 of the ICZN). Moreover, although they were treated as valid names by the two authors mentioned above, the corresponding samples remained undefined and undescribed by them. Thus, their publications do not meet the criteria of Art. 12 of the ICZN, and the names can neither be attributed to Bürchner (1903) nor to Georgalas (1929), who used them.

Depéret (1913), when referring to the material excavated by Skuphos, also uses the first name (as a ‘variation’ of *E. antiquus*, that is of subspecies rank), but with the different spelling ‘*gortyniensis*’, followed by the designation ‘n. var.’. Supposedly, Depéret was aware of the unpublished status of this name and published it, but also in this case without any description of any kind. Since *E. antiquus gortyniensis* lacks a description, it is also a *nomen nudum*, according to the Art. 12 of the ICZN.

Invalid Taxa

In two cases, authors erected new species-group names for elephantid samples from Greece. Both names conform to the requirements of the ICZN, thus they are available, but are considered herein as junior synonyms of pre-existing names.

***Archidiskodon meridionalis proarchaicus* Melentis, 1966 (= *Mammuthus meridionalis*)**

Type Material AMPG 1964/449, left upper third molar (M3); Museum of Paleontology and Geology, University of Athens. Described by Melentis (1966a).

Type Locality Symbolí, (Sérres, E. Macedonia); Early Pleistocene.

Remarks This subspecies was defined on a single molar, described as presenting archaic morphological characters, which allegedly distinguish it as a basal subspecies of *M. meridionalis*. Indeed, the specimen is characterised by low lamellar frequency and thick enamel. However, given the considerable individual and wear-dependent morphological variability of the elephantid molars, a single specimen cannot be considered as a representative of a taxonomically distinct population. Moreover, despite the presence of characters that can be considered ancestral, others are derived (e.g., the molar’s height). In general, the molar AMPG 1964/449 is morphologically and metrically comparable to published samples of *M. meridionalis* (e.g., Maglio 1973; Lister and Sher 2015) and does not present any special features to justify a taxonomic separation. As such, *A. meridionalis proarchaicus* is considered a junior synonym of *Mammuthus meridionalis*. To my knowledge, this species-group name has never been used again for other samples.

***Elephas (Palaeoloxodon) cephallonicus* Theodorou et al., 2018 (= *Palaeoloxodon antiquus*)**

Type Material AMPG 900, fragment of maxilla with molars on both sides; Museum of Paleontology and Geology, University of Athens. Described by Theodorou et al. (2018).

Type Locality North coast of Póros, SE Kephallenía Island; early Late Pleistocene (104.2 ± 18.5 ka) (Theodorou et al. 2018).

Remarks This species was erected as an endemic, incipiently dwarfing *Palaeoloxodon* elephant taxon. The single specimen studied by the authors is dimensionally smaller than some continental samples of *P. antiquus*, but still remains large sized, having molar widths very close to the mean values of *P. antiquus* (according to Maglio 1973). As shown by Athanassiou et al. (2019), the Kephallenía specimen does not differentiate metrically from the mainland *Palaeoloxodon* of Greece, being larger than certain specimens from the Megalopolis Basin. Thus, AMPG 900 is not sufficient for the documentation of a new endemic species, which would require a better statistical sample to show the alleged size reduction trend. The palaeogeography of the area is also not favourable for the isolation of a *Palaeoloxodon* population on the island. During the early Late Pleistocene, when this individual was living, the sea strait separating Kephallenía from the mainland would be less than 8 km wide, a small distance considering the swimming capabilities of the elephants. For these reasons, *P. cephalonicus* is considered herein as a junior synonym of *P. antiquus*.

5 Conclusions

The elephantid fossil record of Greece is known from dental and osteological samples deriving from about 90 sites throughout the country's territory (see Appendix) and spanning geochronologically from the latest Pliocene to the Late Pleistocene (Fig. 13). The best-represented species is *Palaeoloxodon antiquus*, well known from skeletons, cranial, and postcranial material. The genus *Mammuthus* occurs less frequently, but is diverse taxonomically, represented by four species: *M. ex gr. rumanus*, *M. meridionalis*, *M. trogontherii*, and *M. cf. primigenius*. The relative abundance of *Palaeoloxodon* over *Mammuthus* during the Middle and Late Pleistocene is in accordance with the milder climatic conditions of S. Europe, which favoured the temperate species over the cold-adapted ones. Ongoing research in elephantid-bearing sites, particularly those of the Megalopolis Basin, is expected to yield additional data on the morphology and palaeoecology of the family in the SE extremities of Europe.

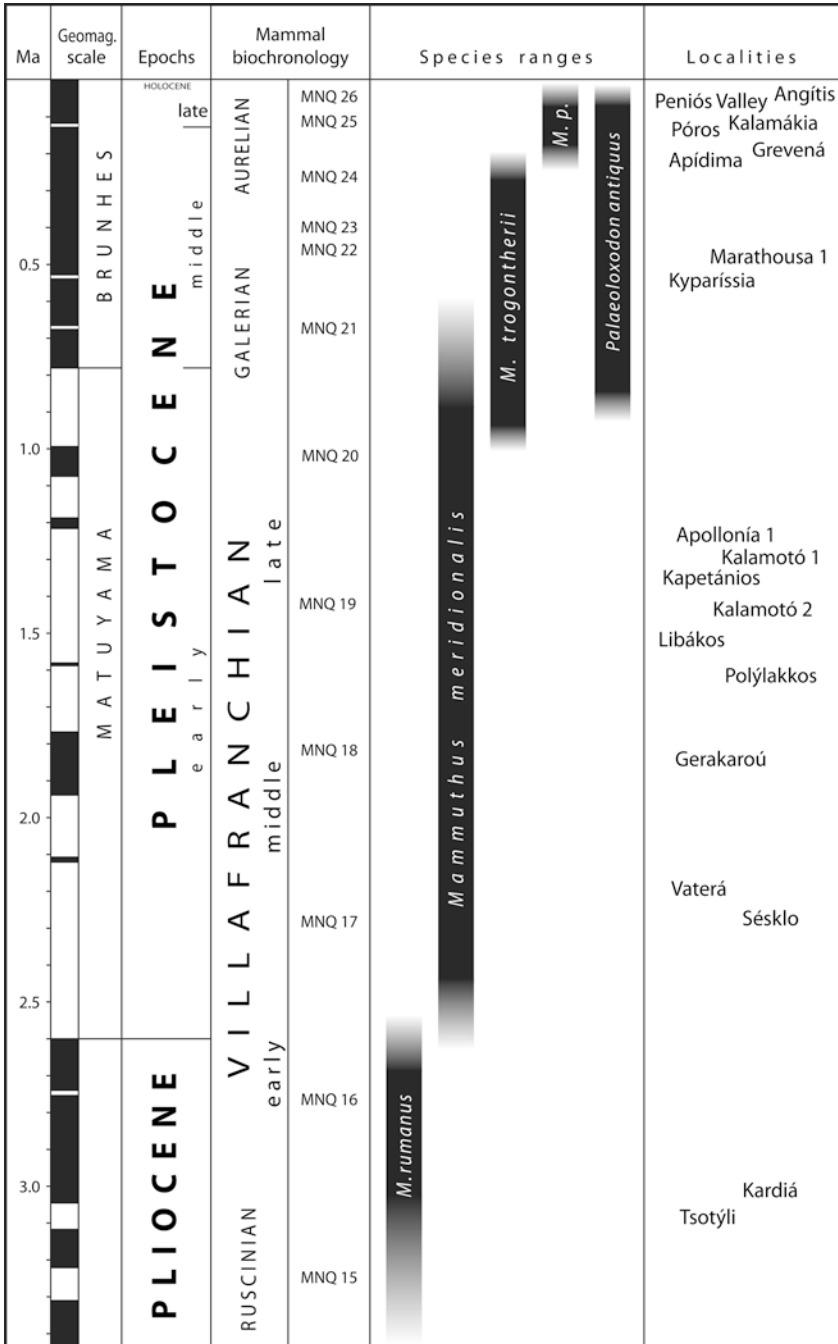


Fig. 13 Geochronologic chart showing the distributions of the elephantid species that occur in Greece and the stratigraphic positions of well-dated *Mammuthus*- and *Palaeoloxodon*-bearing Greek localities. Geochronologic and magnetostratigraphic subdivisions according to Pillans and Gibbard (2012). Mammal biozonation (MNQ zones) according to Guérin (1990). The biochronologic ranges of the *Mammuthus* species follow the concept introduced by Lister et al. (2005). 'M. p.' stands for *Mammuthus primigenius*

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Appendix

List of Greek localities with known occurrences of fossil elephants and mammoths (including some highly tentative ones), arranged in approximate geochronological order. The cited ages are in most cases broadly estimated, based on associated faunas (if any) and the current biostratigraphic framework. The taxonomic identification follows the present revision. Locality numbers refer to the collection numbers of the Paleobiology Database (PBDB)

Localities ^{PBDB No}	Age (biozone or chronometric dating)	Taxon
Angítis ²⁰⁴³⁹¹	Late Pleistocene (34–28 ka)	<i>Mammuthus</i> cf. <i>primigenius</i> ¹
^a Peniós Valley ²⁰⁴³⁹⁷	Late Pleistocene (45–30 ka)	<i>Palaeoloxodon antiquus</i> ²
Kalamákia Cave ¹⁸⁴²⁴⁵	Late Pleistocene (100–40 ka)	<i>Palaeoloxodon antiquus</i> ³
Phílippi ²⁰⁴⁷⁴⁷	Late Pleistocene	<i>Mammuthus</i> cf. <i>primigenius</i> ⁴
Tsákoni ²⁰⁴⁴⁰²	Late Pleistocene	cf. <i>Palaeoloxodon antiquus</i> ⁵
Peniós estuary	Late Pleistocene	<i>Palaeoloxodon antiquus</i> ⁶
Póros (Kephallenía) ²⁰⁴⁴⁰³	early Late Pleistocene (104 ka)	<i>Palaeoloxodon antiquus</i> ⁷
^b Íssoma ²⁰⁴⁵⁴⁶	late Middle (–Late?) Pleistocene	<i>Palaeoloxodon antiquus</i> ^{8,*}
Íssoma KYT	late Middle (–Late?) Pleistocene	<i>Palaeoloxodon antiquus</i> [*]
Symbolí ²⁰⁴⁸⁰⁷	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ⁹
Xeriás ¹⁸²⁶⁷⁹	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ¹⁰
Ravin de l'éléphant ²⁰⁴⁵⁴⁹	Middle–Late Pleistocene	cf. <i>Palaeoloxodon antiquus</i> ^{4,11,*}
Philótas	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> [*]
Pétres	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ^{10,12}
Amýntaio ²⁰⁴⁵⁵⁰	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ¹³
Sotíras ¹⁸²⁶⁷⁸	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ¹⁰
Néa Kómi ²⁰⁴⁷⁵⁴	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ^{14,*}
Perdíkkas ²⁰⁴⁷⁵³	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ^{10,15}
Pentávryssos	Middle–Late Pleistocene	Elephantidae indet. ^{16,*}
Ptolemaís ²⁰⁴⁵⁵²	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ¹⁷
Allatíni	Middle–Late Pleistocene	? <i>Palaeoloxodon</i> sp. ¹⁸
Trílophos ²⁰⁴⁷⁴³	Middle–Late Pleistocene	? <i>Palaeoloxodon</i> sp. ¹⁸
Epanomi ²⁰⁴⁷⁴⁴	Middle–Late Pleistocene	? <i>Palaeoloxodon</i> sp. ¹⁸

Localities ^{PBDB No}	Age (biozone or chronometric dating)	Taxon
Petráloná Cave ¹⁸³¹²³	Middle–Late Pleistocene	Elephantidae indet.*
Kalonéri ¹⁸²⁶⁷⁷	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ¹⁰
°Tsoýli	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ¹⁹
Siátista	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ²⁰
Terpsithéa ¹⁸²⁶⁸⁰	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ¹⁰
Mesorráchi	Middle–Late Pleistocene	Elephantidae indet. ²¹
Chálki	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ²²
Néa Léfkí ¹⁸²⁶⁸¹	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ¹⁰
Lími (Euboea)	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ²⁰
Trichonía	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ²⁰
Patras ²⁰⁴⁵⁵⁴	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ²³
Nissí ²⁰⁴⁵⁵⁵	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ^{24,*}
Canal of Corinth ²⁰⁴⁵⁵³	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ²³
Roupáki ²⁰⁴⁵⁵⁶	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ²⁵
Símiza	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> *
Kálymnos ³⁴⁷⁷⁰	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ²⁶
Apídima Cave C ³²⁰⁸²	Middle–Late Pleistocene	Elephantidae indet. ²⁷
Cape Cheládi, Kýthera ²⁰⁴²⁹⁸	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> ²⁸
Alivéri	Middle–Late Pleistocene	<i>Palaeoloxodon antiquus</i> *
Ambélia (Grevená) ²⁰⁴⁵⁵⁷	late Middle Pleistocene	<i>Palaeoloxodon antiquus</i> ²⁹
Phílippi ²⁰⁴⁷⁴⁹	Middle Pleistocene	<i>Mammuthus trogontherii</i> ⁴
Sotíras ¹⁸²⁶⁷⁸	Middle Pleistocene	<i>Mammuthus trogontherii</i> ^{4,18}
Lágoura (Néo Kostarázi) ²⁰⁴⁵⁵⁸	Middle Pleistocene	Elephantidae indet. ³⁰
Tsoýli ²⁰⁴⁷⁵¹	Middle Pleistocene	<i>Mammuthus</i> cf. <i>trogontherii</i> ⁴
Megálo Monastíri ²⁰⁴⁵⁶⁰	Middle Pleistocene	Elephantidae indet. ³¹
Megalópolis Basin (undefined sites) ¹⁸²⁷²¹	Middle Pleistocene	Elephantidae indet. ³²
Marathóusa 1 ¹⁸⁷⁶³⁷	Middle Pleistocene (0.48–0.42 Ma)	<i>Palaeoloxodon antiquus</i> ³³
Kyparíssia 1 ¹⁹⁴⁴⁷²	Middle Pleistocene	<i>Palaeoloxodon antiquus</i> ³⁴
Kyparíssia 3 ¹⁹⁴⁴⁷⁴	Middle Pleistocene	<i>Palaeoloxodon antiquus</i> ³⁴
Kyparíssia 4 ¹⁹⁴⁴⁷⁵	Middle Pleistocene	<i>Palaeoloxodon antiquus</i> ³⁴
^d Kalývia Karyón	Middle Pleistocene	<i>Palaeoloxodon antiquus</i> ³⁵
°Léfkro	Middle Pleistocene	<i>Palaeoloxodon antiquus</i> ³⁶
Leontári	Middle Pleistocene?	Elephantidae indet. ³⁷
Loussiká ²⁰⁴⁵⁶¹	early Middle Pleistocene	<i>Mammuthus trogontherii</i> ³⁸
Polýlakkos	early Middle Pleistocene?	<i>Mammuthus trogontherii</i> ¹⁸
Apollonía ³⁴⁷⁸⁴	latest Early Pleistocene (MNQ19)	<i>Mammuthus meridionalis</i> ³⁹
Kalamotó-1 ²⁰⁰⁰⁸³	latest Early Pleistocene (MNQ19)	<i>Mammuthus meridionalis</i> ⁴⁰
Kalamotó-2 ²⁰⁰⁰⁸⁴	latest Early Pleistocene (MNQ19)	<i>Mammuthus meridionalis</i> ⁴⁰

Localities ^{PBDB No}	Age (biozone or chronometric dating)	Taxon
Platanochóri-1 ²⁰⁴⁶⁵⁸	latest Early Pleistocene (MNQ19)	Elephantidae indet. ⁴¹
Kapetanios ³⁴⁷⁸¹	Early Pleistocene (MNQ19)	<i>Mammuthus meridionalis</i> ⁴²
Libákos ³⁴⁷⁶⁴	Early Pleistocene (MNQ19)	<i>Mammuthus meridionalis</i> ⁴²
Halykés ³⁴⁷⁸²	Early Pleistocene (MNQ19)	Elephantidae indet. ⁴³
Tsiótra Vryssi	Early Pleistocene (MNQ18–19)	<i>Mammuthus meridionalis</i> ⁴⁴
Gerakarou ³⁴⁶¹⁷	Early Pleistocene (MNQ18)	<i>Mammuthus meridionalis</i> ⁴⁵
Polýlakkos ³⁴⁷⁶³	Early Pleistocene (MNQ18?)	<i>Mammuthus</i> cf. <i>meridionalis</i> ⁴³
Sésklo ³⁴⁶¹⁴	Early Pleistocene (MNQ17)	<i>Mammuthus meridionalis</i> ⁴⁴
Vaterá-DS ¹⁸³³⁴⁴	Early Pleistocene (MNQ17)	<i>Mammuthus</i> cf. <i>meridionalis</i> ⁴⁶
Vaterá-U ¹⁸³³⁴⁶	Early Pleistocene (MNQ17)	<i>Mammuthus</i> cf. <i>meridionalis</i> ⁴⁶
Symbolí ²⁰⁴⁸⁰⁸	Early Pleistocene	<i>Mammuthus meridionalis</i> ^{9,*}
Phílippi ²⁰⁴⁷⁵⁰	Early Pleistocene	<i>Mammuthus meridionalis</i> ⁴
Epanomi ²⁰⁴⁶⁶⁰	Early Pleistocene	<i>Mammuthus</i> cf. <i>meridionalis</i> ⁴⁷
íKípi ²⁰⁴⁹³³	Early Pleistocene	<i>Mammuthus</i> cf. <i>meridionalis</i> ⁴⁸
Peponiá	Early Pleistocene	<i>Mammuthus meridionalis</i> ⁴⁹
Tsotyli	Early Pleistocene	<i>Mammuthus meridionalis</i> ¹⁸
Trapezítsa	Early Pleistocene	Elephantidae indet.*
Q-Profil ³⁴⁸¹²	Early Pleistocene	<i>Mammuthus</i> cf. <i>meridionalis</i> ⁴³
Ioánnina ²⁰⁴⁷⁴⁰	Early Pleistocene	<i>Mammuthus meridionalis</i> ⁵⁰
Gíáltra ²⁰⁴⁸⁰⁴	Early Pleistocene	<i>Mammuthus meridionalis</i> ⁵¹
Reghínio ²⁰⁴⁶⁶¹	Early Pleistocene	<i>Mammuthus</i> cf. <i>meridionalis</i> ⁵²
Zéli	Early Pleistocene?	<i>Mammuthus</i> sp.*
Lefkóchoma ²⁰⁴⁷⁴¹	Early Pleistocene	Elephantidae indet. ⁵³
Vlachiótis ²⁰⁴⁷⁴²	Early Pleistocene	<i>Mammuthus meridionalis</i> ⁵⁴
Antimáchia ²⁰⁷¹³⁰	Early Pleistocene	<i>Mammuthus meridionalis</i> ⁵⁵
Kardámaena ²⁰⁴⁶⁶²	Early Pleistocene	<i>Mammuthus meridionalis</i> ⁵⁶
Almyrí	Early Pleistocene	<i>Mammuthus meridionalis</i> ⁵⁶
Límini (Vromonéra) ²⁰⁴⁹³⁴	Pleistocene	Elephantidae indet. ⁵⁷
Tsotyli ²⁰⁴⁴⁰⁰	late Pliocene	<i>Mammuthus</i> ex gr. <i>rumanus</i> ^{4,58,*}
Kardiá ²⁰⁴⁷⁵²	late Pliocene	<i>Mammuthus</i> ex gr. <i>rumanus</i> ^{4,*}

GPTS Geomagnetic Polarity Time Scale, ELMA European Land Mammal Age, MNQ Mammal Neogene–Quaternary Zone

^aAlso mentioned as ‘Lárisa’ in old publications (e.g., Georgalas 1929; Paraskevaidis 1956)

^bAlso appears in the literature under the names ‘Hágios Ioánnis tis Vathiás Choúnis’ (e.g., Büchner 1903; Melentis 1961) and ‘Grána tou Skoufou’ (Theodorou 2014)

^cAccording to the sketchy map provided by Melentis (1966b), this locality is rather in the area of Kalonéri or Polýlakkos, than Tsotyli

^dAlso appears in the literature as ‘Musaklá’ (Bürchner 1903; Melentis 1961)

^eReported as ‘Biláli’ in the original publication

^fThis locality name is recorded here for the first time, as in the original publication it was referred to vaguely as ‘Neápolis area’

^gThis study

¹Koufos (1981), ²Boessneck in Milójić et al. (1965), Athanassiou (2001, 2011), ³Harvati et al. (2013), ⁴Koulidou (2013), ⁵Athanassiou (2004), ⁶Paraskevaïdis (1977), ⁷Theodorou et al. (2018), Athanassiou et al. (2019), ⁸Melentis (1961, 1963), Theodorou (2014), ⁹Melentis (1966a), ¹⁰Tsoukala et al. (2011), ¹¹de Bonis et al. (1973), ¹²Velitzelos and Schneider (1973), ¹³Kevrekidis and Mol (2016), ¹⁴Mitzopoulos (1967), ¹⁵Poulianos (1986), ¹⁶Stratigopoulos (2008), ¹⁷Astre (1966), ¹⁸Marinos (1964), ¹⁹Melentis (1966b), ²⁰Georgalas (1929), ²¹reported anonymously in the local newspaper ‘Mikrá’, number 305, June 6, (1907), ²²Schneider (1968), ²³Depéret (1913), ²⁴Agiadi and Theodorou (2005), ²⁵Athanassiou (2000), ²⁶Masseti (2006), ²⁷Tsoukala (1999), ²⁸Kuss (1967), Athanassiou et al. (2019), ²⁹Tsoukala and Lister (1998), ³⁰Harvati et al. (2008), ³¹Runnels and van Andel (1993), ³²Sickenberg (1976), ³³Konidaris et al. (2018), ³⁴Athanassiou (2018), ³⁵Melentis (1961, 1963), ³⁶Melentis (1965), ³⁷Mitzopoulos et al. (1862), ³⁸Athanassiou (2012), ³⁹Konidaris et al. (2020), ⁴⁰Tsoukala and Chatzopoulou (2005), ⁴¹Konidaris et al. (2015), ⁴²Steenasma (1988), ⁴³Athanassiou (1998), ⁴⁴Konidaris et al. (2016), ⁴⁵Athanassiou and Kostopoulos (2001), ⁴⁶de Vos et al. (2002), ⁴⁷Athanassiou and Kostopoulos (2010), ⁴⁸Athanassiou (2006b), ⁴⁹Hilber (1894), ⁵⁰Melentis (1960), ⁵¹Psarianos and Thenius (1954), ⁵²Athanassiou (2006a), ⁵³Symeonidis (1970), ⁵⁴Symeonidis and Theodorou (1986), ⁵⁵Forsyth Major (1887), Airaghi (1928), Desio (1931), ⁵⁶Desio (1931), Charrier and Giglio (1969), ⁵⁷Paraskevaïdis (1956), ⁵⁸Kostopoulos and Koulidou (2015)

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