

Review of the Pliocene and Pleistocene Proboscidea (Mammalia) from Greece

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Fossil Proboscidea are common in the Pliocene and Pleistocene sediments of Greece. They have been studied either as parts of a whole fauna, or, as is usually the case, as isolated finds of one or two molars or bones. The only representative of Elephantidae of the Late Pliocene and Early Pleistocene in Europe in general and in Greece in particular is *Mammuthus meridionalis*. In some Late Pliocene localities, this elephant is found together with the gomphothere *Anancus arvernensis*. Some sporadic more advanced forms of the genus *Mammuthus* are identified as *M. trogontherii* (= *M. armeniacus*) and *M. primigenius*. Most of the Late Pleistocene findings belong to *Elephas antiquus*, a species known from numerous continental localities. The same species is also known from insular sites, where it is the main ancestor of the island endemic forms.

Correspondence: C.S. Doukas & A. Athanassiou (to whom correspondence should be addressed), Dept. of Historical Geology and Palaeontology, University of Athens, Panepistimiopolis, GR-157 84 Athens, Greece; email cdoukas@geol.uoa.gr and aathan@cc.uoa.gr

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INTRODUCTION

The Proboscidea is a mammalian order that is currently represented by just two species, but that showed a remarkable diversity and paleogeographical distribution during passed geological epochs. The Greek peninsula was part of this holarctic distribution, including many localities, dated from Middle Miocene to Late Pleistocene (Dermitzakis *et al.* 1982). A short review of the available bibliographical data for the Pliocene and Pleistocene finds is given in this paper. Most of the localities known include Late Pliocene or Pleistocene Elephantidae remains, although Pliocene mastodont fossils, especially those referred to *Anancus*, are also found. Because of the relative complexity of the proboscidean taxonomy and systematics, and as a result of different opinions expressed by the many authors, the genus and species names will be given in

the following review (text and tables) exactly as reported in the relevant papers. In the subsequent discussion, the taxonomy proposed by Maglio (1973) will be used instead, with the exception of *Elephas namadicus*, as the considered synonym *E. antiquus* is still in use for the European material. Each locality name is cited together with a superscript reference number, which corresponds to the geographical position of the locality, as indicated in Figure 1. All tables are listed at the end of this paper.

MAINLAND PROBOSCIDEANS (Tables 1-3)

The fossil elephant findings in Greece are numerous and referred to all known European species of the family Elephantidae. However, the specimens found and described by several

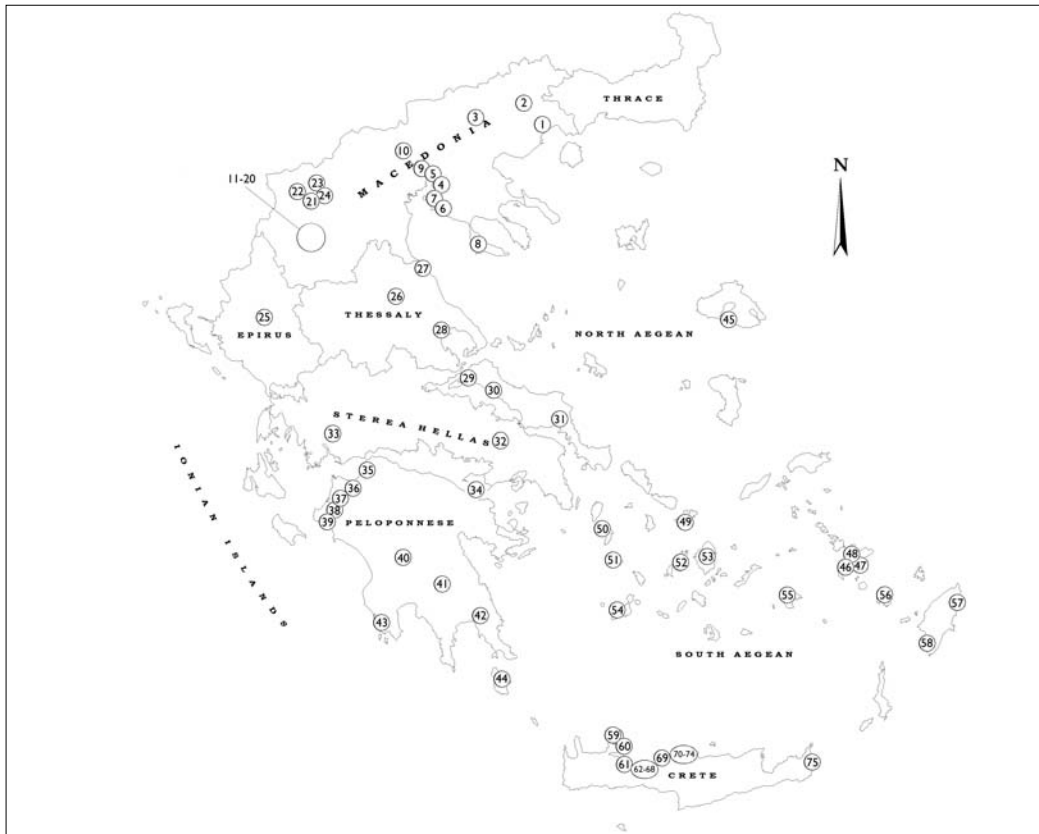


Figure 1 Geographical position of the Greek Pliocene and Pleistocene localities with fossil Proboscidea.

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|---------------------|---------------------|----------------|-----------------------|
| 1 Tenághi Philíppon | 20 Ambéλια | 39 Roupáki | 58 Apolakkiá |
| 2 Aggítis | 21 Perdikkas | 40 Megalópolis | 59 Akrotíri |
| 3 Symbolí | 22 Néa Kómi | 41 Skoúra | 60 Mélekas |
| 4 Allatíni | 23 Sotír | 42 Vlachiótis | 61 Exópolis |
| 5 Trílopho | 24 Pétres | 43 Pýlos | 62 Zourída |
| 6 Epanomí | 25 Ioánnina | 44 Kýthera | 63 Réthymnon fissure |
| 7 Hagía Triáda | 26 Piniós valley | 45 Vaterá | 64 Mavromouíri |
| 8 Sáni | 27 Piniós mouth | 46 Antimáchia | 65 Simonelli |
| 9 Vathýlakkos | 28 Sésklo | 47 Kardámaena | 66 Couúmbes |
| 10 Axiós dam | 29 Aedipsós | 48 R. Almirí | 67 Panagía |
| 11 Miliá | 30 Límnι | 49 Dílos | 68 Gridá Avláki |
| 12 Neápolis | 31 Alivéri | 50 Kýthnos | 69 Skaléta |
| 13 Chorigós | 32 Thíva | 51 Sériphos | 70 Akrotírión Kórakas |
| 14 Tsotýlion | 33 Trichonía | 52 Páros | 71 Kaló Choráphi |
| 15 Klíma | 34 Canal of Corinth | 53 Náxos | 72 Balí |
| 16 Líbakos | 35 Patras | 54 Mílos | 73 Hag. Antónios |
| 17 Polýlakkon | 36 Loussiká | 55 Astypálaea | 74 Koulourídi |
| 18 Kapetánios | 37 Nissíon | 56 Tílos | 75 Charoúmbes |
| 19 Q-Profil | 38 Néa Olga | 57 Erimókastro | |

authors are usually isolated molars or tusks (sometimes broken parts of them) that are found by chance by local people or during field works, without being products of systematic excavations.

Northern Greece

Most localities are in the lacustrine basins in Northern Greece (Macedonia and Thessaly). The lignite basin of Ptolemaís has yielded remains of *Archidiskodon meridionalis archaicus* (Mitzopoulos 1967a). Melentis (1966a) also records the presence of the same species, as well as of *Palaeoloxodon antiquus*, in sites of the nearby upper valley of the river Haliákmon, near the small town of Tsotyílion¹⁴. Another species, *Mammontheus trogontherii*, together with *Archidiskodon meridionalis* and *Palaeoloxodon antiquus antiquus* is reported by Velitzelos & Schneider (1973) from two sites in the Flórina district. Other Macedonian localities are Tenághi Philíppon¹ (with *Archidiskodon meridionalis* and *Mammontheus trogontherii*), Allatíni⁴, Trilopho⁵ and Epanomí⁶ (Thessaloníki district - with *Palaeoloxodon antiquus*; Dermitzakis *et al.* 1982), as well as Symbolí³ (Sérres district - with *Archidiskodon meridionalis* and *Palaeoloxodon antiquus*; Melentis 1966b). Some dental remains from the basin of Dráma (Aggítis² locality, E. Macedonia) are referred to by Koufos (1981) as *Mammuthus* cf. *primigenius*. De Bonis *et al.* (1973) report the presence of *Palaeoloxodon antiquus italicus* from Vathýlakkos⁹ ('Ravin de l'éléphant', Axiós valley), a region rich in Late Miocene mammal remains. More recent field works and excavations at several sites in the Neápolis-Grevená basin (Western Macedonia) yielded remains of *Archidiskodon meridionalis* (Líbakos¹⁶, Polýlakkon¹⁷, Kapetánios¹⁸, Q-Profil¹⁹; Steensma 1988) and *Elephas (Palaeoloxodon) antiquus* (Perdíkkas²¹ and Ambéllia²⁰; Tsoukala & Lister 1998).

Most Thessalian localities are located in Piniós valley²⁶, in the region west of the city of Lárissa. Remains of *Palaeoloxodon anti-*

quus are described by Miloječić *et al.* (1965) and Schneider (1968). The latter author also describes an older finding, referred to as *Archidiskodon meridionalis* cf. *cromerensis*, which comes from the Tertiary hills of the broader Piniós valley area, near Lárissa. Paraskevaidis (1977) reports the presence of *Elephas (Palaeoloxodon) antiquus italicus* together with *Elephas (Archidiskodon) cf. meridionalis* and *Elephas (Mammontheus) cf. primigenius* near the mouth of the same river²⁷. Some skeletal and dental remains of *Mammuthus* are included in the rich Plio-Pleistocene mammal fauna of Sésκλο²⁸ (Athanasioiu 1996).

In Épirus province (NW Greece) there is only one citation of fossil Proboscidea: Melentis (1960) describes a molar referred to *Elephas (Archidiskodon) meridionalis archaicus* from a site near the town of Ioánnina²⁵.

Some recent finds at Vaterá⁴⁵ on Lésbos Island (NE Aegean) -an island that is close to the mainland and has balanced continental faunas- are referred to cf. *Mammuthus meridionalis* (de Vos *et al.* 2002).

Central and Southern Greece

In Central Greece the family Elephantidae is known in the area of Trichonía³³ (Georgalas 1929) and from two localities in Euboea, namely Aedipsós²⁹ (Psarianos & Thenius 1954) and Alivéri³¹ (Dermitzakis & Theodorou, pers. comm. 1990). The Trichonía finds are referred to *Elephas antiquus* and the Euboea finds to *Archidiskodon meridionalis*.

The most important locality of Southern Greece is the basin of Megalópolis⁴⁰ (Peloponnese), where, according to Melentis (1961, 1963), the rich proboscidean fauna consists of several subspecies of normal sized *Archidiskodon meridionalis*, *Palaeoloxodon antiquus* and *Mammontheus primigenius*, as well as a dwarf form (*Palaeoloxodon melitensis*). The presence of a giant and a very small form in the basin was pointed out earlier by Th. Skouphos, professor of the University of Athens and excavator of the

Megalópolis material in the first years of the 20th century (Georgalas 1929). Sondaar & Boekschoten (1967) consider that only *Elephas antiquus* and *Elephas primigenius* are present in the locality, attributing the small size finds to juvenile and not to dwarf individuals. Megalópolis is one of the southernmost localities with *M. primigenius* (the southernmost occurrence of the species in Greece). *Archidiskodon meridionalis* is also reported from Vlachiótis⁴², near Sparta (Symeonidis & Theodorou 1986), as well as from the nearby island of Kýthera⁴⁴ (Psarianos & Kalpakis 1980). Petrochilos (1938) reports the presence of *Elephas antiquus* on the same island. Manolessos (1955) considers that the elephant remains from Kýthera belong to a dwarf form. However, this is not accepted by later authors (Kuss 1967; Sondaar 1971; Dermitzakis *et al.* 1982). Georgalas (1929) reports some remains of *Elephas antiquus* in the areas of Patras³⁵ and of the Canal of Corinth³⁴. Dermitzakis & Theodorou (1980) record the presence of elephant remains in Néa Olga³⁸ (Ilis, NW Peloponnese). Athanassiou (2000) describes remains of *Elephas antiquus* from the nearby locality of Roupáki³⁹. Some fragmentary remains in the broader area of Patras (Loussiká³⁶) may belong to *Elephas antiquus* (personal data). An elephant tusk of presently unknown affinities has been found in the lacustrine deposits of the same region (locality Nissíon³⁷; Theodorou, pers. comm. 1999).

On the island of Kos, which is situated in SE Aegean, close to the mainland, *Elephas meridionalis* remains have been found (Forsyth Major 1887; Airaghi 1928; Desio 1931; Kotsakis *et al.* 1980).

Mastodont findings

The fossil mastodonts in Greece are relatively rare compared to the abundant elephant remains. *Anancus arvernensis* is the most typical as well as the last representative of the mastodonts in the Pliocene faunas. It is known from several localities mainly in Macedonia, such as the Axiós valley (Axiós

dam¹⁰ area; Sakellariou-Mane 1972), the Thessaloníki and Chalkidikí area⁷⁻⁸ (Koufos 1977) and the Neápolis-Grevená basin¹⁵ (Steensma 1988). In Thessaly the species is reported only from Sésklo²⁸ (Symeonidis & Tataris 1983, Athanassiou 1996). Southern occurrences include Thíva³² (a specimen described but not identified by Gidararakos 1938), some Peloponnesian localities (Skoúra⁴¹; Georgalas 1941 and Pýlos⁴²; Mitzopoulos 1967b), as well as the islands of Kos and Rhódos in the Dodecanese, SE Aegean (Forsyth Major 1887, Airaghi 1928, Desio 1931, Theodorou *et al.* 2000). Recent finds at Vaterá⁴⁵, Lésbos Island (NE Aegean) are also referred to this species (de Vos *et al.* 2002). Another Pliocene species, *Mammot borsoni*, is known only from Macedonia (usually referred to as *Zygodolophodon*): in the Neápolis-Grevená basin¹¹ (Brunn 1956, Dermitzakis *et al.* 1982, Tsoukala 2000) and at Vathýlakkos⁹ (Axiós valley; Mitzopoulos 1967b).

ISLAND PROBOSCIDEANS (Table 4)

Proboscidean island populations include mainly Pleistocene insular forms of *Elephas antiquus* (Vaufrey 1929, Osborn 1936-1942; Sondaar 1971, Dermitzakis *et al.* 1982; Theodorou & Dermitzakis 1991). However, normal sized elephant remains are reported from islands that are near the continental coast, like Kos and Lésbos. Most endemic fossil samples come from the islands of Crete and Tílos, while several other island localities have yielded isolated specimens.

Crete

Some authors (Bate 1907; Kuss 1965, 1966) refer elephant remains of moderate size from Crete (caves Charóumbes⁷⁵ III, Panagía⁶⁷ I, Coúmbes⁶⁶ III etc.) to *Elephas antiquus*, attributing some smaller specimens to one or more (up to three or possibly four! - Kuss 1966) endemic species: Bate (1907) establishes the dwarf species *Elephas creticus*. Simonelli (1908) (and Simonelli 1894, 1897 in Dermitzakis 1977) ascribes some middle-

sized finds to *Elephas priscus*. However, Vaufray (1929) considers this species as synonymous with *Elephas antiquus* and Bate's *Elephas creticus* as synonymous with the Maltese dwarf *Elephas melitensis*. Vaufray (1929) also supposes that the fossil remains described by Bate (1907) as *Elephas antiquus* could belong to *Elephas mnaidriensis*. Kuss (1965), accepting the species given by Bate (1907), adds an intermediate species (between *antiquus* and *creticus*) that includes Simonelli's *Elephas priscus*, named *creutzburgi*, which -quite strangely- he classifies with the African genus *Loxodonta*. A year later the same author (Kuss 1966) also refers *creticus* to this genus (*Loxodonta cretica*), while he adds another subspecies to the Cretan elephant fauna: *Hesperoloxodon antiquus falconeri* from Akrotiri⁵⁹. The original taxonomical attribution of all Cretan elephant species to the genus *Elephas* is later accepted by Kuss (1970, 1973). Sondaar & Boekschoten (1967) and Sondaar (1971) do not accept the presence of so many species and reduce their number to two: *Elephas* cf. *antiquus* and *Elephas creticus*. Accordi (1972) describes some remains from the cave 'Simonelli'⁶⁵ as *Elephas priscus* and *Elephas (Palaeoloxodon) creticus*. Melentis (1974) prefers to assign the material from this cave to *Palaeoloxodon* sp., while Malatesta (1980) attributes it to *Palaeoloxodon creutzburgi*. Kotsakis *et al.* (1980) accept again the three-species-scheme proposed by Kuss (1965) for the Cretan fossil elephants, attributing them to the genus *Palaeoloxodon* and assigning the finds from the caves west of Réthymnon (including 'Simonelli' Cave) to *Palaeoloxodon creutzburgi*. De Vos (1984) accepts the taxonomy of Kuss (1973) with three taxa: *Elephas antiquus*, *E. creutzburgi* and *E. creticus*. Mol *et al.* (1996) consider again the presence of two species: *Elephas* cf. *antiquus* and *Mammuthus creticus*, accepting for the latter species a descent from *Mammuthus meridionalis*. This ancestry was also previously implied by Kuss (1973), while Bate (1907) already pointed out many similarities between her new species

and *Mammuthus meridionalis*. Symeonidis & Theodorou (1983) describe a mandible from a cave near Réthymnon (Coúmbes⁶⁶), which could be assigned to a new (not named) subspecies or species. Mol *et al.* (1996) consider it *Elephas* cf. *antiquus*.

Many authors tried to cope with the presence of both, continental and endemic, elephant species of different sizes on the island, suggesting several biostratigraphical and palaeogeographical schemes (Sondaar & Boekschoten 1967; Kuss 1970; Kotsakis *et al.* 1980; Dermitzakis & de Vos 1986; Sondaar *et al.* 1986; Dermitzakis & de Vos 1987; Mol *et al.* 1996; Sondaar *et al.* 1996). However, Theodorou (1986), based on metrical comparisons of the up till then available Cretan material to other endemic and mainland samples, shows that the presence of continental forms on the island cannot be accepted. Mol *et al.* (1996) do not agree with this aspect, accepting the presence of more or less normal sized elephants in the island (*Elephas* cf. *antiquus*).

Tilos

Many other Aegean islands have yielded remains of dwarf elephants, Tilos being the most important of them. In the cave named Charkadió⁶⁶ abundant elephant remains were found that were firstly referred by Symeonidis (1972) to two species: *Palaeoloxodon falconeri* and *P. antiquus melitensis*. Symeonidis *et al.* (1973) adapted the subspecific names of the findings to the nomenclature proposed by Ambrosetti (1968), giving the names *Palaeoloxodon antiquus falconeri* and *Palaeoloxodon antiquus mnaidriensis*. Theodorou (1983) considers the two forms as sexual dimorphs of the same species. He provisionally assigns them to *Palaeoloxodon antiquus falconeri* (although there is no genetic relationship between the populations of Tilos and Malta) until more material facilitates the establishment of a new endemic subspecies for the finds of the island.

Other islands

Remains attributed to *Palaeoloxodon anti-quus mnaidriensis* are described by Marinis & Symeonidis (1973) and Symeonidis *et al.* (1974) from Erimókastró⁵⁷, Rhodes. Scanty remains of dwarf elephants are also known from the islands of Dílos⁴⁹, Páros⁵², Náxos⁵³, Sérifhos⁵¹, Milos⁵⁴, Kýthnos⁵⁰ and Astypálea⁵⁵ (Cayeux 1908; Georgalas 1929; Mitzopoulos 1961; Kuss 1973; Dermitzakis & Sondaar 1979; personal data).

DISCUSSION

The numerous sites with Proboscidean remains show the important role of this order in the fossil faunas of the Greek peninsula. However, despite the abundance and wide dispersion of the localities, the number of the findings is in most cases very low. The specimens were usually found by chance and collected by non-specialists. As a result, little or nothing is known about their exact location, their taphonomy and their stratigraphy. Another related point is that many specific or subspecific identifications are based on the dimensions and morphological characters of a single tooth, or even a part of it (for example Melentis 1960, 1965, 1966b; Mitzopoulos 1967a; Paraskevaïdis 1977). Even when more material is available, there is a tendency to refer the several morphotypes to distinct subspecies, not allowing for any degree of intraspecific morphological variation (i.e. Melentis 1961). Hence, some identifications are quite invalid. The need for systematic excavations is essential, in order to make a systematic revision possible.

Despite these problems, the succession of proboscidean species known from Western Europe is also recorded in the Greek mainland faunas. The older occurrences of *Mammuth borsoni* are replaced by the typical Pliocene species *Anancus arvernensis* and the Plio-Pleistocene *Mammuthus meridionalis*. Some authors report the presence of the more evolved *M. armeniacus*, a species of the Middle Pleistocene, but the scarcity and the absence of diagnostic characters in the availa-

ble material make these identifications rather uncertain. The Late Pleistocene localities have yielded remains of *Mammuthus primigenius* and *Elephas antiquus*.

The problem of poor material is also present in the case of the endemic proboscidean faunas (with the exception of Tilos, where the excavation is still in progress). Many authors tend to classify the finds according to their size, attributing them to the species that were already known from Malta (*Elephas falconeri*, *E. melitensis* and *E. mnaidriensis*). Maglio (1973) agrees with this point of view, finding little biological sense in attributing a different name in each insular population. Some other authors (like Sondaar & Boekschoten 1967; Sondaar 1977; Dermitzakis & Sondaar 1979; Symeonidis & Theodorou 1983; Theodorou 1986) consider that each island colonisation is a unique and independent evolutionary process. It is reasonable that, since the elephant populations on the several islands arose independently from each other and they don't have any genetic contact, they should be classified as distinct taxa. However, no new specific or subspecific name has been given until now to the endemic elephant populations of the Aegean.

CHRONOLOGY

Anancus arvernensis is a typical Pliocene species. During the Early Pliocene it coexisted with *Mammuth borsoni*, a mastodont that did not survive after the arrival of the first primitive elephants (genus *Mammuthus*; *sensu* Maglio 1973). *Anancus* is usually reported together with *Mammuthus* in several localities of Late Pliocene age. This is the case at the localities of the island of Kos⁴⁶⁻⁴⁸, as well as at Sésklo²⁸ (Thessaly). However, there are no precise stratigraphical or taphonomical data for any locality that show the coexistence of the two taxa in the same stratigraphical level. According to Kurtén (1968), *Anancus* ranges up to Early Pleistocene.

The species *Mammuthus meridionalis* shows a gradient of dental characters during the Late Pliocene and Early Pleistocene, the

stratigraphically older specimens having fewer plates, thicker enamel and less hypsodont molars. Several subspecific names have been proposed for distinct stages of this gradient. According to Kurtén (1968), *Mammuthus meridionalis* was not an ecologically specialised animal, living in savannahs, steppes and woodlands. During Middle Pleistocene it was replaced by *Mammuthus armeniacus* (*M. trogontherii*), a more advanced species. The lineage ends up in the latest Pleistocene with the woolly mammoth, *Mammuthus primigenius*, a species adapted to cold steppe environments. Another lineage is represented in the Middle and Late Pleistocene of Europe by *Elephas antiquus* or forest elephant, adapted to the temperate climates of the interglacials. Kurtén (1968) supposes that the South European peninsulas served as refuges for this species during the glacial stages of the Pleistocene.

The insular forms derive from Late Pleistocene *Elephas antiquus* populations, as generally accepted by most authors, with the possible exception of *E. creticus*, which has been also considered as descendant of *Mammuthus meridionalis* (Kuss 1973; Mol *et al.* 1996). The good swimming abilities of the elephants allowed them to colonise islands fairly distant from the mainland, where they became isolated and underwent a progressive reduction of size as an adaptation to the new environment. The dwarf elephants of Tílos Island appeared before 45,000 years and survived until about 4,000 years BP (according to ¹⁴C dates in Symeonidis *et al.* 1973 and Bachmayer *et al.* 1976), being the last elephant population of Europe. An elephant femur from the cave 'Simonelli' in Crete was dated at 49,000 ± 20% yBP and the only known elephant remainder from Kíythnos (a tusk) at 9,160 ± 240 yBP (Reese *et al.* 1996). No other precise chronological data are available for the Cretan and the other Aegean islands dwarf elephants, which are generally dated to the Late Pleistocene.

CONCLUSIONS

The oldest proboscidean species in the Pliocene of continental Greece is *Mammuthus borsoni*. A more advanced gomphothere species, *Anancus arvernensis*, survives until the end of the Pliocene and it is often reported in association with the first representative of the family Elephantidae *Mammuthus meridionalis*, although the coexistence of these two species has not yet stratigraphically and taphonomically been proved. *Mammuthus meridionalis* may have given rise to the Cretan dwarf *Elephas creticus*. The recorded occurrences of *Mammuthus armeniacus* (*M. trogontherii*) are scanty and they possibly need a revision. The end-species of the *Mammuthus* lineage, *M. primigenius*, is present in some localities. The typical European forest elephant *Elephas antiquus* is a very frequent element of the Late Pleistocene faunas of Greece. It is the parent species of most of the endemic island populations of the Pleistocene and Holocene in the Aegean.

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Some new material of relatively large sized elephant remains that was found recently in Crete (Symeonidis *et al.* 2000, 2001; Poulakakis *et al.* 2002) raised again the discussion about the endemic status of the large elephant of Crete. Symeonidis *et al.* (2000, 2001) consider their finds as having sufficient metrical difference from the continental *Elephas antiquus* to erect a new endemic species, *Elephas chaniensis*. Poulakakis *et al.* (2002), in a revision of the taxonomy of the Cretan elephants, consider this difference of subspecific rank and propose the grouping of the large sized elephants under the name *E. antiquus creutzburgi*.

Table 1 Occurrences of Pliocene mastodonts in Greece.

Locality	Taxon	Citation
Kos (Antimáchia) ⁴⁶	<i>Mastodon arvernensis</i>	Forsyth Major (1887)
Kos (Kardámaena) ⁴⁷	<i>Mastodon arvernensis</i>	Charrier & Giglio (1969) [in Kotsakis <i>et al.</i> (1980)]
Kos (R. Almiri) ⁴⁸	<i>Mastodon arvernensis</i>	Desio (1931)
Thíva (Spaídes) ³²	proboscid	Gidakos (1938)
Spárti (Skoúra) ⁴¹	<i>Anancus (Mastodon) arvernensis</i>	Georgalas (1941)
Pýlos ⁴³	<i>Anancus (Bunolophodon) arvernensis</i>	Mitzopoulos (1967b)
Axiós dam ¹⁰	<i>Anancus arvernensis</i>	Sakellariou-Mane (1972)
Hagía Triáda ⁷	<i>Anancus arvernensis</i>	Koufos (1977)
Kassádra (Sáni) ⁸	<i>Anancus arvernensis</i>	Koufos (1977)
Neápolis–Grevená basin	<i>Mastodon borsoni</i>	Brunn (1956)
Vathýlakkos ⁹	<i>Zygodon borsoni</i>	Mitzopoulos (1967b)
Neápolis ¹²	<i>Zygodon borsoni</i>	Dermitzakis <i>et al.</i> (1982)
Chorigós ¹³	<i>Zygodon borsoni</i>	Dermitzakis <i>et al.</i> (1982)
Klíma ¹⁵	<i>Anancus arvernensis</i>	Steensma (1988)
Sésklo ²⁸	<i>Anancus arvernensis</i>	Symeonidis & Tataris (1983)
Sésklo ²⁸	<i>Anancus arvernensis</i>	Athanassiou (1996)
Rhódos (Apolakkiá) ⁵⁸	<i>Anancus arvernensis</i>	Theodorou <i>et al.</i> (2000)
Miliá ¹¹	<i>Mammut borsoni</i>	Tsoukala (2000)
Lésbos (Vaterá) ⁴⁵	<i>Anancus arvernensis</i>	de Vos <i>et al.</i> (2002)

Table 2. Occurrences of the genus *Mammuthus* (sensu Maglio 1973) in Greece.

Locality	Taxon cited	Citation
Kos (Antimáchia) ⁴⁶	<i>Elephas meridionalis</i>	Forsyth Major (1887)
Kos (Kardámaena) ⁴⁷	<i>Elephas meridionalis</i>	Airaghi (1928)
Kos (Kardámaena) ⁴⁷	<i>Elephas (Archidiskodon) meridionalis</i>	Charrier & Giglio (1969) [in Kotsakis et al. (1980)]
Kos (R. Almiri) ⁴⁸	<i>Elephas meridionalis</i>	Desio (1931)
Euboea (Aedipsós) ²⁹	<i>Elephas (Archidiskodon) meridionalis</i>	Psarianos & Thenius (1954)
Tsotýlion ¹⁴	<i>Archidiskodon meridionalis</i>	Psarianos (1958)
Tsotýlion ¹⁴	<i>Archidiskodon meridionalis</i>	Melentis (1966a)
Polýlakkon ¹⁷	<i>Archidiskodon cf. meridionalis</i>	Psarianos (1958)
Polýlakkon ¹⁷	<i>Archidiskodon meridionalis</i>	Steensma (1988)
Ioánnina ²⁵	<i>E. (Archidiskodon) meridionalis archaicus</i>	Melentis (1960)
Megalópolis basin ⁴⁰	<i>Archidiskodon meridionalis meridionalis</i>	Melentis (1961)
Megalópolis basin ⁴⁰	<i>Archidiskodon meridionalis cromerensis</i>	Melentis (1961)
Megalópolis basin ⁴⁰	<i>Mammonteus primigenius primigenius</i>	Melentis (1961)
Megalópolis basin ⁴⁰	<i>Elephas primigenius</i>	Sondaar & Boekschoten (1967)
Megalópolis basin ⁴⁰	<i>Mammuthus (Archidiskodon) meridionalis</i>	Sickenberg (1976)
Piniós valley ²⁶	<i>Archidiskodon meridionalis cf. cromerensis</i>	Schneider (1968)
Symboli ³	<i>Archidiskodon meridionalis proarchaicus</i>	Melentis (1966b)
Néa Kómi ²²	<i>Archidiskodon meridionalis archaicus</i>	Mitzopoulos (1967a)
Perdíkkas ²¹	<i>Archidiskodon meridionalis archaicus</i>	Mitzopoulos (1967a)
Sotír ²³	<i>Archidiskodon meridionalis</i>	Velitzelos & Schneider (1973)
Sotír ²³	<i>Mammontheus trogontherii</i>	Velitzelos & Schneider (1973)
Piniós mouth ²⁷	<i>Elephas (Archidiskodon) cf. meridionalis</i>	Paraskevaidis (1977)
Piniós mouth ²⁷	<i>Elephas (Mammontheus) cf. primigenius</i>	Paraskevaidis (1977)
Kýthera ⁴⁴	<i>Archidiskodon meridionalis</i>	Psarianos & Kalpakis (1980)
Euboea (Alivéri) ³¹	<i>Archidiskodon meridionalis</i>	Dermitzakis & Theodorou (pers. com. 1990)
Euboea (Limni) ³⁰	<i>Archidiskodon meridionalis</i>	Dermitzakis et al. (1982)
Tenághi Philippon ¹	<i>Mammontheus trogontherii</i>	Psarianos (1958)
Tenághi Philippon ¹	<i>Archidiskodon meridionalis</i>	Dermitzakis et al. (1982)
Aggítis ²	<i>Mammuthus cf. primigenius</i>	Koufos (1981)
Vlachiótis ⁴²	<i>Archidiskodon meridionalis</i>	Symeonidis & Theodorou (1986)
Neápolis–Grevená basin	<i>Elephas meridionalis</i>	Hilber (1894) [in Brunn (1956)]
Líbakos ¹⁶	<i>Archidiskodon meridionalis</i>	Steensma (1988)
Kapetánios ¹⁸	<i>Archidiskodon meridionalis</i>	Steensma (1988)
Q-Profil ¹⁹	<i>Archidiskodon meridionalis</i>	Steensma (1988)
Sésklo ²⁸	<i>Mammuthus meridionalis</i>	Athanassiou (1996)
Lésbos (Vaterá) ⁴⁵	<i>cf. Mammuthus meridionalis</i>	de Vos et al. (2002)

Table 3 Occurrences of *Elephas antiquus* in Greece.

Locality	Taxon cited	Citation
Trichonía ³³	<i>Elephas antiquus</i>	Georgalas (1929)
Canal of Corinth ³⁴	<i>Elephas antiquus</i>	Georgalas (1929)
Patras ³⁵	<i>Elephas antiquus</i>	Georgalas (1929)
Roupáki ³⁹	<i>Elephas antiquus</i>	Athanassiou (2000)
Loussiká ³⁶	<i>Elephas antiquus</i>	personal data
Kýthera ⁴⁴ *	<i>Elephas antiquus</i>	Petrochilos (1938)
Kýthera ⁴⁴	<i>Palaeoloxodon</i> (<i>Elephas</i>) <i>antiquus</i>	Dermitzakis et al. (1982)
Megalópolis basin ⁴⁰ **	<i>Palaeoloxodon antiquus antiquus</i>	Melentis (1961)
Megalópolis basin ⁴⁰	<i>Palaeoloxodon antiquus italicus</i>	Melentis (1961)
Megalópolis basin ⁴⁰	<i>Palaeoloxodon antiquus germanicus</i>	Melentis (1965)
Megalópolis basin ⁴⁰	<i>Elephas antiquus</i>	Sondaar & Boekschoten (1967)
Piniós valley ²⁶	<i>Palaeoloxodon antiquus italicus</i>	Milojčić et al. (1965)
Piniós valley ²⁶	<i>Palaeoloxodon antiquus</i>	Schneider (1968)
Piniós valley ²⁶	<i>Palaeoloxodon antiquus italicus</i>	Schneider (1968)
Piniós mouth ²⁷	<i>Elephas</i> (<i>Palaeoloxodon</i>) <i>antiquus italicus</i>	Paraskevaidis (1977)
Symbolí ³	<i>Palaeoloxodon antiquus</i>	Melentis (1966b)
Tsotýlion ¹⁴	<i>Palaeoloxodon antiquus</i>	Melentis (1966a)
Pétres ²⁴	<i>Palaeoloxodon antiquus antiquus</i>	Velitzelos & Schneider (1973)
Vathýlakkos ⁹	<i>Palaeoloxodon antiquus italicus</i>	de Bonis et al. (1973)
Allatíni ⁴	<i>Palaeoloxodon</i> (<i>Elephas</i>) <i>antiquus</i>	Dermitzakis et al. (1982)
Trilopho ⁵	<i>Palaeoloxodon</i> (<i>Elephas</i>) <i>antiquus</i>	Dermitzakis et al. (1982)
Epanomí ⁶	<i>Palaeoloxodon</i> (<i>Elephas</i>) <i>antiquus</i>	Dermitzakis et al. (1982)
Perdíkkas ²¹	<i>Elephas</i> (<i>Palaeoloxodon</i>) <i>antiquus</i>	Tsoukala & Lister (1998)
Ambélia ²⁰	<i>Elephas</i> (<i>Palaeoloxodon</i>) <i>antiquus</i>	Tsoukala & Lister (1998)

* Manolios (1955) assigns the elephant finds from Kýthera to a dwarf form, but Kuss (1967), Sondaar (1971) and Dermitzakis et al. (1982) consider it continental.

** Melentis (1961) reports the presence of the dwarf species *Palaeoloxodon melitensis* in the fauna of Megalópolis, based on some very small molars. However, Sondaar & Boekschoten (1967) consider these specimens to be deciduous molars of *Elephas antiquus*.

Table 4 Endemic forms of elephants in the Greek Archipelago.

Locality	Taxon cited	Citation
Rhódos (Erimókastró) ⁵⁷	<i>Palaeoloxodon antiquus mnaidriensis</i>	Marinos & Symeonidis (1973) Symeonidis et al. (1974) Symeonidis (1972)
Tílos ⁵⁶	<i>Palaeoloxodon falconeri</i> <i>Palaeoloxodon antiquus melitensis</i>	
Tílos ⁵⁶	<i>Palaeoloxodon antiquus falconeri</i> <i>Palaeoloxodon antiquus mnaidriensis</i>	Symeonidis et al. (1973) Bachmeyer et al. (1976)
Tílos ⁵⁶	<i>Palaeoloxodon antiquus falconeri</i>	Theodorou (1983)
Dílos ⁴⁹	<i>Elephas antiquus</i>	Cayeux (1908)
Dílos ^{49?}	<i>Elephas antiquus</i> race <i>mnaidriensis</i>	Vaufrey (1929)
Astypálaea ⁵⁵	dwarf elephant	personal data
Sérifhos ⁵¹	dwarf elephant	Mitzopoulos (1961)
Sérifhos ⁵¹	<i>Elephas (Palaeoloxodon) cf. melitensis</i>	Papp (1953)[in Kuss (1973)]
Mílos ⁵⁴	dwarf elephant	Papp (1953)[in Kuss (1973)]
Náxos (Tripití) ⁵³	<i>Elephas antiquus melitensis</i>	Mitzopoulos (1961)
Páros ⁵²	<i>Elephas antiquus</i>	Georgalas (1929)
Kýthnos ⁵⁰	dwarf elephant	Dermitzakis & Sondaar (1979)
Crete (Mélekas) ⁶⁰	<i>Elephas creticus</i>	Bate (1907)
Crete (Mélekas) ⁶⁰	<i>Elephas antiquus</i> race <i>melitensis</i>	Vaufrey (1929)
Crete (Hag. Antónios) ⁷³	<i>Elephas priscus</i>	Simonelli (1894, 1897) [in Dermitzakis (1977)]
Crete (Charoúmbes) ⁷⁵	<i>Elephas antiquus</i>	Bate (1907)
Crete (Charoúmbes) ^{75?}	<i>Elephas antiquus</i> race <i>mnaidriensis</i>	Vaufrey (1929)
Crete (Koulourídi) ⁷⁴	<i>Elephas priscus</i>	Simonelli (1894, 1897) [in Dermitzakis (1977)]
Crete (Bali) ⁷²	<i>Elephas priscus</i>	Simonelli (1894, 1897) [in Dermitzakis (1977)]
Crete (Gridá Avláki) ⁶⁸	<i>Elephas priscus</i>	Simonelli (1908)
Crete (Gridá Avláki) ⁶⁸	<i>Loxodonta creutzburgi</i>	Kuss (1965)
Crete (Kaló Choráphi) ⁷¹	<i>Loxodonta creutzburgi</i>	Kuss (1965)
Crete (Kaló Choráphi) ⁷¹	<i>Elephas cf. antiquus</i>	Mol et al. (1996)
Crete (Akr. Kórakas) ⁷⁰	elephant	Kuss (1965)
Crete (Exópolis) ⁶¹	? <i>Elephas</i>	Kuss (1965)
Crete (Akrotíri) ⁵⁹	<i>Hesperoloxodon antiquus falconeri</i>	Kuss (1966)
Crete (Coúmbes) ⁶⁶	dwarf elephant	Kuss (1965, 1966)
Crete (Coúmbes III) ⁶⁶	<i>Elephas</i>	Kuss (1970)
Crete (Coúmbes III) ⁶⁶	<i>Palaeoloxodon cf. antiquus</i>	Mol et al. (1996)
Crete (Coúmbes) ⁶⁶	<i>Palaeoloxodon antiquus</i> n. ssp.	Symeonidis & Theodorou (1983)
Crete (Coúmbes Ib) ⁶⁶	large elephant	de Vos (1984)
Crete (Panagía I) ⁶⁷	<i>Elephas</i>	Kuss (1970)
Crete (Panagía II) ⁶⁷	elephant	Lax (1996)
Crete (Skaléta) ⁶⁹	<i>Loxodonta creutzburgi</i>	Kuss & Misonne (1968)
Crete (Mavromóuri IV) ⁶⁴	elephant	Kuss (1970)
Crete (Mavromóuri) ⁶⁴	<i>Elephas cf. antiquus</i>	Dermitzakis & Sondaar (1979)
Crete (Mavromóuri IV) ⁶⁴	<i>Elephas creutzburgi</i>	de Vos (1984)
Crete (Mavromóuri VI) ⁶⁴	elephant	Lax (1996)
Crete (Simonelli cave) ⁶⁵	<i>Elephas priscus</i> <i>Elephas (Palaeoloxodon) creticus</i>	Accordi (1972)
Crete (Simonelli cave) ⁶⁵	<i>Palaeoloxodon</i> sp.	Melentis (1974)
Crete (Simonelli cave) ⁶⁵	<i>Palaeoloxodon creutzburgi</i>	Malatesta (1980)
Crete (Simonelli II cave) ⁶⁵	<i>Palaeoloxodon cf. antiquus</i>	Mol et al. (1996)
Crete (Zourída) ⁶²	<i>Elephas creutzburgi</i>	de Vos (1984)
Crete (Réthymnon fiss.) ⁶³	<i>Elephas creutzburgi</i>	de Vos (1984)