



A REVIEW OF THE PLEISTOCENE DWARFED ELEPHANTS FROM THE AEGEAN ISLANDS, AND THEIR PALEOGEOGRAPHIC CONTEXT

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Abstract: This paper provides a synthesis of the present knowledge on dwarfed endemic elephants from the Pleistocene of the south Aegean islands. Pleistocene elephants are quite well documented from Crete and Tilos, but with scarce remains on other islands. The systematics and affinities of these elephants are discussed here in the light of recent knowledge on their dispersal history and morphological features. There were apparently three different species on Crete, an older species of Early Pleistocene age and related to *Mammuthus*, and two others of Middle or Late Pleistocene age, namely *Palaeoloxodon creutzburgi* and *P. chaniensis*. The unique m3 from Kassos is similar in size and morphology to *P. creutzburgi*. From the other islands, the most famous and particularly well-documented species is *P. tiliensis* from Tilos. It was a dwarfed form estimated as being 1.8 m at the shoulders. Other important records are from the islands of Rhodos, Naxos, Dilos, Kalymnos and Kythera. These islands yielded palaeoloxodontine elephant fossils presumably of the Middle-Late Pleistocene age. The pattern of their dentition and the character of the limb bones, when known, resemble those of the European straight-tusked elephant *P. antiquus*, and the general opinion is that they were derived from this species. The main question discussed in the present study is the relationship between the elephant occurrences and palaeogeographic evolution of the Aegean domain. It appears that elephants populated Crete at least twice at different times using sweepstake roots. On other islands, elephants probably became isolated because of the subsidence of the Aegean domain and the sea level rise during the Late Pleistocene, which reduced land surfaces and food resources. Hence different degrees of dwarfism existed in these elephants and varied from one island to another.

Key words: Elephantidae, Aegean islands, *Palaeoloxodon*, dwarfism, Pleistocene, palaeogeography

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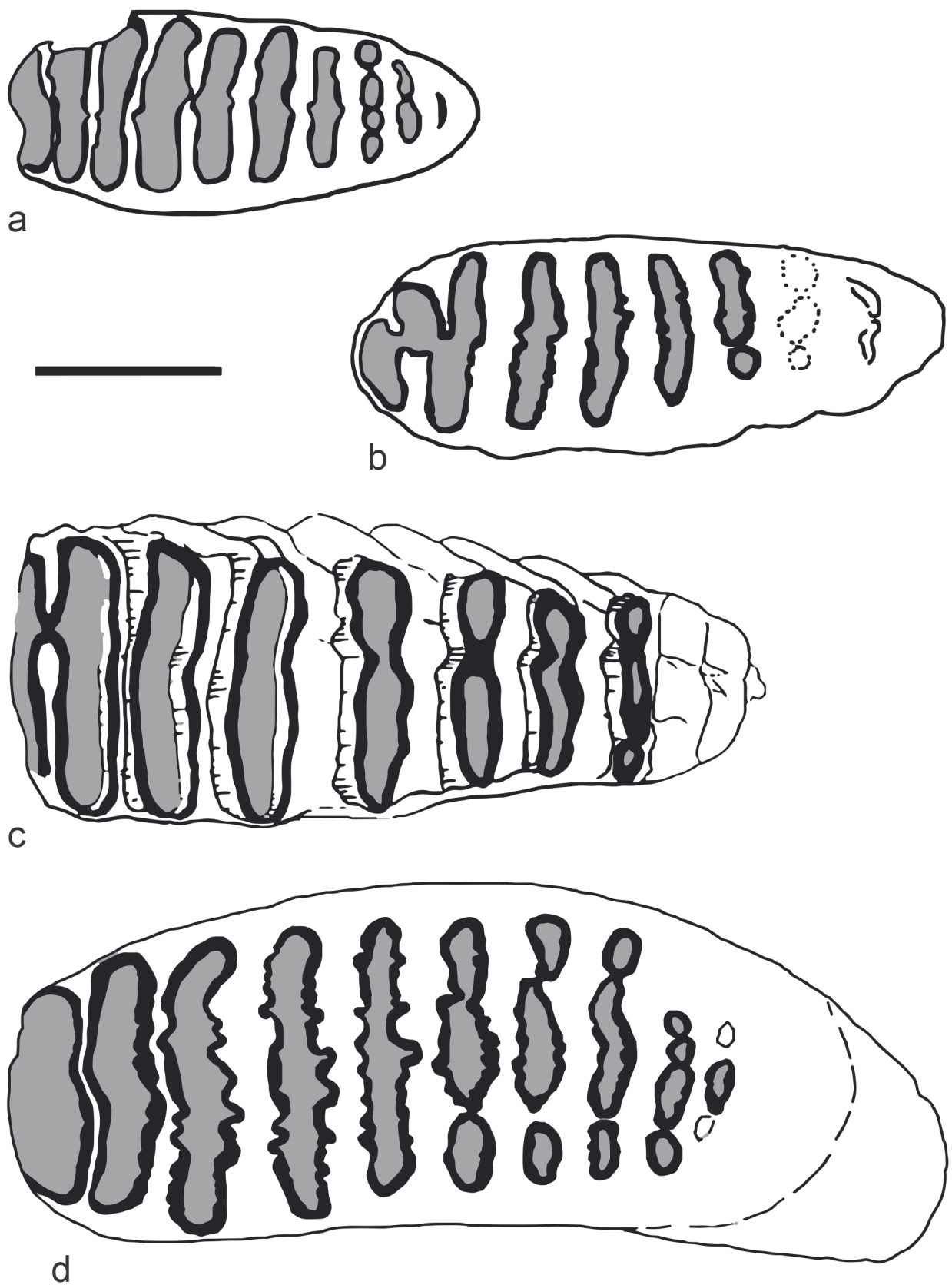
Introduction

Elephants inhabited several Mediterranean islands during the Pleistocene. Their fossils are known since the 17th century in Malta (Abela 1647), since the 18th century in Crete (Pococke 1745), and probably since the antiquity in Sicily (Adams 1870). They are quite abundant in western Mediterranean islands (Sicily, Sardinia, Malta and Favignana) (Palombo 2004), but much less so in eastern Mediterranean islands where the best records are from Cyprus, Crete and Tilos (Doukas and Athanassiou 2003).

The present paper only concerns elephants from the Aegean islands. It does not bring any new record of fossil elephants, but it presents a synthesis of all the available records with comments on the morphology of their dentition, their systematics and palaeobiogeographic significance. This is the first such synthesis to date. Their occurrence on the Aegean islands is discussed in the light of recent knowledge on the palaeogeographic evolution of the Aegean domain.

The occurrence of elephants and other terrestrial vertebrates on islands provides information on the palaeogeographic context of islands, in particular on their proximity and/or possible connections with the mainland. Moreover, these fossil data document the evolution of these insular biota and environments through time, such as food resource richness to shelter terrestrial vertebrate populations. Discoveries and studies over the last century have shown that Pleistocene terrestrial vertebrate faunas on most Mediterranean islands are composed of endemic species that are different from those from the mainland. The composition of island faunas differs from one island to another, even when only a short marine barrier separates these islands (Palombo 2007, Van der Geer et al. 2010, Masseti 2012).

The Aegean realm is limited to the north by Macedonia and Thrace, to the south by the Hellenic arc between the Peloponnese peninsula and Rhodos Island, to the west by the Greek mainland and to the east by Western Anatolia. This marine realm is open to the Mediterranean Sea via



Text-fig. 1. Upper third molars (M3) of some dwarfed elephants from the Aegean islands discussed in the text, in comparison with an M3 of the continental strait tusked elephant *Palaeoloxodon antiquus*. (a) *P. tiliensis* from Tilos (redrawn from Theodorou 1983: pl. II, fig. 8), (b) *P. lomoloini* from Naxos (redrawn from Van der Geer et al. 2014: fig. 5), (c) *P. sp.* from Dilos (redrawn from Vaufrey 1929: fig. 38), (d) *P. antiquus* from Penios Valley, Peloponnesus, Greece (redrawn from Athanassiou 2000: pl. 2). All the teeth are illustrated as left M3, but (a), (b), and (c) reversed. Note that the scale bar is 5 cm for three island species, but 10 cm for *P. antiquus*. The blackened lines represent enamel; gray areas dentine; white areas generally covered by cement.

various straits between the Hellenic arc islands, whereas the Dardanelles strait connects the Aegean Sea with the Sea of Marmara and then the Black Sea. The Aegean archipelago is composed of over 2,000 islands and islets of which only some 200 are inhabited. The Aegean Sea is a part of the Western Anatolian-Aegean continental block that had been expanding since the Miocene. To the south of the Aegean realm, the Cretan Basin reaches a depth of 3,543 m northeast of Crete, but elsewhere most parts of the sea are shallower than 500 m.

The palaeogeography of the Aegean region underwent continuous changes during the Cenozoic, from a marine domain of the Neotethys during the early Cenozoic to an uplifted continental bridge between Asia and Europe in later epochs (Rögl 1998, Popov et al. 2004, 2006, Barrier and Vrielynck 2008). During the Middle Miocene, a continuous emerged land extended in this region from Iran to the Balkans, and separated the Paratethys and Mediterranean seas. According to the above authors, this continental bridge lasted till the end of the Late Miocene, ca. 5.3 Ma, although some intermittent marine connections may have existed across the Aegean between the Paratethys and Mediterranean during the Tortonian (early Late Miocene). During the Messinian, the Aegean realm became a dry land connecting Anatolia and the Balkans (Rögl 1998). Further evolution of the region was controlled by tectonics, climate and sea-level fluctuations throughout the Pliocene and the Quaternary. As we will discuss below, the dispersal of elephants in the Aegean islands during the Pleistocene as well as the diminution of their size and body mass are greatly related to the palaeogeographic evolution of this region.

Pleistocene elephants on the Aegean islands

The English bishop and traveller Richard Pococke (1704–1765) was the first to report the presence of fossil bones in a cave near Chania on the island of Crete, without however any species identification (Pococke 1745: 264). During the second half of the 19th century, several European scholars recorded the presence of Pleistocene mammals in karstic deposits (caves and fissures) on the northern coast of Crete and on the Katharo plain as summarized by Dermitzakis (1973, 1977), Dermitzakis and De Vos (1987) and Poulakakis et al. (2002). Despite these early studies, the English lady Dorothea Bate (1878–1951) was the first to describe the fossil elephants of Crete (Bate 1907) as *Elephas creticus* from a cave at Cape Melekas and as *Elephas antiquus* FALCONER et CAUTLEY, 1847 from karstic deposits in Charoumbes bay in the Sitia district. The Italian traveler Vittorio Simonelli (1894) also reported the occurrence of Pleistocene mammals in cave deposits along the northern coasts of Crete, between the districts of Agios Nikolaos and Mavro Muri, about 3 kilometres west of Rethymnon. He found there “sometimes even the skeletons of mammals” and “magnificent remains of *Elephas priscus* (mandible, complete humerus, atlas, several ribs, etc.)” in the caves of Agios Antonios, Kuluridi and Bali, and he noted their “diminutive stature”. He later described some of these fossils under the name of *E. priscus* GOLDFUSS, 1821, and he illustrated several jaw and bone fragments (Simonelli 1908).

Since then, the occurrence of more or less dwarfed Pleistocene elephants and associated mammals on Aegean islands became a major topic of research and contributed to the debate on the origin of island mammals, their adaptation to island conditions, body size and body mass modifications, and the unbalanced nature of island faunas. The present study aims to provide a new synthesis of the available data on fossil elephants from all Aegean islands. The literature dealing with them is not always easy to access, and the elephant fossils from these islands are presented under various names and often with succinct descriptions and comparisons.

Remains of more or less dwarfed Pleistocene elephants are known from the following Aegean islands: Astypalea, Crete, Dilos, Kalymnos, Kassos, Kos, Kythera, Kythnos, Milos, Naxos, Paros, Rhodos, Serifos and Tilos (Doukas and Athanassiou 2003, Tsoukala et al. 2011, Masseti 2012, Sen et al. 2014, Van der Geer et al. 2014). These islands are all in the southern Aegean, and some of them are part of the Hellenic arc (Crete, Kassos, Kythera and Rhodos) whereas others islands belong to the Cycladic arc. The presence of Pleistocene elephants in the islands of Astypalea, Kythnos, Milos, Paros and Serifos is mentioned in the literature (see in particular Kotsakis 1990, Doukas and Athanassiou 2003, and references therein) but without any description or illustration (see a recent review in Van der Geer et al. 2014). The elephant fossils from the other islands are briefly described herein in alphabetic order.

Crete

Dwarf elephants are best known from Crete, with three species being distinguished: *Mammuthus creticus* (BATE, 1907), *Palaeoloxodon creutzburgi* (KUSS, 1965) and *P. chaniensis* (SYMEONIDIS, THEODOROU et GIANNOPOULOS, 2000) (see below).

Bate (1907) described a small species of elephant, that she named *Elephas creticus*, from the Early-Middle Pleistocene site of Cape Melekas in northwestern Crete. The type material consists of “nine imperfect molars and a few fragments, among which are a portion of an incisor and the dorsal half of a vertebra” (p. 239). Bate (1907: 243) noted that “except with regard to the immense difference in size the characteristics of the molars (from Cape Melekas), more especially in the lowness of the crowns, appear to resemble more closely those of *Elephas meridionalis* than any other of the larger Elephants of the Mediterranean region”. At the same site, P. Y. Sondaar discovered a lower molar together with a lower jaw of the murid *Kritimys kiridus* (BATE, 1942) (Mol et al. 1996, Van der Geer and Lyras 2011). Herridge and Lister (2012) reported additional specimens from this site. All these authors reconsidered the systematic status of this dwarf elephant and confirmed its affinities with *Mammuthus meridionalis* (NESTI, 1825). *M. creticus* has molars with a reduced number of lamellae, low crown, wide occlusal surface, broad cement areas, and simple enamel bands. Poulakakis et al. (2006) studied ancient DNA (aDNA) from a rib bone fragment from Cape Melekas which evidenced the affinities of this small elephant with *Mammuthus* BROOKES, 1828. However, Binladen et al. (2007) and Orlando et al. (2007) considered that the 43 bp sequence used by Poulakakis

et al. (2006) was not the most appropriate for determining the generic status of the Cretan elephant. Lastly, Herridge and Lister (2012) studied the Bate's collection housed at the Natural History Museum in London, plus some new fossils, and confirmed the morphological evidence suggesting some ancestral relationship between *M. creticus* and the Early Pleistocene *M. meridionalis* or the Late Pliocene *M. rumanus* (ȘTEFĂNESCU, 1924). These authors estimated that *M. creticus* may have had an average body mass of about 310 kg and shoulder height of 1.13 m (see also Poulakakis et al. 2002, Lomolino et al. 2013). *M. creticus* was found associated with the murid *Kritimys kiridus*, and they apparently reached Crete during the first migration wave of land mammals during the Early Pleistocene (Mayhew 1977, 1996), i.e. ca. 0.9 My ago (Reese et al. 1996, Sondaar and Van der Geer 2005, Van der Geer et al. 2010, Van der Geer and Lyras 2011). However, Stuart and Lister (2012) claimed that this date is not accurate and needs to be checked using new dating methods. According to Dermitzakis and De Vos (1987: 400), *M. creticus* "became extinct during higher sea level stand of an interglacial, when Crete supposedly became subdivided into different smaller islands, not large enough to support elephant populations". This period could have been the Günz-Mindel interglacial which lasted between ca. 0.75–1.0 Ma.

The second elephant species from Crete is *P. creutzburgi* (KUSS, 1965) (Text-fig. 2). Its type locality Kalo Chorafi in northern Crete yielded three cheek teeth (P2, P3 and m1; Text-fig. 2c) and some tooth and bone fragments (Kuss 1965). Poulakakis et al. (2002) enumerated 22 localities in Crete, all supposedly of latest Middle or Late Pleistocene age, that yielded remains of this palaeoloxodontine elephant. The material from most localities is fragmentary and not adequately studied. The best fossils referred to this species from Crete are, in addition to the type material from Kalo Chorafi cave, a damaged mandible of an old individual, an atlas and a femur from Krida Avlaki (Simonelli 1908, Palombo and Petronio 1989), a damaged mandible with m2 and m3 from Kharoumes Bay (Bate 1907), an m3 from Simonelli Cave (Text-fig. 2e; Kotsakis 1980) and an m2 from Katharo plain (Poulakakis et al. 2002), all referred to *P. creutzburgi* by the last authors. This is a large sized form having palaeoloxodontine characters in its dentition: straight or gently curved tusks, narrow lamellae separated by cement areas that are narrower than the plates, gently folded enamel, anterior and/or posterior enamel bulges on the plates. Using the humerus length (790 mm) and the femur length (950 mm), Lomolino et al. (2013) estimated the body mass of this species as about 3,000 kg, i.e., half the weight of the European straight-tusked elephant *P. antiquus* (FALCONER et CAUTLEY, 1847), from which it probably derived.

Belluomini and Delitala (1983) dated an elephant femur from the Simonelli Cave in Crete to $49,000 \pm 20\%$ BP using the Amino Acid Racemization method. This femur was determined as belonging to *P. creutzburgi* (Palombo and Petronio 1989; see also Reese et al. 1996). No other chronological data are available for the localities that yielded *P. creutzburgi*, which are tentatively correlated to the Late Pleistocene.

Several authors mentioned the presence of a third species of elephant in Crete which would have been larger than

P. creutzburgi from the Kalo Chorafi Cave and about 20% smaller than the mainland species *P. antiquus*. This form was initially referred to *P. antiquus* or *P. cf. antiquus* (Kuss 1973, Dermitzakis and Sondaar 1979, Symeonidis and Theodorou 1982, Dermitzakis and De Vos 1987, Mol et al. 1996). Symeonidis et al. (2000) recorded 41 well-preserved limb bones from a submerged cave close to Vamos in northwestern Crete, and they erected a new species *Elephas chaniensis* based on this material (see also Symeonidis et al. 2001, Poulakakis et al. 2002). They also referred to this species a well-preserved complete lower jaw bearing the m3s from Coumbes Cave near Rethymnon (Text-fig. 2b) that Symeonidis and Theodorou (1982) initially identified as "a new endemic Pleistocene subspecies of *P. antiquus*". Symeonidis et al. (2000: 106) diagnosed this species as "Endemic elephant of relatively large dimensions about 20% smaller than continental *P. antiquus*".

The cheek teeth are the most diagnostic elements for species distinction. As it can be seen in Tables 1 and 2, the number of teeth referred to *P. creutzburgi* and *E. chaniensis* is still too limited to discriminate between the two different palaeoloxodontine species in Crete. In all these specimens, the plates are narrow, the interplate cement areas are narrower than the plates, the central part of the plates is a little larger (mesio-distal) than the lateral parts, the plates bear anterior and/or posterior enamel bulges in their central part, the enamel is gently folded but much less so than in the teeth of *P. antiquus* in a similar stage of wear, the slightly abraded plates are composed of one wide central loop and two or more lateral ellipsoid or rounded rings, and the lamellar frequency is quite similar. Consequently, Poulakakis et al. (2002) suggested the synonymy of the large elephant from Vamos Cave and Coumbes Cave with *P. creutzburgi*. Fieldwork carried out during the last two decades did not provide any additional fossil material, except for "a part of deciduous molar of a dwarf elephantid" from the Koutalas Cave (Chania) that Iliopoulos et al. (2010: 5) referred to *Elephas* sp. The systematic status of this large elephant from Crete was not discussed in later studies dealing with the Crete elephants, such as by Van der Geer and Lyras (2011), Herridge and Lister (2012), Lomolino et al. (2013) and Van der Geer et al. (2014, 2016). Consequently, we suggest to maintain the species distinction of "*E. chaniensis*" pending a systematic review of the Late Pleistocene elephants of Crete.

In summary, at least two, probably three species of elephants inhabited Crete during the Pleistocene. Taking into consideration their systematic affinities and their degree of dwarfism, it appears that elephants reached Crete in three successive waves of migration, some together with cervids, hippos and murids. The paleobiogeographic context of these dispersal events will be discussed in the next chapter.

Dilos

The tiny island of Dilos (3.5 km²) is part of the Cyclades and it is situated some 20 miles northwest of the large island of Naxos, and between the islands of Rhinia and Mykonos. The Ecole française d'Athènes undertook archaeological excavations in 1873 to bring to light the mythical city of Dilos in this sacred island of Apollo. The investigations

Table 1. Comparative measurements and ratios of the third lower molars (m3, except an m1 from Kalo Chorafi and an m2 from Katharo) of Elephantidae from several localities in Greece, Bulgaria and Italy. N = number of specimen, N of plates = number of preserved plates, x = talon, p = plate, Hyps. index = hypsodonty index, LF = lamellar frequency. Measurements in mm.

Species	Locality	N	N of plates	Length	Width	Height	Hyps. index	LF	Enamel thickness	References
<i>Palaeoloxodon creutzburgi</i> (m1)	Kalo Chorafi Cave, Crete, Greece	1	>7p	>121.3	75.2	>79.4	–	5.2	<4.0	Kuss 1965
<i>P. creutzburgi</i> (m2)	Katharo Basin, Crete, Greece	1	>8p	>140	67	104	1.55	8.0	1.8–2.88	Poulakakis et al. 2002
<i>P. aff. creutzburgi</i>	Kassos, Greece	1	x>9p	>165	54	72.9	1.35	6.5	1.8–2.2	Sen et al. 2014
<i>P. creutzburgi</i>	Kharoumes, Crete, Greece	1	x>8p	?	47	95.3	–	9.0	1.0–2.5	Bate 1907, Kuss 1966
<i>P. aff. creutzburgi</i>	Coumbes Cave, Crete, Greece	2	x>9p	165–181	63	–	–	5.5–6.0	3.0–3.5	Symenoidis and Theodorou 1982
<i>P. creutzburgi</i>	Grida Avlaci, Crete, Greece	1	–	>125	60	–	–	>4.5	2.5	Simonelli 1908
<i>P. creutzburgi</i>	Simonelli Cave, Crete, Greece	1	x9p	216	64	133	2.1	4.75	2.5	Kotsakis 1980
<i>P. creutzburgi</i>	Simonelli Cave II, Crete, Greece	1	–	>125	56	–	–	?	1.5–2.5	Mol et al. 1996
<i>Palaeoloxodon</i> sp.	Kythera Island, Greece	1	x12p	>180	75	–	–	6.6–7	3.0	Kuss 1967
<i>P. tiliensis</i>	Tilos Island, Greece	3	x11p	>110–160	48–53	–	–	6.5–7.7	2.5–3.0	Theodorou 1983
<i>Mammuthus creticus</i>	Cape Malekas, Crete	2	x12p	145	33–41	39–50	1.2	10.0	–	Bate 1907
<i>P. mnaidriensis</i>	Puntali Cave, Sicily, Italy	2	x10p	170–174	60	–	–	6.0–7.0	–	Ferretti 2008
<i>P. antiquus</i>	Grevena, Greece	1	x14p	242	83	–	–	6.0	2.3–3.3	Tsoukala and Lister 1998
<i>P. antiquus</i>	Ryahovo, Bulgaria	1	x17p	370	86	172	2.0	5.5	2.5	Markov 2007

continued up to 1968 with, however, two major breaks during the first and second world wars. In this context, the French geologist Lucien Cayeux (1864–1944) was inspired to study the geology of the island. He published his results in 1911 in a volume entitled “Description physique de l’île de Délos”. In a survey excavation to study the substrate of some monuments to the east of the Apollo temple, an elephant molar was found (Text-fig. 1c) near the bottom of a pit, in the alluvial deposits of the Inopos River, four meters above sea level (Cayeux 1908). Cayeux (1908) identified this molar as an M3 of *Elephas antiquus* FALCONER et CAUTLEY, 1847, following the advice of Professor Marcellin Boule (1861–1942) from the Natural History Museum of Paris. Later on, Vaufrey (1929: fig. 38) illustrated this molar and debated whether this belonged to *Elephas mnaidriensis* ADAMS, 1874, a species previously defined on the basis of fossils from Malta, or to the small species *E. antiquus*. This record was often mentioned in the literature (e.g. Dermitzakis and Sondaar 1979, Symeonidis and Theodorou 1982, Kotsakis 1990, Caloi et al. 1996, Poulakakis et al. 2002, Doukas and Athanassiou 2003, Tsoukala et al. 2011), but most of these authors noted that this molar belonged to a somewhat dwarfed elephant but without any precise systematic assignment. A cast of this molar is preserved in the collections of the Muséum national d’Histoire naturelle in Paris. The label on this cast mentions that the original specimen is housed in the Archaeological Museum of Dilos. I went to this Museum on May 6, 2014 and asked to see this molar. The curator from the Dilos Museum told to me that this specimen does not exist in their collections. A. van

der Geer from Leiden Museum wrote to me that she had also wanted to see this molar some three years ago and had received the same answer (e-mail on May 29, 2014).

Sen et al. (2014) redescribed and illustrated the Dilos molar. It is a left M3, it tapers backwards and has a talon typical for a last upper molar. Its occlusal surface is almost flat. It consists of nine plates plus the talon. The degree of attrition, quite advanced, suggests that some anterior plates may have been lost. The wear is progressive backwards, and the two last plates are not yet abraded. The lamellar frequency is 6.1. The crown height rapidly increases from the first preserved plate to the 7th plate, and then slightly decreases backwards. In occlusal view, the plates form narrow lamellae, almost perpendicular to the longitudinal axis. The first six preserved plates are composed of two unequal enamel loops, which are more or less confluent depending on the degree of wear; the lingual loop is larger than the labial one. The remaining three plates each display a big central ring and two small lateral rings. The enamel is delicately folded and the enamel wear surfaces are inclined mesially. The talon is a small cusp at mid depth of the crown. The roots are not preserved (Text-fig. 1c).

The Dilos M3 is a little larger and more hypsodont than the M3s preserved on a palate from Naxos (see below). However, the pattern of the occlusal surface is very similar in having an equal number of plates, narrow shape, asymmetric enamel loops, gently folded enamel, and three loops on the unworn plates. Based on the tooth pattern similarities, it can be hypothesized that the Dilos and Naxos specimens may belong to the same species, *Palaeoloxodon lomolinoi*

VAN DER GEER, LYRAS, VAN DEN HOEK OSTENDE, DE VOS et DRINIA, 2014, hence different from *P. tiliensis* THEODOROU, SYMEONIDIS et STATHOPOULOU, 2007 and *P. creutzburgi*. To assume such a hypothesis, more material from Cycladic islands is needed to appreciate the size and morphological variability in this species.

Kalymnos

This Island (110 km²) is situated about 15 miles west of the Bodrum peninsula, off the western coasts of Turkey. Masseti (2009, 2012) illustrated a lower jaw fragment that bears an incomplete molar identified as an m3. The photography was communicated to the author by “Toula Marketou, 22nd Ephorate of Prehistoric and Classical Antiquities, Rhodes” (Masseti 2012: 16). According to the picture published by this author, the anterior and posterior parts of the molar are broken, and the total number of lamellae cannot be estimated. The characters of the occlusal pattern fit with that of palaeoloxodontine elephants: the eight preserved lamellae are narrow, separated by narrower interplate cement bands, the lamellae have a central part slightly larger than lateral and medial parts, and the enamel is delicately wrinkled. The size of this specimen cannot be accurately evaluated based on the scale given in the picture since the value of the scale is not indicated. Van der Geer et al. (2014: 139) suggest that “a number of elephant fossils from southern Aegean islands belong to mainland *P. antiquus*. These islands were connected to the mainland and include Kalymnos (... specimen figured in Masseti, 2009, fig. 6), Kythera and Ikaria”. Although Masseti (2009, 2012) and Van der Geer et al. (2014) identify the Kalymnos elephant as *P. antiquus*, a detailed comparison of its morphological characters and size with other palaeoloxodontine elephants is needed to confirm this assignment.

Kuss and Storch (1978) reported an Early Pleistocene small mammalian fauna from Kalymnos, which is relatively diversified and does not bear any endemic character. This fauna shows great taxonomic affinities with those of the continent and it is correlated to the early Biharian, ca. 1.0–1.5 Ma.

Kassos

The island of Kassos (66 km²) is part of the Hellenic arc, and it is situated between the large islands of Crete and Karpathos. Kassos is separated from Crete by a large deep channel, but is closer to the neighboring island of Karpathos and separated from it by a narrow shallow channel. Kuss (1969) reported remains of Pleistocene cervids from brecciated deposits on the northern coasts of the island. He identified them as *Cervus cretensis* (SIMONELLI, 1907), i.e. similar to those from Crete.

X. Crété, an inhabitant of this island, discovered an isolated molar embedded in a breccia matrix at the foot of a fault scarp in the northwestern part of the island. It is a third lower molar (preserved length × width = 165 × 54 mm) similar in size and dental morphology to *P. creutzburgi* from Crete (Sen et al. 2014). This molar bears nine plates plus the talon. In occlusal view, it is moderately curved laterally, and tapers backwards. The lamellar frequency is 6.5. From the occlusal view, the plates form narrow and slightly oblique

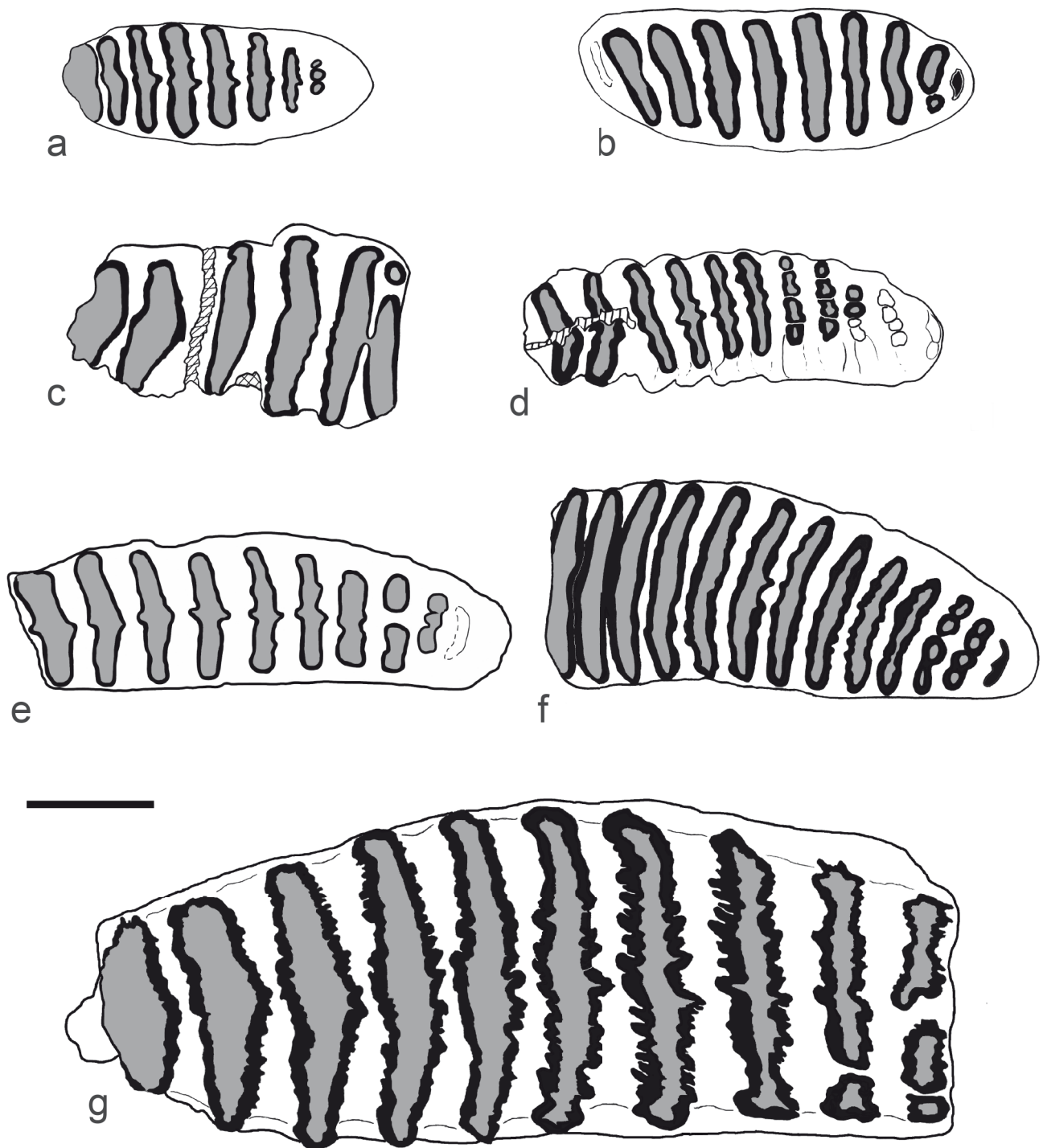
ridges with almost regular antero-posterior width. The enamel bands are delicately wrinkled. The enamel thickness varies between 1.8–2.2 mm. The cement areas between the plates are narrower than or the same width as the plates (Text-fig. 2d).

As shown in Table 1, the size and dental parameters of this molar are in the range of variability of the Cretan species *P. creutzburgi*. However, it cannot be unquestionably assimilated to this species due to limited knowledge of the morphological and size variability of this species. In addition, the island of Kassos is separated from Crete by a 30 miles large channel in which the depth exceeds 1,000 m. We hypothesize that Crete and Kassos were never connected during the Pleistocene, and consequently the Kassos elephant may well represent a different species.

Kythera

This Island (280 km²) is situated less than one mile south of the Peloponnese peninsula, and is on the Hellenic arc. The Italian naturalist Lazzaro Spallanzani (1729–1799) in 1785 discovered a great quantity of bones on the “montagna delle ossa” in the southern part of the island during a forced stop en route to Constantinople by ship. In the paper he published, Spallanzani (1786) stated that the brecciated and clayey sediments in large areas in southern part of the island are full of petrified bones, and that he had recognized human and animal remains. Unfortunately, Spallanzani did not give further details of these fossils. When he visited Pavia, Georges Cuvier (1769–1832) went to examine the fossils that Spallanzani had collected in Kythera. In the first volume of his “Recherches sur les ossements fossiles”, Cuvier (1812: 83) wrote: “J’ai examiné à Pavie les groupes d’ossements rapportés par Spallanzani, de l’île de Cérigo; et, malgré l’assertion de cet observateur célèbre, j’affirme également qu’il n’y en a aucun dont on puisse soutenir qu’il est humain [I examined at Pavia the groups of bones found by Spallanzani in the island of Cérigo; and, despite the assertion of this famous observer, I affirm that there is none of which that can be argued as human]”. In other words, Cuvier’s aim was to demonstrate that fossil quadrupeds and men had not lived together.

Despite these early discoveries of terrestrial vertebrate fossils in Kythera, nothing was done during one and half centuries to discover what kind of mammals inhabited this island. Petrochilos (1938: 59) was the first author to report the discovery of elephant fossils “à l’Est de la petite montagne Saint-Hélias, 20 m au-dessus de la mer et dans une petite ravine”. He referred his findings to *P. antiquus*, without any description or illustration. He concluded that this island was isolated from the continent after the Riss glacial period on the basis of the occurrence of elephants, deer and antelopes, contrary to previous geological studies that suggested the isolation of Kythera occurred during the Neogene. Kuss (1967) studied Pleistocene mammals from Kythera and identified *P. antiquus* and *Cervus dama* LINNAEUS, 1758. For the first species, he described a complete right m3 of an elephant that was quite large. This m3 bears 12 lamellae plus the talon. A few anterior plates might have been lost. Its length is 180 mm and its width is 75 mm (Tab. 1, Text-fig. 2f). Such values indicate



Text-fig. 2. Lower molars of some dwarf elephants from the Aegean islands discussed in the text, in comparison with an m3 of the continental strait tusked elephant *P. antiquus*. (a) *P. tiliensis* from Tilos (redrawn from Theodorou 1983: pl. III, fig. 5), (b) *P. chaniensis* from Coumbes cave in Crete (redrawn from Symeonidis and Theodorou 1982: pl. V), (c) holotype m1 of *P. creutzburgi* from Kalo Chorafi Cave in Crete (redrawn from Kuss 1965: pl. III), (d) *P. cf. creutzburgi* from Kassos (redrawn from Sen et al. 2014: fig. 3), (e) *P. creutzburgi* from Simonelli Cave in Crete (redrawn from Kotsakis 1980: pl. I, fig. 4), (f) *Palaeoloxodon* sp. from Kythera (redrawn from Kuss 1967: pl. II), (g) *P. antiquus* from Penios Valley, Peloponnesus, Greece (redrawn from Athanassiou 2001: fig. 2b). Note that all molars are presented as from the left side, but (f) and (g) reversed. Scale bar 5 cm for all molars. The blackened lines represent enamel; gray areas dentine; white areas generally covered by cement.

that it is about 20% smaller than the average values for *P. antiquus* (Tab. 1). The occlusal surface tapers backwards and is curved labially. The plates are curved forward, unlike in *P. antiquus*, which has rather straight plates. Interplate cement areas are narrow, the enamel is gently folded, and some plates bear, in their middle part, tiny anterior and posterior enamel bulges. The general pattern of this molar fits that of *P. antiquus*, except the arcuate shape of the plates and its smaller dimensions. Despite these differences, Sondaar (1971) considered that the Kythera elephant should belong to *P. antiquus*. More material and a new detailed comparative study of this m3 are needed to determine the degree of dwarfism and the appropriate identification of the elephant from Kythera.

Kythnos

Kythnos (99 km²) is a small island in the western Cyclades at some 60 miles southeast of Piraeus. Honea (1975) discovered an apparent preceramic camp and cemetery with human burials on the Maroula site to the northeast of Kythnos. Northwest of the island, this author also recovered the distal end of a small elephant tusk exposed in the wall of an ancient artificial hollow. C14 analysis of the tusk fragment provided an age of 9,160 ± 240 yrs BP (Honea 1975). However, this author noted (p. 279) that “the specimen was air-exposed and it has been subjected to continual wetting, and thus contamination... The true age of the tusk is probably much in excess of the above apparent date”. This author did not comment on the systematic status of this tusk fragment, and he did not indicate where it is stored.

Naxos

Naxos is one of the largest islands of the Aegean archipelago, and the largest island of the Cycladic arc. Mitzopoulos (1961) described the palate of a small sized elephant, found in the Trypiti ravine near the eastern coast of the island. The palate bears both M3s which are well preserved. He tentatively attributed this specimen to *Elephas melitensis* FALCONER, 1968, a species initially known from the Middle Pleistocene of Malta.

The maximum width of the maxillae is 149 mm. The palate enlarges backward; its minimum width between the fourth lamellae of the M3s is 37.3 mm and its maximum width between the posterior edges of the molars is 72.1 mm. The choanae are V shaped. The teeth (length = 125 and 127 mm) are smaller than the Dilos M3, although their proportions and lamellar frequency are almost identical (Tab. 2). The pattern of the occlusal surface is also very similar in having an equal number of plates, narrow lamellae that bear two unequal enamel loops (labial loop smaller than lingual loop on worn plates), gently folded enamel, and three loops on the unworn plates (Text-fig. 1b). In a recent note, Van der Geer et al. (2014) redescribed this specimen and recognized it as a new species, *Palaeoloxodon lomolinoi*. These authors estimated its body mass as about ten percent that of *P. antiquus*, i.e. between 400–500 kg. Despite some size differences, the similarities in dental morphology suggest a close relationship between the Naxos and Dilos elephants.

Rhodos

Symeonidis et al. (1974) described postcranial bones of a dwarf elephant from a cave in the eastern slope of Eremocastro hill near Ladiko in NE Rhodos. The material consists of numerous limb bones, vertebrae and a tusk fragment. Despite the lack of cheek teeth or skull fragments, the morphology of the limb bones resembles that of *P. antiquus* although considerably smaller. For instance the length of metacarpal II (Mc II) from Ladiko is 115.5 mm contra 203 mm on a Mc II of *P. antiquus* from Soulac (France; Beauval et al. 1998) and 227 mm on a Mc II on a skeleton from Upnor (Great Britain; Andrews and Forster-Cooper 1928). The same size difference is also noted for a distal part of a femur from Ladiko (distal transverse diameter 113 mm) compared to six femora from Italy (average distal transverse diameter 250 mm; Marra 2009). Despite this size difference, the Mc II from Ladiko has the typical characters of *Palaeoloxodon* being shaped, in lateral view, like an hourglass, while in *Mammuthus* the shaft of Mc II becomes thinner dorsally (Ziegler 2001). Symeonidis et al. (1974) suggested that the elephant remains from Ladiko might belong to a local *Palaeoloxodon* species of Late Pleistocene age. Van der Geer et al. (2014, 2016) estimated the body mass of the Rhodos elephant to be about 1,500 kg, on the basis of the femur dimensions.

Tilos

This small island (about 60 km²) belongs to the Dodecanese group of islands, between the large islands of Rhodos and Kos. It is situated a few miles away from southwestern Anatolian shores. Symeonidis (1972) was the first to report the presence of dwarfed elephants in the Charkadio Cave. He provisionally referred the fossils to *Elephas antiquus mnaidriensis* ADAMS, 1874 and *E. antiquus falconeri* BUSK, 1867, based on the fact that the sample includes small sized specimens (*E. antiquus falconeri*), but also large sized specimens (*E. antiquus mnaidriensis*). Bachmayer and Symeonidis (1975) and Bachmayer et al. (1976) maintained the opinion that there are two species of different size. In his PhD thesis, Theodorou (1983) provided a detailed description of the elephant remains from Charkadio Cave. He concluded that there was one species, with a great size variation and sexual dimorphism. Finally, Theodorou et al. (2007) erected a new species for the Tilos elephant, *Palaeoloxodon tiliensis* THEODOROU, SYMEONIDIS ET STATHOPOULOU, 2007.

Symeonidis and his collaborators have excavated this cave over several years and collected abundant cranial, dental and postcranial remains of dwarfed elephants. They were represented by several individuals of different age classes (more than 15,000 specimens according to Theodorou et al. 2007, or about 13,300 identified specimens plus fragments according to Mitsopoulou et al. 2015). Excavations in the Charkadio Cave are still actively pursued by a team from the University of Athens. More recently Mitsopoulou et al. (2015) used imaging technologies for modeling and 3D printing of elephant bones that they applied for taphonomical purposes.

The first C14 dating of bones yielded ages of 4,390 ± 600 years and 7,090 ± 680 years, suggesting that these elephants

Table 2. Comparative measurements and ratios of the upper molars of some dwarfed elephants from Aegean islands in comparison with the mainland species *Palaeoloxodon antiquus* from Italy, Greece and Bulgaria. N = number of specimen, N of plates = number of preserved plates, x = talon, p = plate, Hyps. index = hypsodonty index, LF = lamellar frequency. Values for *P. antiquus* from Italy represents average value of the sample. Measurements in mm.

Species (tooth)	Locality	N	N of plates	Length	Width	Height	Hyps. index	LF	Enamel thickness	References
<i>P. creutzburgi</i> (P2)	Kalo Chorafai Cave, Crete, Greece	1	>5p	73.8	63.3	>45	–	7.1	3.8	Kuss 1965
<i>P. creutzburgi</i> (P3)	Kalo Chorafai Cave, Crete, Greece	1	>5p	94.6	64.8	>66	–	5.9	3.0	Kuss 1965
<i>P. lomolinoi</i> (M3)	Naxos, Greece	2	>9p	122–128	43–48	101–104	2.17	7.1	2.0–3.0	Van der Geer et al. 2014
<i>Palaeoloxodon</i> sp. (M3)	Dilos, Greece	1	>9p	156	59	110	1.86	6.1	1.5–3.0	Sen et al. 2014
<i>P. tiliensis</i> (M3)	Tilos, Greece	3	>7–11p	>95–124	47–53	86	1.72	7.7–9.0	2.0–2.9	Theodorou 1983
<i>P. antiquus</i> (M3)	Italy, various locs	6–35	x15p	280	90	170	1.92	5.0	2.6	Palombo and Ferretti 2005
<i>P. antiquus</i> (M3)	Penios Valley, Greece	2	x19p	340–355	93–95	220–250	>2.37–2.63	5.4	1.7–3.9	Athanassiou 2000
<i>P. antiquus</i> (M3)	Ryahovo, Bulgaria	1	x14p	>230	71	>183	>2.58	6.5	2.0	Markov 2007

lived on this island up to the Holocene, well beyond their last occurrence on other Mediterranean islands, and in Europe (Symeonidis et al. 1973). Additional radiochronologic datings and correlation of the cave stratigraphy with the Quaternary glacial and interglacial periods provided a new time range for the Tilos elephant. According to Poulakakis et al. (2002, 2006) and Theodorou et al. (2007), *Palaeoloxodon tiliensis* inhabited Tilos Island between ca. 45,000 to 4,000 BP.

This species is smaller than *P. creutzburgi* from Crete, and also smaller than other palaeoloxodontine elephants from the Aegean islands. Its size is estimated as being about 50% of the medium values of the continental species *P. antiquus*, with a shoulder height of about 180–190 cm (Theodorou et al. 2007). Lomolino et al. (2013) estimated the body mass of this elephant as between 630–831 kg by using the length of humerus, femur and tibia (see also Van der Geer et al. 2016). This elephant had slender limb bones allowing movement on rough terrain. The combined proximal surface of all metacarpals and all metatarsals is less stretched than in other *Palaeoloxodon* species. However, the characters of its cheek teeth such as lamellar frequency, enamel thickness, slightly folded enamel, lamellae with parallel enamel bands, oblique position of the lamellae on the posterior half of m3, presence of a small central loop on the lamellae and crown height of upper molars indicate that this species belongs to the *Palaeoloxodon* group (Text-figs 1a, 2a, Tabs 1, 2).

Hans Brinkerling from the Natural History Museum of Rotterdam sculptured a life-like reconstruction of this elephant which is on exhibit at the Palaeontological Museum of the University of Athens (Mol 2002).

The presence of a dwarfed elephant on a wall painting in the 18th Dynasty tomb of Rekh-mi-Ré at Thebes (Egypt), i.e., between 1,543–1,292 BC, led Masetti (2001: 405) to suggest that dwarf elephants from Aegean islands, such as those from Tilos Island, “could have been exported to a mainland area where it could have represented a precious and rare curiosity to be exchanged as costly gift between Aegean, Near Eastern and Egyptian rulers”. This implies

that dwarf elephants would have lived in the Aegean islands during these historical periods. Indeed, elephants lived on Tilos Island during the historical times (ca. 3,500–4,000 BP according to Theodorou et al. 2007: 25), whereas the age of fossils is either older or unknown on other islands.

Origin and affinities of dwarf elephants from the Aegean islands

As we noted above, there are two groups of dwarfed elephants that inhabited Aegean islands. One is *M. creticus*, which is recorded to date only at the locality of Cape Melekas near Rethymnon in northern Crete. The elephants of the second group are affiliated to the Eurasian straight-tusked elephant *P. antiquus*, and they are recorded from many Aegean islands, as enumerated above.

M. creticus is a very small sized elephant and it has peculiar molar characters (reduced number of lamellae, low crown, wide occlusal surface, broad cement areas, simple enamel bands). As Bate (1907) noted when she defined this species, its dentition shows great affinity with *M. meridionalis* which inhabited southern Europe and southwestern Asia between ca. 2.5–1.5 My ago. *M. meridionalis* is also a well-known taxon from Greece and Turkey (Doukas and Athanassiou 2003, Albayrak and Lister 2011).

The age of *M. creticus* is debatable. It was found associated with the murid *K. kiridus*. Based on the affinities of this murid and the succession of murid species in Cretan sites, Mayhew (1977, 1996) suggested an Early Pleistocene age for this pigmy elephant. It apparently reached Crete during the first migration wave of land mammals in the Early Pleistocene or ca. 0.9 Ma ago (Reese et al. 1996, Sondaar and Van der Geer 2005, Van der Geer et al. 2010). However, all these dates need to be further substantiated or checked with newer dating methods (Stuart and Lister 2012).

Lastly, studying Bate’s collection at the Natural History Museum in London plus some new findings, Herridge and Lister (2012) confirmed the morphological evidence of

its ancestral relationships with the Early Pleistocene *M. meridionalis* or even with the Late Pliocene *M. rumanus*.

With the exception of *M. creticus* from Crete and *M. lamarmorae* (MAJOR, 1883) from Sardinia, all other elephants from Mediterranean islands, from Cyprus to Malta, belong to the palaeoloxodontine group. It is generally accepted that all the palaeoloxodontine elephants from the Mediterranean islands were derived from *P. antiquus*. This species inhabited Europe, from Spain to Ural, including British Islands and Anatolia during the Middle and Late Pleistocene, ca. between 750 and 40 ky ago (Stuart and Lister 2012). It is well represented on the continent surrounding the Aegean Sea. It has also been recorded from at least 23 Pleistocene localities in Greece (Tsoukala and Lister 1998, Athanassiou 2001, Doukas and Athanassiou 2003, Tsoukala et al. 2011) as well as in the Balkans (Markov 2007) and Asia Minor (Becker-Platen and Sickenberg 1968, Albayrak and Lister 2011). The major question is when and how this species reached these islands.

Concerning the Aegean region, all available radiochronologic and biochronologic data indicate that palaeoloxodontine elephants were present in the southern Aegean islands by the Middle-Late Pleistocene transition. However, the available radiochronologic ages from Crete (Belluomini and Delitala 1983) and Tilos (Symeonidis et al. 1973, Poulakakis et al. 2002, 2006, Theodorou et al. 2007) date the occurrence of palaeoloxodontine elephants to the Late Pleistocene, which probably does not represent the initial dispersal of palaeoloxodontine elephants in the southern Aegean islands. In addition, palaeontological correlations are difficult to use due to the endemic nature of terrestrial mammals of the islands. New radiochronological dating and well-documented biostratigraphic correlations are needed to evidence their appearance in these islands.

Palaeogeographic context of elephants from the Aegean islands

During the Pleistocene, elephants reached the Aegean islands in at least two waves of dispersal: during the Early Pleistocene, ca. 900 ky ago or earlier, and during Middle or Late Pleistocene, ca. 200 ky ago or later. *M. creticus* from Crete attests to the first dispersal event whereas the second wave is documented by elephants remains from several islands in the southern Aegean. The latter belong to the *Palaeoloxodon* group, and the elephants of this group are diversified in size and in molar morphology. Consequently these fossils are referred to several species differentiated under an insular context. As noted above, the numerical ages of these findings were obtained using the Amino Acid Racemization (AAR) method for some specimens from Crete (Belluomini and Delitala 1983, Reese et al. 1996), with the C14 dating of a tusk fragment from Kythnos (Honea 1975) and bones from Tilos (Theodorou et al. 2007). Stuart and Lister (2012) questioned the AAR ages, especially those obtained for the elephants from Crete, but they did not provide any alternative ages for these fossils.

Whatever the uncertainties about the time of dispersal of elephants within the Aegean islands, it appears that (1) *M. creticus* was derived from the Early Pleistocene *M.*

meridionalis and it probably reached Crete during the Early Pleistocene, (2) the elephants of the *Palaeoloxodon* group dispersed in the southern Aegean islands much later, and (3) Pleistocene mammalian faunas in all the southern Aegean islands are ecologically unbalanced, indicating that they evolved in insular conditions.

The Aegean area is specific in being situated in a tectonically active belt, subject to changing paleogeography during the Neogene and Quaternary. The main tectonic features that shaped southern Aegean geography during late Neogene and Quaternary can be summarized as follows:

- Subduction of the Arabo-African plate under Eurasia, and in the Aegean domain under the plate “Aïgais”;

- Extension of the Aegean domain to the south-southwest due to the rollback of the Hellenic arc at a speed of about 33 mm/year in Crete (McClusky et al. 2000, Philippon et al. 2014);

- Thickening of the Earth’s crust, resulting from the orogeny in the Hellenic arc and the formation of a volcanic belt to the north (Cycladic arc);

- Southwestward motion of the Anatolian plate along the North Anatolian slip fault system at an average speed of 21 mm/year (Sengör et al. 2005, Philippon et al. 2014);

- Clockwise rotation (25° during the last 13 My) of continental Greece and the southwestern Aegean islands, and anticlockwise rotation (more than 20°) of the southeastern Aegean islands and South-West Anatolia (Laj et al. 1982, Duermeijer et al. 1998, Kondopoulou 2000, Van Hinsbergen et al. 2007);

- Subsidence of basins located back to the Hellenic arc.

Geologists intensively explored all these issues during the last 50 years, and proposed several models to explain the tectonic features of the region. Consequently, the literature dealing with one or more aspects of Aegean tectonics is particularly abundant, and thus the references cited above are a few of them. Regarding the recent evolution of the area, the most important feature is the subsidence of southern Aegean basins during the Plio-Pleistocene.

When visiting the Aegean islands, especially those situated on the Cycladic and Hellenic arcs, one is astonished by their specific relief. Almost all these islands have a very rugged topography, consisting of mountains and hills that are cut by deep valleys. The height of the mountains may exceed 1,000m, which is amazingly high in comparison with the reduced size of these islands. Plains are rare, except at the mouth of some rivers where they appear as small deltas. Otherwise, most of the rivers are seasonal streams fed by heavy rainfall. The coastlines of these islands often have a jagged outline, and are delimited by high cliffs; sandy beaches are rare and limited to small creeks. The general impression is that a continent sank in the sea, and only the mountain peaks still emerge from the waves. It is no coincidence that the legend of Atlantis was born in this country at the time of ancient Greece (see Vidal-Naquet 1964, 2005).

Indeed, the southern Aegean realm has been subsiding at least since the end of the Miocene (Lykousis 2009, Philippon et al. 2014, Simaiakis et al. 2017, and references therein). The seismic reflection profiles showed that after the Messinian Salinity Crisis, in the Early Pliocene the sea occupied the Myrtoon Basins and Saronikos Gulf, east of Peloponnese



Text-fig. 3 Simplified palaeogeographic reconstruction of the Aegean region during the ^{18}O Marine Isotopic Stage MIS 6 (low sea-level of the glacial period Riss/Saalian) between 180–140 ky ago (modified from Lykousis 2009). Schematized strait tusked elephant pictures and the names of the islands indicate the main occurrences of more or less dwarfed elephants in the Aegean as discussed in this paper.

and south of Attiki respectively. The Island of Crete became definitively isolated from the continent in Early Pliocene (Piper and Perissoratis 2003, Perissoratis and Conispoliatis 2003, Anastasakis et al. 2006, Lykousis 2009). The rest of the southern Aegean domain remained connected to the continent and mostly occupied by lakes. During the Late Pliocene – Early Pleistocene, between 3.2–2.0 My ago, the sea invaded much larger areas, in particular by penetrating the Evoikos Gulf to the east of Attiki (Anastasakis et al. 2006). This is also the time interval during which a new marine connection between the southern and northern Aegean basins settled (mid Aegean trench), thus separating the eastern and western parts of the Aegean domain. Despite a progressive

marine transgression, most parts of the Cyclades remained as land and connected to Attiki up to the Middle Pleistocene (Lykousis 2009, Simaiakis et al. 2017). It was also the case for the Dodecanese islands which remained connected to the southwestern coast of Anatolia up to the Middle Pleistocene (Perissoratis and Conispoliatis 2003). In the southern Aegean realm, only Crete and Karpathos-Kassos formed islands that have persisted since the Early Pliocene.

Since the pioneering work of Creutzburg (1963), several palaeogeographic maps of the Aegean region for the successive periods of the Neogene and Quaternary were proposed (Dermitzakis and Papanikolaou 1981, Dermitzakis 1990, Anastasakis and Dermitzakis 1990, Perissoratis and

Conispoliatis 2003, Anastasakis et al. 2006, Lykousis 2009, Poulakakis et al. 2015, Simaiakis et al. 2017). Lykousis (2009) used data from seismic reflection profiles, subsidence rates, land observations (terraces and faults) and sea-level fluctuations during the glacial and interglacial periods to calculate the subsidence rates for the second half of the Quaternary in different domains of the Aegean. For instance, in the eastern Cycladic Plateau, the subsidence rate between the Marine Isotopic Substage MIS 8.2 (ca. 250 ky BP) and the Marine Isotopic Substage MIS 2.2 (ca. 18 ky BP) was 0.44 m/ky, i.e. 102.5 m of subsidence over 232 ky. For the northern margin of the Cycladic Plateau, the subsidence rates range between 0.40–0.55 m/ky for the same time interval.

In addition to the impact of tectonic events on the palaeogeography of the Aegean realm, global sea-level fluctuations have impacted the extension of emerged areas. Lykousis (2009), Kapsimalis et al. (2009) and Simaiakis et al. (2017) showed that the Cyclades were separated from mainland Greece during the Middle Pleistocene. The Mega-Cyclades palaeo-island became fragmented into separate islands after the Last Glacial Maximum (LGM) due to the combined sea-level rise and subsidence. Simaiakis et al. (2017) quantified sea-level rise since the LGM, i.e., ca. 21 ky BP, as 145 m near Crete and 120 m at the Northern Aegean Sea coasts. Consequently, “the sea-level rise, from 21 kyr BP to present time, reduced the total area of the Aegean island by >70%, from 83,000 to 22,000 km²” (Simaiakis et al. 2017: 112). These authors also noted that the reduction in land surface was not regular during this interval, and the emerged area sharply decreased between 15 and 10 ky BP. This clearly shows that the present day southern Aegean islands were much larger, connected to each other, and/or connected to the mainland as peninsulas, up to the Late Pleistocene, except for Crete and Kassos-Karpathos that had remained as islands since the Early Pliocene (see above) (Text-fig. 3).

In such a paleogeographic context, the dispersal of terrestrial mammals including elephants into the southern Aegean islands is better explained by the tectonic events that controlled land-sea distribution. As discussed above, the elephant *M. creticus*, together with *Hippopotamus* LINNAEUS 1758, and the murid *Kritimys* KUSS et MISONNE, 1968, which appeared almost simultaneously on the Island of Crete and had reached this island via sweepstake routes, probably from continental Greece, at a time of sea-level lowstand (Sondaar 1971, 1977, 1986, Dermitzakis and Sondaar 1979, Sondaar et al. 1996, Mitsopoulou and Iliopoulos 2001, Sondaar and Van der Geer 2005, Masseti 2009, Herridge and Lister 2012, Van der Geer et al. 2014).

The first occurrence of palaeoloxodontine elephants on the southern Aegean islands was much later. Most islands of the Cyclades and Dodecanese were part of continental peninsulas during the Middle Pleistocene and earlier, and they became progressively covered by the sea due to subsidence of these regions. As shown in the paleogeographic maps drawn by Lykousis (2009), the ongoing subsidence of the southern Aegean area has progressively reduced the emerged areas. Most islands that hosted elephants became isolated during the Marine Isotope Substage MIS 5.5 (Riss-Würm interglacial or Tyrrhenian), at about 130 ky ago (Waelbroeck et al. 2002, Antonioli et al. 2006, Lykousis 2009).

Poulakakis et al. (2002: 177) suggested that “the most probable scenario for colonization of Crete by Middle and Late Pleistocene mammals (such as *Palaeoloxodon creutzburgi*) was the ‘Island Sweepstakes’ route”, which was also probably the case for *M. creticus* in the Early Pleistocene. It is generally accepted that *P. creutzburgi* is closely related to the straight-tusked continental species *P. antiquus* which is well known from the continents surrounding the Aegean Sea. It seems that the dwarf elephant species of the various southern Aegean islands are each the result of independent isolation events on the individual islands, hence their different degrees of dwarfism and morphological differences (Van der Geer et al. 2014). Finally, Van der Geer et al. (2016) studied the relationships between the degree of dwarfism in elephants and island conditions, and they concluded that the body size of elephants was influenced much more by the island surface and ecological competitors than the duration of a population’s isolation on an island. This would explain the strong dwarfism of elephants in the smaller islands such as Tilos, Dilos or Naxos.

Conclusions

Miocene and Pliocene mammalian faunas from the Aegean islands do not present any endemic character, and they are similar to contemporaneous faunas from Greece and Turkey (Koufos in press, and references therein). However, Pleistocene mammals from the southern Aegean islands show a marked endemic character due to the insular conditions of the area. This is particularly well expressed in the elephants of the Aegean islands, which are more or less dwarfed depending on several ecological parameters such as the island surface, food resources, isolation, competition and niche partitioning.

Compared to Sicily and Malta, elephants are poorly documented in the southern Aegean islands. The best fossil record is from Crete where three species have been identified from more than twenty localities. On the other islands, the fossil record is poor, generally limited to isolated discoveries, except for Tilos where a small sized elephant, *P. tiliensis*, is well documented with several thousand specimens. Despite the scarcity of fossil remains, the more or less dwarfed elephants occur in nine southern Aegean islands (in alphabetic order Crete, Dilos, Kalymnos, Kassos, Kythnos, Kythira, Naxos, Rhodos and Tilos) and other potential occurrences from other islands are just mentioned without any precise report or identification (see Doukas and Athanassiou 2003).

Recent studies on the insular mammals show that their isolation on islands leads to mammals becoming genetically derived, and thus forming new species (Berry 1986, Van der Geer et al. 2010). The old tendency was to lump together fossil elephants from the islands in the same species because of their similarity in size and features of their dentition even though the islands were sometimes separated from each other by hundreds of miles. Therefore, based on the observation of extant island populations, the systematics of insular mammals has been analyzed in the light of potential genetic isolation of populations and this related to the speciation rate on each island. This hypothesis could also be applied to

the fossil elephants of the Aegean islands, since the islands that they reached became progressively isolated from the surrounding continent and also from the neighbouring islands due to the active tectonics of the Aegean area. The dispersal of the Aegean island elephants was highly dependent on the palaeogeographic evolution of the region which was shaped by both regional tectonics and sea-level changes. The three elephant species from Crete, *M. creticus* from the Early Pleistocene, and *P. creutzburgi* and *P. chaniensis* from the Middle-Late Pleistocene, probably reached this island using sweepstake roots, as initially hypothesized by Sondaar (1971). It is also probably the case for the elephant from Kassos. All palaeogeographic reconstructions show that Crete and Kassos-Karpathos had been isolated since at least the Early Pliocene. Their Pleistocene mammalian faunas are unbalanced and composed of endemic species. In the other southern Aegean islands, Pleistocene elephants are poorly documented, except for *P. tiliensis* from Tilos. The appearance of elephants in these islands was initially attributed to sweepstake migration roots (Sondaar 1977, Dermitzakis and Sondaar 1979). Recent developments on the tectonic evolution of the Aegean domain indicate that all Cycladic and Dodecanese islands were connected to the mainland up to the Middle Pleistocene, and became isolated islands because of the ongoing subsidence of the Aegean basins (subsidence rate between 0.40–0.55 m/ky) and sea-level high stand during the Marine Isotope Substage MIS 5.5 at about 130 ky ago. We hypothesize that the palaeoloxodontine elephants may have reached these islands as well via land connections or using sweepstake roots. After their arrival on these islands, each island population evolved independently, and finally became extinct because of the progressive subsidence and reduced space there. In summary, the occurrence, dwarfism and extinction of elephants on the Aegean islands were mainly controlled by local tectonics and sea-level changes.

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