Ann. Zool. Fennici 51: 27–42 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 7 April 2014

Late Pleistocene dwarf elephants from the Aegean islands of Kassos and Dilos, Greece

Sevket Sen[1,*], Eric Barrier[2] & Xavier Crété[3]

[1)] *Laboratoire de Paléontologie du Muséum, CR2P-CNRS-UPMC, 8 rue Buffon, F-75005 Paris, France (*corresponding author's e-mail: sen@mnhn.fr)*
[2)] *iSTeP, Université Paris 6, CNRS, Case 129, 4 Place Jussieu, F-75252 Paris, France*
[3)] *280 Chemin de la Villa des Chênes, F-30250 Aubais, France*

Received 17June 2013, final version received 3 Jan. 2014, accepted 20 Jan. 2014

Sen, S., Barrier, E. & Crété, X. 2014: Late Pleistocene dwarf elephants from the Aegean islands of Kassos and Dilos, Greece. — *Ann. Zool. Fennici* 51: 27–42.

Dwarf elephants are quite well known from the western Mediterranean islands, but they are still poorly documented in most eastern Mediterranean islands. This paper reports on the discovery of a third lower molar of a dwarf elephant from the island of Kassos, which is situated in the southern Aegean, between Crete and Karpathos. This molar is determined as *Palaeoloxodon* aff. *creutzburgi*, a dwarfed species known from the Late Pleistocene caves and deposits in Crete and derived from the mainland straight-tusked elephant *P. antiquus*. An upper molar (M3) from the island of Dilos, previously referred to *Elephas antiquus* or *E. mnaidriensis*, is also redescribed. It is almost identical to the upper molars of a paleoloxodontine elephant from Naxos. Its small size and lack of sufficient comparative material lead us to determine it as *Palaeoloxodon* sp. The palaeogeographic evolution of the Aegean region during the Pleistocene and its impact on the dispersal of elephants in the Aegean islands are discussed.

Introduction

Endemic insular mammals are commonly recorded in Pleistocene deposits and cave infill of Mediterranean islands. They display particular adaptational features and evolutionary trends, different from that of their continental relatives. Elephants, hippos and ruminants (in particular deer) for large mammals, and a few murids and insectivores for small mammals are the main mammalian taxa settled in the Mediterranean islands during the Quaternary (Masseti 2009, 2012). They apparently reached islands when particular conditions favored their dispersal. Azzaroli (1977) hypothesized that terrestrial mammals reached Mediterranean islands through temporary land bridges. Sondaar (1977) proposed another alternative, assuming that the large mammals may have reached islands by swimming and small mammals by passive transport on natural rafts. Whatever the way terrestrial mammals used to reach and to populate Mediterranean islands, their affinities with mainland mammals indicate palaeobiogeographic relationships of islands with the surrounding mainland.

The "island rule" in mammals, i.e. impact of island conditions on the trends towards dwarfism of large mammals and towards gigantism of small mammals, is also an interesting phenomenon that is largely discussed in the literature (*see* e.g., Foster 1964, Van Valen 1973, Palombo 2007, and references therein). These authors and others (e.g. Thaler 1973, Case 1978, Lomolino 1985, 2005, Angerbjörn 1986, Damuth 1993, Palombo, 2004, 2007, 2009, Meiri *et al*. 2006, Raia & Meiri 2006, 2011, Van der Geer *et al*. 2010, Lomolino *et al*. 2012) provided several explanations for these trends. Among them the surface of the island and its distance to the mainland, its food resources, intra- and interspecific competition, and absence of predation pressure are considered the main factors that impacted on the evolution of island populations.

The occurrence of Pleistocene endemic mammals on Mediterranean islands indicates that they had particular ecosystems quite different from that of the surrounding mainland, due to their isolated conditions. Their mammalian faunas are unbalanced, and the lack of carnivorous predators is particularly noticeable. Among these endemic mammals, elephants are particularly remarked because of the spectacular reduction of their size. Dwarf elephants are also known from the western Mediterranean islands such as Malta, Sicily, Sardinia, and from the eastern Mediterranean islands such as Cyprus, Crete and several Aegean islands.

This paper reports on the discovery of a small elephant molar from the Late Pleistocene on Kassos and reviews the systematic assignment of another elephant molar from Dilos.

European Pleistocene elephants are grouped in the genera *Mammuthus* Brookes, 1828 (*M. meridionalis*, *M. trogontherii*, *M. primigenius*) and *Elephas* Linnaeus, 1758 or *Palaeoloxodon* Matsumoto, 1924. Opinions differed during the last half-century on the generic attribution of the species grouped under the last two genera names. Maglio (1973) included the species *antiquus* in the genus *Elephas*, while Aguirre Enríquez (1968–1969) preferred the genus name *Palaeoloxodon* to distinguish fossil Eurasian strait-tusked elephants from the extant and subfossil Asian *Elephas*. Since that time, the species *antiquus* waltzed between *Elephas* and *Palaeoloxodon* or was nominated as *Elephas (Palaeoloxodon) antiquus* (Mol *et al*. 2007). This was also the case for the Mediterranean island elephants presumably derived from the species *antiquus*. During the last two decades, several fossil-elephant experts recognized the genus status of *Palaeoloxodon* (e.g. Caloi *et al*. 1996, Doukas & Athanassiou 2003, Inuzuka & Takahashi 2005, Stuart 2005, Ferretti 2008, Herridge & Lister 2012). We decided to follow them.

The systematic status of island elephants is also the subject of current debate. For instance, Vaufrey (1929) referred to *Elephas falconeri* the specimens from Sicily and Malta, but also from Cyprus and Crete. Later studies recognized the distinct species status of elephants from the eastern Mediterranean islands (*see* Sondaar & Boekschoten 1967, Kuss 1970, 1973, Mol *et al*. 1996, Poulakakis *et al*. 2002a and references therein). However, during the last decade, several authors questioned the occurrence of some dwarfed elephant species on several islands. Consequently, elephant populations on each isolated island should have evolved independently (Palombo 2004, 2007, Theodorou *et al*. 2007, Ferretti 2008, Herridge & Lister 2012). Concerning the Aegean realm, this question is crucial for the systematic attribution of elephant remains that are known from several islands. The only named Pleistocene elephants species are from Crete: the small *Mammuthus creticus* (Bate 1907), the average-sized *Palaeoloxodon creutzburgi* (Kuss 1965) and a possible third large-sized species that is compared to *P. antiquus* (Falconer & Cautley 1847) (Mol *et al*. 1996, Poulakakis et *al*. 2002a and references therein). Elephant fossils that belonged to a species of the size of *P. creutzburgi* or larger have also been found on several south Aegean islands: Naxos, Dilos, Kythnos, Serifos, Milos, Paros, Kalymnos, Rhodos and recently Kassos (Sondaar 1971, Kuss 1973, Dermitzakis & Sondaar 1979, Caloi *et al*. 1996, Palombo 2001, Doukas & Athanassiou 2003, Tsoukala *et al*. 2011, Masseti 2012). The remains from Kythnos, Serifos, Milos and Paros are just mentioned in the literature without any description and illustrations (Palombo 2001, 2004) while the specimens from other islands are better known. In the present paper, we also discuss the systematic status of some findings from these islands based on morphological comparisons with the Kassos and Dilos molars. The tooth terminology follows Maglio (1973).

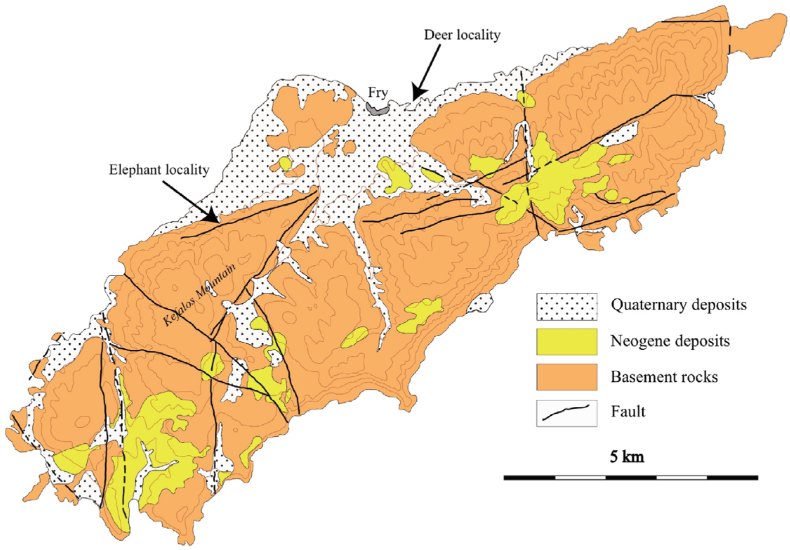

Fig. 1. Simplified geological map of Kassos Island (modified after Barrier 1984). The arrows indicate the localities where the elephant molar and deer fossils were found.

Localities and their geological context

The small island of Kassos (surface 49 km^2) is situated in the southern part of the Aegean Sea, between the large islands of Crete and Karpathos. It is a mountainous island whose highest peak reaches 601 m a.s.l. It is mainly formed of Mesozoic and Palaeogene limestones; in the lowlands of the island some marine Neogene deposits unconformably cover the substratum. Quaternary deposits are piedmont screes and alluvions in riverbeds, especially in the northern and western parts of the island (Barrier 1979, 1984), in addition to karstic deposits that may have been formed locally in caves, fissures or fault scarps. These Quaternary deposits are not known as fossiliferous, except in a locality at about 600 meters east of the last houses of the capital Fry, on the coast, where Kuss (1969) recorded cranial and postcranial remains of a fossil deer in cemented alluvial fan deposits. He referred these fossils to *Cervus cretensis*, and later (Kuss 1975) to *Candiacervus cerigensis*, which he had described from Late Pleistocene of the neighbouring island of Karpathos. Dermitzakis and Sondaar (1979) suggested that the occurrence of the same species on both islands indicates the lack of a real barrier between Kassos and Karpathos. For Sondaar *et al*. (1996: 63) "the Karpathos/Kasos deer must be a different and probably new genus". According to De Vos (2006: 129) the Kassos deer "is a species on its own and different from *Candiacervus cerigensis*". The occurrence of an elephant on Kassos is new, and its discovery contributes to a better understanding of Pleistocene palaeobiogeographic context of this island.

One of us (Xavier Crété) discovered the Kassos elephant molar when he was hiking in early August 2011 along the northwestern slopes of the Kefalos Mountain (465 m) in the western part of the island. The geographical coordinates and the altitude of the site where he found this molar are 35°23´45.6´´N and 26°24´´24.7´´E, and 165–170 m a.s.l., respectively (Figs. 1 and 2). The elephant molar was in a loose block probably fallen from a nearby karstic infill. Indeed, to the north of the Kefalos Mountain, an approximately E–W trending normal fault forms cliffs in the Eocene limestones (Figs. 1 and 2). Along these fault cliffs, occasional fissure fillings and footwall accumulations contain brecciated red deposits. They are strongly eroded because of the young topography and barren landscapes. The age of this fault as well as of sediments that are accumulated on its footwall is not known. The sediment in which the elephant molar was preserved is a pinkish-reddish brecciated marl, consolidated by a calcareous

Fig. 2. Northwestern slopes of the Kefalos Mountain on Kassos. The arrow indicates the site where the elephant molar was found. Note the fault cliffs along the slopes of the mountain marked by light-coloured rock outcrops at the level of the arrow.

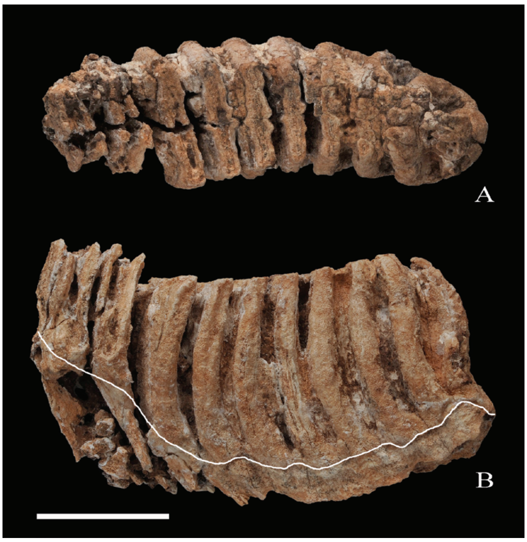

Fig. 3. A lower left third molar (m3) of *Palaeoloxodon* aff. *creutzburgi* from Kassos, Greece. (**A**) Occlusal view, and (**B**) lateral view with an indication (white line) of the crown-root limit. Scale bar = 5 cm.

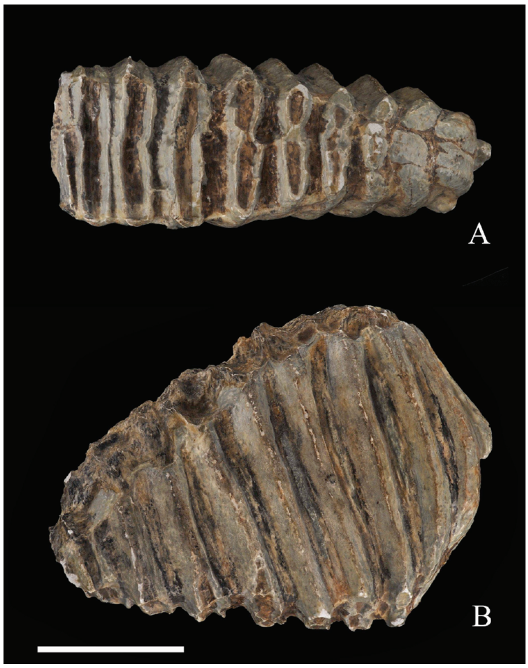

Fig. 4. An upper left third molar (M3) of *Palaeoloxodon* sp. from Dilos, Greece (cast, original stored at Dilos Archeology Museum). (**A**) Occlusal view, and (**B**) lateral view. Scale bar = 5 cm.

cement. It was prepared at the Natural History Museum of Paris, using successive baths of 5% diluted formic acid.

In addition to the Kassos elephant molar (Fig. 3), we redescribe a third upper molar from Dilos (Fig. 4). The tiny island of Dilos (3.5 km^2) is part of Cyclades, and is situated some 20 miles northwest of the large island of Naxos, and between Rhinia and Mykonos. Cayeux (1908) reported on the discovery of an elephant molar in the alluvions of the Inopos River at the northern part of Dilos. This molar was found during a survey excavation to study the substrate of the monuments in the ancient city of Dilos, to the east of the Apollo temple, 4 m a.s.l. (Cayeux 1908). He referred it to *Elephas antiquus* Falconer & Cautley, 1847. Later, Vaufrey (1929: fig. 38) illustrated this molar and speculated whether it belongs to *Elephas mnaidriensis* Adams, 1874, a species previously defined from Malta, or to a small sized *Elephas antiquus*. This record was often mentioned in the literature (e.g. Dermitzakis & Sondaar 1979, Symeonidis & Theodorou 1982, Kotsakis 1990, Caloi *et al*. 1996, Poulakakis *et al*. 2002a, Doukas & Athanassiou 2003, Tsoukala *et al*. 2011); most of these authors noted that this molar belonged to a somewhat dwarfed elephant without however suggesting any systematic assignment. Its similarities in size and dental pattern to the Kassos molar led us to restudy the Dilos molar from a cast kept at the Paris Museum.

The southern Aegean region is formed of several tectonic structures, the most prominent of them being (1) the south Aegean volcanic arc, which extends approximately from the Gulf of Corinth in the west to Kos in the east (including Cyclades), (2) the Cretan arc, which extends from Peloponnese to Rhodos via the largest Aegean island of Crete, and (3) the Cretan Basin that separates these two arcs. South and southwest of the Cretan arc, the Hellenic trench is a subduction zone where the African plate plunges beneath Eurasia. On the other hand, the Anatolian plate is extruded southwestward under the effect of the collision of the African plate with the Anatolian plate in southeastern Turkey. The southward extension of the Aegean–West Anatolian region since the late Miocene onwards is related to a differential advancement of the upper plates (Greece and Anatolia) over the African plate (Piper & Perissoratis 2003, Agostini *et al*. 2010). In other words, the southern Aegean realm is subsiding since at least the early Pliocene. The effects of the subsidence on the dispersal of Pleistocene elephants in the southern Aegean realm will be discussed in the Discussion.

Systematic study

Palaeoloxodon aff. *creutzburgi* (Kuss, 1965)

Order Proboscidea Illiger, 1811
Family Elephantidae Gray, 1821
Genus *Palaeoloxodon* Matsumoto, 1924

Type locality: Kalo Chorafi cave, Rethymnon, Crete.
Holotype: left m1, Nr 22/1963 (Kuss 1965: pl. 3).

Material from Kassos Island

An isolated left third lower molar (m3) labelled as KAS-1 (Fig. 3). Its basal length is 165 mm; preserved crown length 162 mm; maximum width 54 mm at the level of 3rd plate; maximum crown height 72.9 mm at the 7th plate. This specimen is stored at the Arhaeological Museum of Kassos, and its casts are available at the Natural History Museums of Paris (MNHN) and London (NHM).

Description

In occlusal view, the Kassos molar is moderately curved laterally, so its labial face is concave. The occlusal surface is concave and progressively tapers backwards. The stage of wear indicates that it belonged to an adult individual. It bears nine plates plus talon. The advanced stage of wear of the anterior plates, which are also partly damaged, and the lack of the anterior root indicate that some anterior plates may have been lost. All plates but the last one are progressively abraded. The lamellar frequency is 6.5. The talon forms a narrow platelet as high as the last plate. The crown height increases from the first preserved plate to the 7th plate, and then it slightly decreases towards the back. On the occlusal view, the plates form narrow and slightly oblique ridges with almost regular antero-posterior width. In other terms, the width of the plates does not change significantly in their central, lateral and medial parts, except when there is anterior and/or small posterior enamel bulges near the center. The enamel bands are delicately wrinkled. The enamel thickness varies between 1.8–2.2 mm depending on the wear stage. On the occlusal surface, the enamel loops of the plates and the cement areas between the plates occupy similar surfaces. The roots are not preserved. The Kassos molar is determined as an m3 based on the following characters:

1. In occlusal view, its distal part is laterally curved from the 6th plate backward. The curve makes an angle of 160°. In that it is similar to the left m3 from Simonelli Cave in Crete illustrated by Kotsakis (1980) and

referred to *P. creutzburgi*, as well to the left m3 of *P. tiliensis* from Tilos (Theodorou 1983: pl. 3, fig. 1), right m3 of "*Elephas antiquus*" from Kythera Island (Kuss 1967, fig. 2), and many other m3 referred to *Palaeoloxodon* sp. from the European mainland and Mediterranean islands. The m3s from Coumbes Cave (Crete) are less curved than the above-mentioned specimens (Symeonidis & Theodorou 1982). The holotype of *P. creutzburgi*, and the only lower molar from the type locality Kalo Chorafi (Crete), is a worn left m1 (Kuss 1965). Its occlusal surface is straight. Theodorou (1983) also illustrated two m2 from Tilos, the one with a similar occlusal wear, and these molars are barely curved, nothing to compare with the curvature seen on the Kassos molar. The general curvature trend on the m3 of *Palaeoloxodon* sp. is that the less a tooth is abraded the more it appears to be laterally curved [e.g. curved m3 in Bate (1907: pl. 22, fig. 6) and Palombo & Ferretti (2005: fig. 12), but almost not curved m3 from Coumbes Cave (Symeonidis & Theodorou 1982: pl. 3–5)].

2. The distal part of the Kassos molar tapers backward. In a similar degree of attrition, the m1 from Kalo Chorafi as well as the m2 from Tilos Island have the distal edge rather rounded and lack the talon.
3. The Kassos tooth is worn up to its eight preserved plate. In such a degree of attrition, the distal face of an m1 or an m2 should have a pressure mark of the following tooth. This is not the case on the Kassos molar. For the identification of a molar from Simonelli Cave in Crete, Kotsakis (1980: 115) compared it with the lower molars of *Palaeoloxodon antiquus*, and observed that on m2s "there is always a flattening however small, on the posterior side due to the contact with the growing m3". Such a contact is not observed on the Kassos molar.

Comparison of the Kassos m3

Dwarf elephants are best known from the neighbour island Crete with two species: *Mammuthus creticus* (Bate 1907) and *Palaeoloxodon creutzburgi* (Kuss 1965). Some papers mentioned the presence of a third form a little larger than the type specimens of *P. creutzburgi* from Kalo Chorafi cave and about 20% smaller than the mainland species *Palaeoloxodon antiquus*; this third form was referred to *P. antiquus*, *P.* cf. *antiquus* or to a new species, *Palaeoloxodon chaniensis* (Kuss 1973, Dermitzakis & Sondaar 1979, Symeonidis & Theodorou 1982, Dermitzakis & de Vos 1987, Symeonidis *et al*. 2000, 2001, Poulakakis *et al*. 2002a).

Mammuthus creticus from the Early-Middle Pleistocene site of Cape Meleka near Rethymnon 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) clearly different from that of the Kassos molar. Bate (1907: 243) noted that "except with regard to the immense difference in size the characteristics of the molars (of Cape Meleka), more especially in the lowness of the crowns, appear to resemble more closely those of *E. meridionalis* than any other of the larger Elephants of the Mediterranean region". Lastly, studying the Bate's collection at the NHM-London and some new material, Herridge and Lister (2012) confirmed morphological evidence on its ancestral relationships with Early Pleistocene *Mammuthus meridionalis* or even with Late Pliocene *M. rumanus*. These authors estimated that *M. creticus* may have a body mass about 310 kg and shoulder height 1.13 m. *Mammuthus creticus* was found associated with the murid *Kritimys kiridus*, and it apparently reached Crete during the first migration wave of land mammals in Early Pleistocene (Mayhew 1977, 1996), or ca. 0.9 Ma ago (Reese *et al*. 1996, Sondaar & Van der Geer 2005, Van der Geer *et al*. 2010). However, all these dates need to be confirmed or evaluated with new dating methods and more accurate analyses, as noted by Stuart and Lister (2012).

A second elephant species from Crete is *Palaeoloxodon creutzburgi* (Kuss 1965). It was recorded in Crete at more than 15 localities, all supposedly of latest Middle or Late Pleistocene age (Poulakakis *et al*. 2002a). This is a large sized form having palaeoloxodontine affinities in its dentition. The systematic status of palaeoloxodontine elephant remains from Crete has been debated since 1960s. Lastly Poulakakis *et al*. (2002a) reviewed the material from the Cretan localities and retained two subspecies, *Elephas* (*Palaeoloxodon*) *antiquus creutzburgi* for specimens similar in size to that of the Kalo Chorafi cave, and *Elephas* (*Palaeoloxodon*) *antiquus chaniensis* for the larger sized elephant remains from the caves of Vamos and Coumbes in Crete. We estimate that the taxon *creutzburgi* deserves the species status, and here it will be retained as *P. creutzburgi*. Its type material from the Kalo Chorafi cave includes two upper-cheek teeth identified as P2 and P3, and one damaged and worn m1 (Kuss 1965). This m1 is clearly wider than the Kassos m3 (75.2 mm contra 54 mm) and also all m3s of "large elephant" known from other sites in Crete. However, it should be noted that the anterior molars, in particular when they are well worn, might be larger than the m3, as already noted by Bate (1907) on the mandible with the m2–m3 from Kharoumes Bay in Crete. Concerning the size of molars, it is not possible to distinguish any size group among the available specimens from Crete, as well as including the m3s from Kythera and Naxos islands (Mitzopoulos 1961, Kuss 1967). The size and different ratios of the Kassos m3 fall close to the average values of palaeoloxodontine elephants from Crete (Table 1).

The lower molar morphology is best observed on the type specimen (m1) from Kalo Chorafi, on the m2 (not M2 as determined by Poulakakis *et al*. 2002a) from Katharo Basin, on the m2–m3 from Kharoumes Bay (Bate 1907) and on the m3s from Grida Avlaci, Simonelli Cave and Coumbes Cave (Simonelli 1908, Kotsakis 1980, Symeonidis & Theodorou 1982). In all these specimens, as well as on the Kassos m3, the plates are narrow, the interplate cement areas are narrower than the plates, the central part of plates is a little larger (mesio-distal) than the lateral parts, the plates bear anterior and posterior enamel bulges in their central part, the enamel is gently folded but much less than in *Palaeoloxodon antiquus* molars of similar wear stage, the plates slightly abraded are composed of one wide central loop and two or more lateral rounded rings. In all these features, the Kassos m3 cannot be distinguished from the lower molars of Cretan localities that Kuss (1965), Kotsakis (1980) and Poulakakis *et al*. (2002a) referred to *P. creutzburgi*.

From other Aegean islands some elephant remains of the size of *P. creutzburgi* were also recovered. From Rhodos, Symeonidis *et al*. (1974) recorded postcranial remains of a dwarfed elephant that they tentatively referred to a possible subspecies of *P. antiquus*. From Naxos, Mitzopoulos (1961) described a palate with both M2 that Symeonidis *et al*. (2000) referred to their new species *Elephas chaniensis*. An M3 from Dilos (*see* below) that Cayeux (1908) determined as *Elephas antiquus* also represents a dwarfed elephant. All these findings cannot be compared with the Kassos m3.

Elephas tiliensis Theodorou *et al*. (2007) from Charkadio Cave on Tilos is well documented with many skeletal parts, cranial and postcranial bones, and several cheek teeth. They were extensively described and illustrated by Theodorou (1983) who referred it in his Ph.D. thesis, following Symeonidis (1972), to *Palaeoloxodon antiquus falconeri*. Later on, Theodorou *et al*. (2007: 23) referred the Tilos elephant to a new species because (in the diagnosis): "even if its dimensions and morphology were equal to other endemic Mediterranean elephants, its isolation is more than adequate for the description of a new endemic species". In other words, this species is new not because it is morphologically different from the other elephant species, but because it is endemic to Tilos, and thus it is supposed to be genetically isolated from the other elephants hence deserving a new species status. According to the measurements given by Theodorou (1983), the size of the molars of this species is smaller than or in the lower range of variation of *Palaeoloxodon creutzburgi* from Crete (Table 1). The characters of cheek teeth such as lamellar frequency, enamel thickness, slightly folded enamel, lamellae with parallel enamel bands, oblique position of the lamellae in the posterior half of the m3, presence of a small central loop on the lamellae and crown height of upper molars are also similar to that of *P. creutzburgi*. According Poulakakis *et al*. (2002b, 2006) and Theodorou *et al*. (2007), *Elephas tiliensis* inhabited Tilos between ca. 50 000 and 4000 BP, i.e. at least partly contemporaneous with *P. creutzburgi*. Although smaller, the mor-

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 specimens, x = talon, p = plate, *L/W* = length/width ratio, LF = lamellar frequency. '>' = part of the tooth missing.

Species	Locality	*n*	Number of preserved plates	Length (mm)	Width (mm)	*L/W*	Height (mm)	Hypsodonty index	LF	Enamel thickness (mm)	References
Palaeoloxodon creutzburgi (m1)	Kalo Chorafi cave, Crete	1	>7p	121.3*	75.2	1.6*	79.4*		5.2	less than 4	Kuss 1965
P. creutzburgi (m2)	Katharo Basin, Crete	1	>8	140*	67	2.1*	104	1.55	8	1.8–2.88	Poulakakis *et al.* 2002
P. aff. *creutzburgi*	Kassos, Greece	1	x>9p	165*	54	3.06*	72.9	1.35	6.5	1.8–2.2	This paper
Palaeoloxodon creutzburgi	Kharoumes, Crete	1	x>8p	?	47		95.3		9	1–2.5	Bate 1907, Kuss 1966
P. aff. *creutzburgi*	Coumbes Cave, Crete	2	x>9p	165–181	63	2.62–2.87	–		5.5–6	3–3.5	Symenoidis & Theodorou 1982
Palaeoloxodon creutzburgi	Grida Avlaci, Crete	1		125*	60				4.5*	2.5	Simonelli 1908
Palaeoloxodon creutzburgi	Simonelli Cave, Crete	1	x9p	216	64	3.38	133	2.1	4.75	2.5	Kotsakis 1980
Palaeoloxodon creutzburgi	Simonelli Cave II, Crete	1		125*	56				?	1.5–2.5	Mol *et al.* 1996
Palaeoloxodon sp.	Kythera Island, Greece	1	x12p	180*	75	2.4*			6.6–7	3	Kuss 1967
Elephas tiliensis	Tilos Island, Greece	3	x11p	110–160*	48–53	3.2			6.5–7.7	2.5–3.0	Theodorou 1983
Mammuthus creticus	Cape Maleka, Crete	2	x12p	145	33–41	3.9	39–50	1.2	10		Bate 1907
Palaeoloxodon mnaidriensis	Puntali Cave, Sicily	2	x10p	170–174	60	2.87	–	–	6–7		Ferretti 2008
Palaeoloxodon antiquus	Grevena, Greece	1	x14p	242	83	2.92			6	2.3–3.3	Tsoukala & Lister 1998
Palaeoloxodon antiquus	Ryahovo, Bulgaria	1	x17p	370	86	4.3	172	2	5.5	2.5	Markov 2007

* measured from incomplete tooth, true value greater than the given one.

phological pattern of its cheek teeth shows great similarities with that of *P. creutzburgi*.

Kuss (1967) described and illustrated a right m3 from Kythera as belonging to *Elephas antiquus*. This m3 is larger than any other m3 from Crete and Kassos (Table 1), it has more plates preserved, although it is in other characters quite similar to both *P. antiquus* and *P. creutzburgi*. However, the lack of central enamel bulges on the plates resembles more the pattern of *P. antiquus*. Masseti (2009, 2012) referred to *P. antiquus* a lower jaw fragment from Kalymnos with the m3 (?), which has the anterior and posterior parts damaged. Masseti did not provide any measurements for this molar but he illustrated it with a scale. Using this scale, the estimated maximum width of this molar should be less than 40 mm, which is smaller than any other lower molar referred to *P. creutzburgi*, and of course infinitely small as compared with the molars of *P. antiquus*. This molar bears seven preserved plates that are similar in shape and pattern to that of *P. creutzburgi* and *P. tiliensis*. The size of the Kalymnos molar makes it the smallest palaeoloxodontine elephant of the Aegean islands. We have to emphasize that Kalymnos is close to the western Anatolian coasts and it is on the continental plateau. The status of the Kalymnos specimen cannot be solved without a detailed comparative study.

Despite the great similarities of the Kassos molar with those from Crete, we preferred to determine it as *P.* aff. *creutzburgi*, due to the fact that *P. creutzburgi* is still poorly documented in Crete (limited number of lower molars to be compared with Kassos molar), and that only a more abundant material from the type locality of *P. creutzburgi* or from similar age localities in Crete can solve its taxonomic status.

***Palaeoloxodon* sp.**

Material from Dilos

An isolated left third upper molar (M3) (Fig. 4). Preserved crown length 156 mm; maximum width 59 mm at the level of 3rd plate; maximum crown height 110 mm at the 7th plate. A cast of this specimen is preserved at MNHN. According to the label of this cast, the original specimen is stored at the Archaeological Museum of Dilos Island. This label also mentions that this tooth "was found in the sandy alluvium of the former torrent Inopos, during the excavations near the sanctuary of Apollo".

Description

The Dilos molar should be an M3 because it tapers backward though the wear abraded almost all plates except the last two, and there is a talon typical for a last upper molar. Its occlusal surface is almost flat. It preserves nine plates plus talon. The advanced wear degree suggests that some anterior plates may have been lost. The wear is progressive backward, 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 it slightly decreases towards the back. 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 display each one big central 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 the mid depth of the crown. The roots are not preserved.

Comparison

As noted above, Cayeux (1908) described this tooth from Dilos as a last upper milk molar of *Elephas antiquus*. According to Vaufrey (1929) who gave an illustration, the Dilos specimen is the last molar (M3) and it can be referred to *Elephas mnaidriensis*, a species previously known from Malta and Sicily. Since that time the systematic status of this specimen remained open.

As shown above, this specimen is a left M3 belonging to an adult individual. Its narrow plates, unequal rings and gently folded enamel bands indicate a palaeoloxodontine elephant. Its size is about 60% of the strait-tusked continental

Table 2. Comparative measurements and ratios of the upper molars of Elephantidae from several localities in Greece, Bulgaria and Italy. x = talon, p = plate, *L/W* = length/width ratio, LF = lamellar frequency. '>' = part of the tooth missing.

Species (tooth, number of specimens)	Locality	Number of preserved plates	Length (mm)	Width (mm)	*L/W*	Height (mm)	Hypsodonty index	LF	Enamel thickness (mm)	References
P. creutzburgi (P2, 1)	Kalo Chorafi cave, Crete	>5	73.8	63.3	1.17	45*		7.1	3.8	Kuss 1965
P. creutzburgi (P3, 1)	Kalo Chorafi cave	>5	94.6	64.8	1.46	66*		5.9	3	Kuss 1965
Palaeoloxodon sp. (M2, 2)	Naxos, Greece	>9	125–127	45–46	2.77	101–104	2.31	6.9–7.2	2–3	Mitzopoulos 1961
Palaeoloxodon sp. (M3, 1)	Dilos, Greece	>9p	156	59	2.64	110	1.86	6.1	1.5–3	This paper
P. tiliensis (M3, 3)	Tilos, Greece	>7–11	95–124*	47–53	2.28	86	1.72	7.7–9	2–2.9	Theodorou 1983
P. antiquus (M3 average, 6)	Italy, various locs	x14p	280	90	3.11	170	1.92	5.0	2.6	Palombo & Ferretti 2005
P. antiquus (M3, 2)	Penios Valley, Greece	x19p	340–355	93–95	3.70	220–250	2.37–2.63*	5.4	1.7–3.9	Athanassiou 2001
P. antiquus (M3, 1)	Ryahovo, Bulgaria	x14p	230*	71	3.2	183*	2.58*	6.5	2.0	Markov 2007

* measured from incomplete tooth, true value greater than the given one.

elephant *P. antiquus*. Upper cheek teeth of large sized palaeoloxodontine elephants from Aegean islands are poorly documented: one P2 and one P3 from the Kalo Chorafi cave in Crete referred to *P. creutzburgi* (Kuss 1965, 1973), a palate with both M2s from Naxos tentatively referred to *Elephas melitensis* (Mitzopoulos 1961) and several upper cheek teeth from Tilos referred to a new species *Elephas tiliensis* (Theodorou 1983, Theodorou *et al*. 2007). The Dilos M3 is a little larger and more hypsodont than the specimens from Naxos (Table 2). On the contrary, the pattern of the occlusal surface is very similar in having equal number of plates, a narrow shape, unequal enamel loops, gently folded enamel, and three loops on the unworn plates. The M3s from Tilos are smaller than those of Dilos and Naxos, with however a similar occlusal pattern. The lamellar frequency is quite similar on the Dilos and Naxos molars, but higher on the Tilos molars (Table 2). Based on the size and tooth pattern of these molars, it can be supposed that the Dilos and Naxos specimens belong to the same species, while those from Tilos probably belonged to a different species. Concerning the P2 and P3 from the Kalo Chorafi cave in Crete, the type locality of *P. creutzburgi*, it will be hazardous to compare them with the Dilos M3. They apparently represent a larger sized form, and the plates are not divided in unequal loops as on the Dilos and Naxos molars. In summary, the poor available knowledge on the upper dentition of palaeoloxodontine elephants from the Aegean islands does not allow a definite systematic assignment of the Dilos M3, hence its determination as *Palaeoloxodon* sp.

Discussion

Pleistocene dwarf elephants are well known from the western Mediterranean islands of Malta and Sicily. Palaeoloxodontine species from these islands are, from the smaller to the larger, *Palaeoloxodon falconeri* (Busk, 1867), *Palaeoloxodon melitensis* (Falconer 1862, in Busk 1867) and *Palaeoloxodon mnaidriensis* (Adams, 1874) (Ambrosetti 1968, Caloi *et al*. 1996, Palombo 2001, Marra 2005, Ferretti 2008, Masseti 2009), although the possible synonymy between these species is discussed since Pohlig (1893) (*see* also Ambrosetti 1968, Caloi *et al*. 1996, Ferretti 2008). These authors demonstrated the affinities of these species with the "normal" sized strait tusked elephant of Europe, *Palaeoloxodon antiquus*. Some of these western Mediterranean Pleistocene elephants are in some extent similar in size and morphology to the elephants of the Aegean islands. For instance, *Palaeoloxodon mnaidriensis* is similar in size to *Palaeoloxodon creutzburgi* from Crete (Table 1). The length/width ratio, number of lamellae and lamellar frequency, gently folded enamel bands and the progress of the occlusal wear on cheek teeth are also characters shared by *P. mnaidriensis* and *P. creutzburgi*.

However, the similarities of their tooth pattern are the characters inherited from their common ancestor *Palaeoloxodon antiquus*. These are also reliable differences between these two species, for instance for the m3, sharp lamellar edges in *P. mnaidriensis* but square shaped in *P. creutzburgi*, lamellae generally curved backward in the first, straight in the second, and so on. Despite the above-mentioned similarities, it is assumed here that the dwarfed elephants of Malta and Sicily have an independent evolutionary history from their mainland relatives as well as from the other island elephants. Consequently, they represent independent species. Indeed, the western Mediterranean islands have their own palaeobiogeographic context (Marra 2005). During the Pleistocene they were never connected to the Aegean islands, neither had they any mammalian exchange.

This is also the case for Cyprus, which became definitely isolated from the mainland after flooding of the Mediterranean at the end of the Messinian Salinity Crisis, ca. 5.3 Ma (Hadjisterkotis *et al*. 2000). The dwarf elephant *Palaeoloxodon cypriotes* (Bate 1903) inhabited Cyprus during the Middle-Late Pleistocene (Simmons 1999). It is probably derived from *Palaeoloxodon antiquus* although remarkably reduced in size, i.e. about 1 to 1.2 m at the withers (Davies & Lister 2001; G. Iliopoulos unpubl. data). Its molar pattern displays the primitive characters of the paleoloxodontine type with low-crowned cheek teeth, gently folded enamel and low lamellar frequency. *Palaeoloxodon cypriotes* is different from the elephant of Kassos and Dilos in being significantly smaller and in having lower crowned cheek teeth. Boekschoten and Sondaar (1972) reported the presence of a larger elephant in Cyprus based on some tooth fragments that are not reliable for any comparisons.

How many elephant species did inhabit the Aegean islands during the Pleistocene? This crucial question is difficult to answer reliably due to the fact that the elephant remains from many islands, except in Tilos, are still quite scarce and fragmentary. The available material and the state of paleontological studies do not allow for estimating variations in size and morphology because of sexual dimorphism, intra-specific variation or degree of dwarfism.

Another major question currently debated concerns the endemic evolution of island elephants, and consequently the occurrence of independent species on each island (Palombo 2004, 2009, Theodorou *et al*. 2007, Ferretti 2008). This view assumes a genetic isolation of elephants after they reached the islands, and consequently they became independent species on each island. For instance Palombo (2004, 2009) and Ferretti (2008) questioned the species identity of Sicilian and Maltese elephants despite their great size and morphological similarities. It is conceivable that elephants may have evolved independently on islands that remained isolated from the mainland (e.g. Cyprus and Malta). We do not know for certain how and when the Aegean islands became isolated from the mainland, and also from each other, in particular when Pleistocene elephants inhabited these islands. As seen in Fig. 5, the distances between the Aegean islands that yielded elephant fossils are short.

In addition, we have to take into account the fact that the Aegean region is currently undergoing a widespread regional extension, which can be dated back at least to the Late Miocene. This is due to the convergence of the Afro-Arabian and Eurasian plates and the southwestward motion of the Anatolian block. Using seismic reflection profiles and available chronostratigraphic data, Piper and Perissoratis (2003) estimated the southward Quaternary extension rate of the Aegean realm as 37 mm/year and the subsidence rates for the last 0.2 Myr at about 2.5 m/kyr in the Santorini-Anafi Valley region,

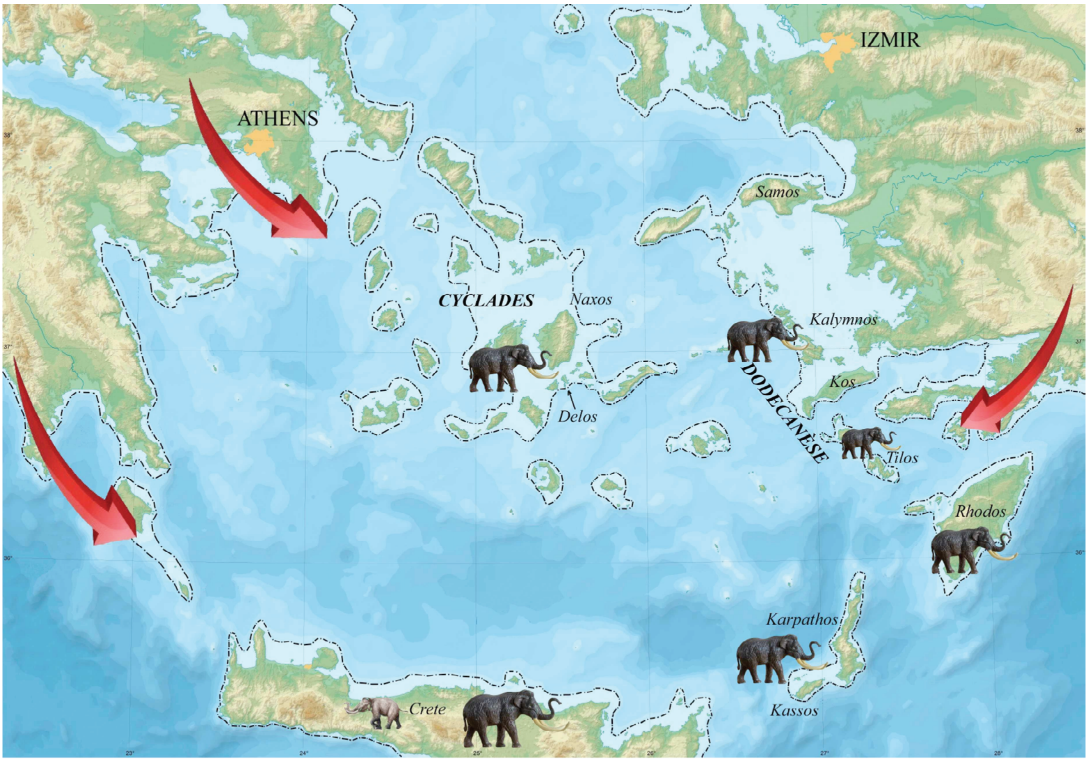

Fig. 5. Present day map of the southern Aegean, showing the islands inhabited by *Mammuthus creticus* (Crete), *Palaeoloxodon creutzburgi* (Crete), *Palaeoloxodon* spp. (Kassos, Rhodos, Dilos, Naxos and possibly Kalymnos) and *Palaeoloxodon tiliensis* (Tilos). The dashed lines around the islands and continent indicate –100 m depth that was exceeded during the last glacial sea level drop. The red arrows indicate the possible dispersal routes of island elephants.

and up to 1.6 m/kyr on the North Aegean Shelf. According to Agostini *et al*. (2010), the subduction rates in the southern Aegean may reach 4 cm/year during the Quaternary. Indeed, a final tectonic phase beginning at about 0.8 Myr ago markedly changed the fault pattern in the South Aegean arc, and all the Aegean Basin underwent a fault-controlled subsidence (Piper & Perissoratis 2003). Thus, when *P. creutzburgi* and its relatives inhabited the southern Aegean islands, one can speculate how large these islands were (possibly even larger than today), and how deep were the channels in between. This implies that these islands may have intermittently been connected to the mainland and/or the area of the Aegean Pleistocene islands was larger than today. They might have sheltered larger sized individuals and the elephants might not have been totally isolated from their mainland relatives as it happened for species such as *Mammuthus creticus* in Crete and *Palaeoloxodon cypriotes* in Cyprus. In addition, the available fossil documentation does not inform us on the possible sexual dimorphism and/or size variability of the palaeoloxodontine elephants on Aegean islands.

Poulakakis *et al*. (2002a) discussed the possible origination of the elephant species in Crete. It is hypothesized that the pigmy elephant *Mammuthus creticus* is derived from *Mammuthus meridionalis* based on its older age (ESR dates ranging from 846 000 to 475 550 years; Reese *et al*. 1996, *see* above) and the similarities of its dental pattern with the Mediterranean mammoth. This species may have reached Crete during the sea level lowering in the late Early Pleistocene.

For the entrance in Crete of the less dwarf elephant *Palaeoloxodon creutzburgi*, Poulakakis *et al*. (2002a: 177) suggest that “the most probable scenario for colonization of Crete by Middle and Late Pleistocene mammals was the ‘Island

Sweepstakes' route". Fossil elephant researchers generally accept that *P. creutzburgi* is probably derived from the strait-tusked continental species *P. antiquus*. This species is well represented on the continents surrounding the Aegean Sea. It has been recorded in at least 23 Pleistocene localities all over Greece (Tsoukala & Lister 1998, Athanassiou 2001, Doukas & Athanassiou 2003, Tsoukala *et al*. 2011) as well in the Balkans (Markov 2007) and Asia Minor (Becker-Platen & Sickenberg 1968, Albayrak & Lister 2011).

Indeed, the sea level dropped several times during the Pleistocene. For instance, the sea level was about –120 m during the Marine Isotopic Stage 6 (MIS) (about 140 kyr ago), –100 m during MIS 4 (about 60 kyr ago) and –125 m during MIS 2 (about 20 kyr ago) (Antonioli *et al*. 2006). In such a palaeogeographic context, several Aegean islands, today isolated and far from the continent, became connected to the mainland (Greece or Turkey) or their distance from the mainland considerably diminished (Fig. 5). In addition, we have to take into account the current regional extension and fault-controlled subsidence of the Aegean region since the Late Miocene. All these parameters indicate that during the Pleistocene, the island surfaces and environmental conditions were probably different of their present conditions. These events may have facilitated the dispersal to these islands of deer, elephants and hippopotamuses that were common on the mainland, hence their occurrence in Crete and several other Aegean islands. When sea level rose, these islands became isolated and their inhabitants evolved under the new insular conditions.

Conclusion

The present study describes a newly-discovered elephant m3 from Kassos and provides a new systematic assessment for an M3 from Dilos. The Kassos M3 is referred to *Palaeoloxodon* aff. *creutzburgi* (Kuss 1965), which is a species quite abundant in Crete during the Late Pleistocene. This species is related to the straight-tusked elephant of Eurasia, *P. antiquus*. *Palaeoloxodon creutzburgi* has a reduced body mass that Palombo (2007) estimated as 67% of the mainland species *P. antiquus*. The size of the Kassos and Dilos molars indicates individuals smaller than *P. creutzburgi* from its type locality the Kalo Chorafi cave in Crete.

Immigration of elephants as well as of other mammals onto the Aegean islands probably occurred in several phases, the one in the Early Pleistocene with *Mammuthus creticus*, which is known only from Crete, and the second during the late Middle or Late Pleistocene with the palaeoloxodontine elephants. This latter group is much less dwarfed than the first one, and it inhabited several south Aegean islands, i.e. Crete, Kassos, Rhodos, Kalymnos, Dilos and probably Naxos. Its occurrence on these islands is probably due to sea level lowering during the Middle-Late Pleistocene.

Acknowledgements

It is a great pleasure for us to contribute to this volume in honour of Mikael, with whom one of us (S. Sen) hunted mammalian fossils in Turkey, China and more recently in Iran, and shared some exciting discussions making and unmaking the systematics and palaeobiogeography of many groups of mammals. We would like to thank Anu, Suvi and Jussi for inviting us to join the group of Mikael's friends. Pascal Tassy (MNHN, Paris) and Marco Masseti (Firenze) provided useful comments and literature on fossil elephants. Vincent Pernègre (MNHN, Paris) hunted all fossil elephant molars in the palaeontology collections of the Natural History Museum of Paris to be compared with the Kassos and Dilos elephants. Philippe Loubry (CNRS-MNHN, Paris) made the photos. Philippe Richir prepared the cast of the Kassos elephant molar. We are grateful to the referees Victoria Herridge, Juha Saarinen and an anonymous referee for their valuable comments and suggestions that allowed to greatly improve this paper.

References

Agostini, S., Doglioni, C., Innocenti, F., Manetti, P. & Tonarini, S. 2010: On the geodynamics of the Aegean rift. — *Tectonophysics* 488: 7–21.

Aguirre Enríquez, E. 1968–1969: Revisión sistemática de los Elephantidae por su morfología y morfometría dentaria. — *Estudios geologicos* 24: 109–167; 25: 123–177 and 317–367.

Albayrak, E. & Lister, A. M. 2011: Dental remains of fossil elephants from Turkey. — *Quaternary International* 276–277: 198–211.

Ambrosetti, P. 1968: The Pleistocene dwarf elephants of Spinngallo. — *Geologica Romana* 7: 277–397.

Angerbjörn, A. 1986: Gigantism in island populations of wood mice (Apodemus) in Europe. — *Oikos* 47: 47–56.

Antonioli, F., Kershaw, S., Renda, P., Rust, G., Belluomini, G., Cerasoli, M., Radtke, U. & Silenzi, S. 2006: Elevation of the last interglacial highstand in Sicily (Italy): a benchmark of coastal tectonics. — *Quaternary International* 145–146: 3–18.

Athanassiou, A. 2001: New findings of fossil large mammal remains in the Penios Valley (area of Larissa, Thessaly, Greece). — *Bulletin of the Geological Society of Greece* 34: 533–539.

Azzaroli, A. 1977: Considerazioni sui mammiferi fossili delle Isole Mediterranee. — *Bolletino di Zoologia* 44: 201–211.

Barrier, E. 1979: Précisions sur l'édifice des nappes helléniques dans l'arc égéen oriental: le jalon de Kassos (Dodécanèse, Grèce). — *Comptes rendus de l'Académie des Sciences de Paris* D289: 453–456.

Barrier, E. 1984: *Geological map of Greece, 1/50 000, Kassos Island*. — Institue of Geology and Mineral Exploration, Athens.

Bate, D. M. A. 1903: Preliminary note on the discovery of a pygmy elephant in the Pleistocene of Cyprus. — *Proceedings of the Royal Society of London* 71: 498–500.

Bate, D. M. A. 1907: On elephant remains from Crete, with description of *Elephas creticus* sp. n. — *Proceedings of the Zoological Society of London* 77: 238–250.

Becker-Platen, J.-D. & Sickenberg, O. 1968: Die unterpleistozaenen Kiese von Eskisehir (Anatolien) und ihre Saugertierfauna. — *Mitteilungen des Geologischen Instituts der Technischen Hochschule in Hannover* 8: 7–20.

Boekschoten, G. J. & Sondaar, P. Y. 1972: On the fossil Mammalia of Cyprus. — *Proceedings of Koninklijke Nederlandse Akademie van Wetenschappen B* 75: 306–338.

Busk, G. 1867: Description of the remains of three extinct species of elephant, collected by Capt. Spratt, C.B.R.N., in the ossiferous cavern of Zebbug, in the island of Malta. — *Transactions of the Zoological Society of London* 6: 227–306.

Caloi, L., Kotsakis, T., Palombo, M. R. & Petronio. C. 1996: The Pleistocene dwarf mammoths of Mediterranean islands. — In: Shoshani, J. & Tassy, P. (eds.), *The Proboscidea, evolution and palaeoecology of elephants and their relatives*: 234–239. Oxford University Press, United Kingdom.

Case, T. J. 1978: A general explanation for insular body size trends in terrestrial vertebrates. — *Ecology* 59: 1–18.

Cayeux, L. 1908: Découverte de l'Elephas antiquus à l'île de Délos (Cyclades). — *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences* 147: 1089–1090.

Damuth, J. 1993: Cope's rule, the island rule and the scaling of mammalian population density. — *Nature* 365: 748–750.

Davies, P. & Lister, A. M. 2001: *Palaeoloxodon cypriotes*, the dwarf elephant of Cyprus: size and scaling comparisons with *P. falconeri* (Sicily–Malta) and mainland *P. antiquus*. — In: Cavarretta, G., Gioia, P., Mussi, M. & Palombo, M. R. (eds.), *La terra degli Elefanti, The World of Elephants*: 479–480. Consiglio Nazionale delle Ricerche, Roma.

De Vos, J. 2006: Notes about the parallels in evolution of the Pleistocene cervids from Greece (Crete, Kassos and Karpathos), Japan (the Ryukyu-islands) and Philippines (Masbate). — *Hellenic Journal of Geosciences* 41: 127–140.

Dermitzakis, M. D. & Sondaar, P. Y. 1979: The importance of fossil mammals in reconstructing paleogeography with special reference to the Pleistocene Aegean archipelago. — *Annales géologiques des Pays helléniques* 29: 808–840.

Dermitzakis, M. D. & De Vos, J. 1987: Faunal succession and the evolution of mammals in Crete durin the Pleistocene. — *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 173(3): 377–408.

Doukas, C. S. & Athanassiou, A. 2003: Review of the Pliocene and Pleistocene Proboscidea (Mammalia) from Greece. — *Deinsea* 9: 97–110.

Ferretti, M. P. 2008: The dwarf elephant *Palaeoloxodon mnaidriensis* from Puntali Cave, Carini (Sicily; late Middle Pleistocene): Anatomy, systematics and phylogenetic relationships. — *Quaternary International* 182: 90–108.

Foster, J. B. 1964: Evolution of mammals on islands. — *Nature* 202: 234–236.

Hadjisterkotis, E., Masala, B. & Reese, D. 2000: The origin and extinction of the large endemic Pleistocene mammals of Cyprus. — *Biogeographia Anatolia* 21: 593–606.

Herridge, V. L. & Lister, A. M. 2012: Extreme insular dwarfism evolved in a mammoth. — *Proceeding of the Royal Society B* 279: 3193–3200.

Inuzuka, N. & Takahashi, K. 2005: Discrimination between the genera *Palaeoloxodon* and *Elephas* and the independent taxonomical position of *Palaeoloxodon* (Mammalia: Proboscidea). — In: Baquedan, E. & Rubio, S. (eds.), *Miscelanea en homenaje a Emiliano Aguirre*, Zona Arqueológica 4: 234–244. Museo Arqueologico Regional, Madrid.

Kotsakis, T. 1980: Short account on the elephant remains of the Simonelli Cave. — *Quaderno Accademia Nazionale dei Lincei* 249: 115–120.

Kotsakis, T. 1990: Insular and non insular vertebrate fossil faunas in the eastern Mediterranean islands. — *Accademia Nazionale dei Lincei* 85: 289–334.

Kuss, S. E. 1965: Eine Pleistozäne Säugetierfauna der Insel Kreta. — *Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau* 55: 271–348.

Kuss, S. E. 1966: Beiträge zur Pleistozänen-Fauna der Insel Kreta. I. Die von D. Bate 1904 gesammelten Elephantenund Cerviden-Reste. — *Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau* 56: 169–181.

Kuss, S. E. 1967: Pleistozäne Säugetierfunde auf den ostmediterranen Inseln Kythera und Karpathos. — *Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau* 57: 207–216.

Kuss, S. E. 1969: Die erste pleistozäne Säugetierfauna der Insel Kasos (Griechenland). — *Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau* 59:

169–177.

Kuss, S. E. 1970: Abfolge und Alter der pleistozänen Saugetierfaunen der Insel Kreta. — *Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau* 60: 35–83.

Kuss, S. E. 1973: Die Pleistozänen Säugetierfaunen der ostmediterranen Inseln. — *Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau* 63: 49–71.

Kuss, S. E. 1975: Die pleistozänen Hirsche der ostmediterranen Inseln Kreta, Kassos, Karpatos und Rhodos (Griechenland). — *Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau* 65 (1-2): 25–79.

Lomolino, M. V. 1985: Body size of mammals on islands. The island rule re-examined. — *American Naturalist* 125: 310–316.

Lomolino, M. V. 2005: Body size evolution in insular vertebrates, generality of the island rule. — *Journal of Biogeography* 32: 1683–1699.

Lomolino, M. V., Sax, D. F., Palombo, M. R. & Van der Geer, A. 2012: Of mice and mammoths : evaluations of causal explanations for body size evolution in insular mammals. — *Journal of Biogeography* 39: 842–854.

Maglio, V. J. 1973: Origin and evolution of the Elephantidae. — *Transactions of the American Philosophical Society* 63: 1–149.

Markov G. N. 2007: *Elephas antiquus* (Mammalia: Proboscidea) in Bulgaria. — *Historia naturalis bulgarica* 18: 161–166.

Marra, A. C. 2005: Pleistocene mammals of Mediterranean islands. — *Quaternary International* 129: 5–14.

Masseti, M. 2009: Mammals of the Mediterranean islands: homogenization and the loss of biodiversity. — *Mammalia* 73: 169–202.

Masseti, M. 2012: *Atlas of terrestrial mammals of the Ionian and Aegean islands*. — Walter de Gruyter GmbH, Berlin/Boston.

Mayhew, D. F. 1977: The endemic Pleistocene murids of Crete. — *Proceedings of Koninklijke Nederlandse Akademie van Wetenschappen B* 80: 182–214.

Mayhew, D. F. 1996: The extinct murids of Crete. — In: Reese, D. S. (ed.), *Pleistocene and Holocene fauna of Crete and its first settlers*: 167–171. Monographs in World Archaeology 28, Prehistory Press, Madison, Wisconsin.

Meiri, S., Simberloff, D. & Dayan, T. 2006: The generality of the island rule re-examined. — *Journal of Biogeography* 33: 1571–1577.

Mitzopoulos, M. 1961: Uber einen Pleistozänen Zwergelefanten von der Insel Naxos (Kykladen). — *Praktika Akademia Athinon* 36: 332–340.

Mol, D., De Vos, J., van den Bergh, G. D. & Sondaar, P. Y. 1996: The taxonomy and ancestry of the fossil elephants of Crete: faunal turnover and a comparison with Proboscidean faunas of Indonesian islands. — In: Reese, D. S. (ed.), *Pleistocene and Holocene fauna of Crete and its first settlers*: 81–98. Monographs in World Archaeology 28, Prehistory Press, Madison, Wisconsin.

Mol, D., De Vos, J. & Van der Plicht, J. 2007: The presence and extinction of *Elephas antiquus* Falconer and Cautley, 1847, in Europe. — *Quaternary International* 169–170: 149–153.

Palombo, M. R. 2001: Endemic elephants of the Mediterranean islands: knowledge, problems and perspectives. — In: Cavarretta, G., Gioia, P., Mussi, M. & Palombo, M. R. (eds.), *La terra degli Elefanti, The World of Elephants*: 486–491. Consiglio Nazionale delle Ricerche, Roma.

Palombo, M. R. 2004: Dwarfing in insular mammals: the endemic elephants of Mediterranean islands. — In: Baquedan, E. & Rubio, S. (eds.), *Miscelanea en homenaje a Emiliano Aguirre*, Zona Arqueológica 4: 354–371. Museo Arqueologico Regional, Madrid.

Palombo, M. R. 2007: How can endemic proboscideans help us understand the ''island rule''? A case study of Mediterranean islands. — *Quaternary International* 169–170: 105–124.

Palombo, M. R. 2009: Body size structure of Pleistocene mammalian communities: what support is there for the "island rule"? — *Integrative Zoology* 4: 341–356.

Palombo, M. R. & Ferretti, M. P. 2005: Elephant fossil record from Italy: knowledge, and perspectives. — *Quaternary International* 126–128: 107–136.

Piper, D. J. W. & Perissoratis, C. 2003: Quaternary neotectonics of the South Aegean arc. — *Marine Geology* 198: 259–288.

Pohlig, H. 1893: Eine Elephantenhole Siciliens und der erste Nachweis des Cranial-domes von *Elephas antiquus*. — *Abhandlungen Bayerische Akademie der Wissenschaften* 18: 73–100.

Poulakakis, N., Mylonas, M., Lymberakis, P. & Fassoulas, C. 2002a: Origin and taxonomy of the fossil elephants of the island of Crete (Greece): problems and perspectives. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 186: 163–183.

Poulakakis, N., Theodorou, G., Zouros, E. & Mylonas, M. 2002b: Molecular phylogeny of the extinct Pleistocene dwarf elephant *Palaeoloxodon antiquus falconeri* from Tilos Island, Dodekanisa, Greece. — *Journal of Molecular Evolution* 55: 364–374.

Poulakakis, N., Parmakelis, A., Lymberakis, P., Mylonas, M., Zouros, E., Reese, D. S., Glaberman, S. & Caccone, A. 2006: Ancient DNA forces reconsidération of evolutionary history of Mediterranean pigmy elephantids. — *Biology Letters* 2: 451–454.

Raia, P. & Meiri, S. 2006: The island rule in large mammals: paleontology meets ecology. — *Evolution* 60: 1731–1742.

Raia, P. & Meiri, S. 2011: The tempo and mode of evolution: body sizes of island mammals. — *Evolution* 65: 1927–1934.

Reese, D. S., Belluomini, G. & Ikeya, M. 1996: Absolute dates for the Pleistocene fauna of Crete. — In: Reese, D. S. (ed.), *Pleistocene and Holocene fauna of Crete and its first settlers*: 47–51. Monographs in World Archaeology 28, Prehistory Press, Madison, Wisconsin.

Simmons, A. H. 1999: *Faunal extinction in an island society: Pygmy hippopotamus hunters of Cyprus*. — Kluwer Academic/Plenum Publishers, New York.

Simonelli, V. 1908: Mammiferi quaternari dell 'isola di Candia. Memoria seconda. — *Memorie della Royale*

Accademia delle Scienze dell'Instituto di Bologna 6(5): 103–111.

Sondaar, P. Y. 1971: Paleozoogeography of the Pleistocene mammals from the Aegean. — *Opera Botanica* 30: 65–69.

Sondaar, P. Y. 1977: Insularity and its effects on mammal evolution. — In: Hecht, M. K., Goody, P. C. & Hecht, B. M. (eds.), *Major patterns of vertebrate evolution*: 671–707. Plenum Press, New York.

Sondaar, P. Y. & Boekschoten, G. J. 1967: Quaternary mammals in the South Aegean island arc; with notes on other fossil mammals from coastal regions of the Mediterranean. — *Proceedings of Koninklijke Nederlandse Akademie van Wetenschappen B* 70: 556–576.

Sondaar, P. Y. & Van der Geer, A. 2005: Evolution and extinction of Plio-Pleistocene island ungulates. — *Quaternaire, International Journal of the French Quaternary Association* hors-série 2005, 2: 241–256.

Sondaar, P. Y., Dermitzakis, M. D. & De Vos, J. 1996: The paleogeography and faunal evolution of the land mammals of Crete. — In: Reese, D. S. (ed.), *Pleistocene and Holocene fauna of Crete and its first settlers*: 61–65. Monographs in World Archaeology 28, Prehistory Press, Madison, Wisconsin.

Stuart, A. J. 2005: The extinction of woolly mammoth (*Mammuthus primigenius*) and straight-tusked elephant (*Palaeoloxodon antiquus*) in Europe. — *Quaternary International* 126–128: 171–177.

Stuart, A. J. & Lister, A. 2012: Extinction chronology of the woolly rhinoceros *Coelodonta antiquitatis* in the context of late Quaternary faunal extinctions in northern Eurasia. — *Quaternary Science Reviews* 51: 1–17.

Symeonidis, N. K. 1972: Die entdeckung von Zwergelefanten inder Hohle "Charkadio" auf der insel Tilos (Dodekanes, Griechenland). — *Annales géologiques des Pays helléniques* 24: 445–461.

Symeonidis, N. & Theodorou, G. 1982: [New finds of fossil elephants on Cretan islands]. — *Annales Géologiques des Pays Helléniques* 31: 113–129. [In Greek].

Symeonidis, N., Bachmayer, F. & Zapfe, H. 1974: Entdeckung von Zwergelefanten auf der Insel Rhodos (Ausgrabungen 1973). — *Annalen des Naturhistorischen Museums in Wien* 78: 193–202.

Symeonidis, N. K., Theodorou, G. E. & Giannopoulos, B. 2000: [The new species *Elephas chaniensis* from the submerged Pleistocene deposits of Vamos Cave at Chania, Crete]. — *Bulletin de la Société Spéléologique de Grèce* 22: 95–108. [In Greek].

Symeonidis, N. K., Theodorou, G. E. & Giannopoulos, B. 2001: New data on *Elephas chaniensis* (Vamos cave, Chania, Crete). — In: Cavarretta, G., Gioia, P., Mussi, M. & Palombo, M. R. (eds.), *La terra degli Elefanti, The World of Elephants*: 510–513. Consiglio Nazionale delle Ricerche, Roma.

Thaler, L. 1973: Nanisme et gigantisme insulaire. — *La Recherche* 4: 741–750.

Theodorou, G. 1983: *The dwarf elephants of the Charkadio cave on the island of Tilos (Dodekanese, Greece)*. — Ph.D. thesis, Athens University.

Theodorou, G. E., Symeonides, N. & Stathopoulou, E. 2007: *Elephas tiliensis* n. sp. from Tilos Island (Dodecanese, Greece). — *Hellenic Journal of Geosciences* 42: 19–32.

Tsoukala, E. & Lister, A. 1998: Remains of strait-tusked elephant, *Elephas (Palaeoloxodon) antiquus* Falc. & Caut. (1847) ESR dated oxygen isotope Stage 6 from Grevena (W. Macedonia, Greece). — *Bollettino della Società Paleontologica Italiana* 37: 117–139.

Tsoukala, E., Mol, D., Pappa, S., Vlachos, E., van Logchem, W., Vaxevanopoulos, M. & Reumer, J. 2011: *Elephas antiquus* in Greece: new finds and a reappraisal of older material (Mammalia, Proboscidea, Elephantidae). — *Quaternary International* 245: 339–349.

Van der Geer, A., Lyras, G., De Vos, J. & Dermitzakis, M. 2010: *Evolution of island mammals — adaptation and extinction of placental mammals on islands*. — Wiley-Blackwell, Oxford.

Van Valen, L. M. 1973: Pattern and the balance of nature. — *Evolutionary Theory* 1: 31–49.

Vaufrey, R. 1929: Les Eléphants nains des îles méditerranéennes et la question des isthmes Pléistocènes. — *Archives de l'Institut de Paléontologie Humaine* 6: 1–220.