PALAEO 3

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A dwarf elephant and a rock mouse on Naxos (Cyclades, Greece) with a revision of the palaeozoogeography of the Cycladic Islands (Greece) during the Pleistocene

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ABSTRACT

During the Late Pleistocene, Naxos and adjacent areas, including Delos and Paros, constituted a mega-island, here referred to as palaeo-Cyclades. The extensive low-lying plains with lakes and rivers provided a suitable habitat for elephants. Due to long-term isolation from the mainland and mainland populations, these elephants evolved miniature size. The species found on Naxos had a body size of about ten percent of that of the mainland ancestor, *Palaeoloxodon antiquus*. During the glacial periods of the Late Pleistocene, *P. antiquus* may have migrated eastwards and southwards in search of better conditions and reached the islands. The dwarf species of the various Southern Aegean islands (e.g. Crete, Tilos, Rhodos, palaeo-Cyclades) are each the result of independent colonisation events. The very small size of the Naxos species respective to the dwarf elephants from Crete is explained as due to the lack of competitors. The only other elements of the contemporaneous fauna were a rock mouse (*Apodemus* cf. *mystacinus*) and a shrew (*Crocidura* sp.). Submergence of the area, climate change, volcanism, hunting by humans or a combination of these factors during the terminal Pleistocene may have caused the extinction of this endemic fauna.

1. Introduction

Dwarf elephants were relatively common elements in insular faunas worldwide in the past. The diminutive size of these fossil insular proboscideans started to attract the attention of naturalists in the 19th century (e.g. Sciná, 1831; Leith Adams, 1863; Spratt, 1867). This interest continued throughout the 20th century and is still a significant topic of scientific research. There are numerous recent studies on this subject (e.g. Van den Bergh, 1999; Palombo, 2007; Ferretti, 2008; Herridge, 2010; Herridge and Lister, 2012; Liscaljet, 2012), which re-examine old specimens, and in some cases describe recently collected ones, and put their analyses under the perspective provided by the latest developments in ecology, biogeography and palaeogeography.

There is, however, a set of elephant fossils, known to science since several decades that has been ignored in these works. They are the fossils found on the Cyclades (Southern Aegean Sea, Greece), a group of islands (archipelago) that have recently become disconnected from each other and the mainland by rising sea level (continental shelf islands sensu Whittaker, 1998). The Cyclades, located between the Greek

peninsula in the west and the coast of Asia Minor in the east, consists mainly of metamorphic and igneous rocks (Hejl et al., 2002). The sedimentary deposits, including those in caves, are limited. Therefore, on the contrary to the overwhelming amount of fossils known from other Mediterranean islands with endemic mammals, the fossils from the Cycladic archipelago are limited to a few sporadic findings (see Section 2) and this is the main reason why they escaped attention. Originally, the dwarf elephant of Naxos was attributed to *Elephas antiquus melitensis* (Mitzopoulos, 1961), the species from Late Pleistocene Malta. This original nomenclature is invalid because it can by no means be conspecific with a dwarf elephant that is endemic to Sicily at the other side of the Mediterranean. Exchange of genetic material between the Siculo-Maltese and Cycladic populations could not have taken place. The consensus view is that dwarf elephants are restricted in distribution with each (palaeo-) island harbouring its own endemic species (Azzaroli, 1982; Herridge, 2010). That said, Naxos and adjacent parts cannot have shared the same species with any other Mediterranean island.

In addition to the description and taxonomy of the mammal fauna, new data are here put in a broader biogeographic context. Despite the scantiness of the material, a re-appreciation within the latest developments in palaeogeography and palaeobiogeography is most needed. Today all endemic mammals are extinct from the Cyclades. The islands however, continue to host an interesting fauna of endemic reptiles and invertebrates (Wettstein, 1953; Sfenthourakis and Legakis, 2001). The

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effect of the original palaeogeography continues to give a strong signal to the remaining composition of Cycladic fauna (e.g. Sfenthourakis, 1996; Fattorini, 2002; Hausdorf and Hennig, 2005) and flora (e.g. Bittkau and Comes, 2005). The now extinct mammalian fauna is a lost component of the Cycladic ecosystem. Therefore, any contribution towards a better understanding of these missing elements is most valuable.

The scope of this contribution is to describe in detail the Late Pleistocene mammals from Naxos, to address their taxonomy and to infer palaeobiogeographical and palaeoecological implications.

2. History of fossil findings from the Cyclades

The earliest finding is from Delos, from where Cayeux (1908) reported the discovery of an isolated incomplete third upper molar found near the Apollo temple in a deposit of the Inopos River. Cayeux (1908) referred the specimen tentatively to *Elephas antiquus* Falconer and Cautley, 1847, although he remarked that the interplate distance is too large for this species. Vaufrey (1929: 126) lists the specimen under *E. antiquus* race *mnaidriensis* based on size but depicts it (Vaufrey, 1929: Fig. 38) as *E. antiquus*. The second fossil was found on Naxos in sediments of the Trypiti River. The specimen, an upper jaw of a dwarf elephant, was described by Mitzopoulos (1961) as *Palaeoloxodon antiquus melitensis*. A tip of an elephant tusk was found exposed in an ancient artificial hollow on a valley slope in northwest Kythnos (Honea, 1975). The larger portion of the tusk was still in situ at the base of a 4 m tick deposit of cemented breccia associated with fossil bones and quartz tools at the time of the report. The present situation is unknown. The tusk's dating (9160 ± 240 C14 yrs BP) is likely much underestimated as the specimen was air-exposed and subjected to regular wetting due to seasonal rise in ground-water level (Honea, 1975). The tusk itself was never described and its size therefore unknown. The rest of the fossil findings from the Cyclades are merely anecdotal reports without proper description or depiction and for which in some cases any evidence is missing. These are unspecified elephant fossils from Paros (*E. antiquus* in Georgalas, 1929), Milos (dwarf elephant in Papp, 1953) and Seriphos (dwarf elephant in Papp, 1953; *Elephas (Palaeoloxodon)* cf. *melitensis* in Kuss, 1973). In the 1970s also a large *Apodemus* was found on Naxos near or at the elephant locality (Sondaar, 1971), later referred to as *Apodemus* cf. *mystacinus* (Dermitzakis and Sondaar, 1978). The same sample also contained insectivore remains (labelled as *Crocidura* sp.), but these were not reported in any publication. Kuss (1973) further mentioned the presence of endemic deer (resembling *Cervus* (= *Candiacervus*) *cretensis*) and some micromammals from Amorgos. The Cycladic findings were cited as such in faunal lists and overview papers (e.g. Dermitzakis and Sondaar, 1978; Sondaar and Dermitzakis, 1982; Alcover et al., 1998; Doukas and Athanassiou, 2003), without further examination of any of these fossils or their context.

3. Materials and methods

3.1. Fossil material

The mammalian fossils described here are a complete elephant maxilla (left and right side; AMPG), a number of murid and insectivore teeth and fragmentary mandibles (GIU). All material originates from Naxos (Cyclades, Greece). The specimen from Delos was not available to us and the depiction of Vaufrey (1929: 131) is used instead. The whereabouts of the Paros fossil(s) is uncertain as they were only briefly mentioned without institutional information in an article on extinct elephants in a Greek encyclopaedia. Subsequent authors only quoted this reference without tracking the fossil or its history. Equally uncertain and without any formal description or institutional information are the fossils from the remainder of the Cycladic islands (Milos, Kythnos, Serifos, Amorgos). However, these specimens are less relevant to the present discussion as these islands have an independent history (see Section 3.3).

The elephant maxilla described here was found in the Trypiti River, south of Cape Moutsouna (eastern Naxos), about 150 m from the river mouth (Fig. 2). The murid and insectivore remains also originate from the Pleistocene deposits exposed in a dry river in the same area. Absolute datings are not available.
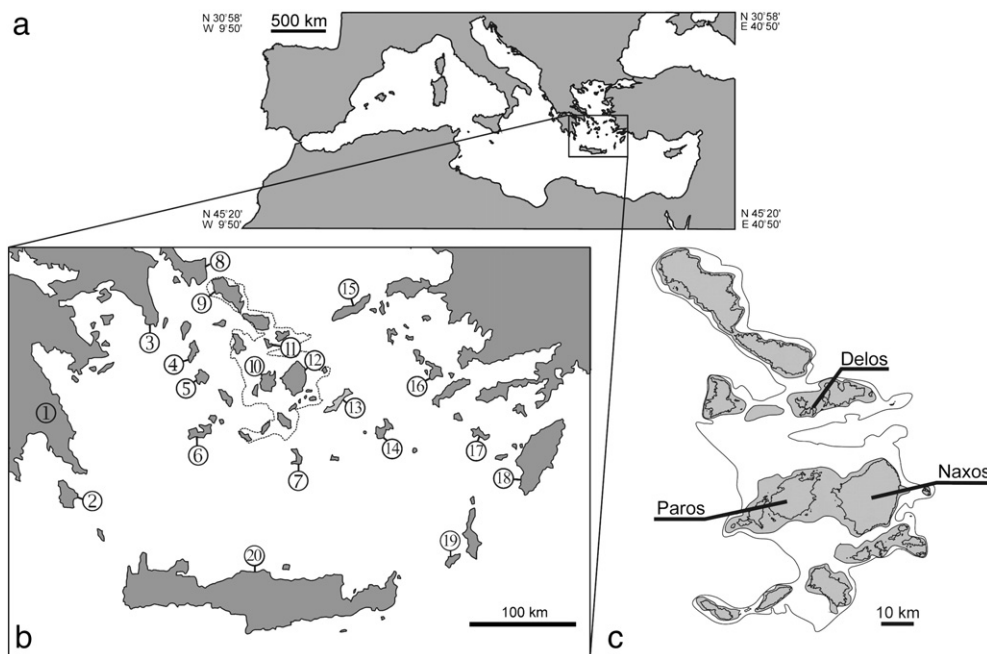

Fig. 1. Map of the Mediterranean (a) with Southern Greece (b) indicating the islands mentioned in the text. The dashed line is the 100-m isobath and approximately indicates the extent of the Cyclades Plateau. (c) Map of the central Cyclades corresponding to the 100-m isobath as given in (b). The grey areas correspond to the 50-m isobath. During periods of 50 m sea-level drop, Naxos clusters together with Paros. At periods of more extensive sea-level drops (e.g. 100 m), a single mega-island is formed. 1: Peloponnesos; 2: Kythera; 3: Sounio (province of Attika); 4: Kythnos; 5: Serifos; 6: Milos; 7: Santorini (Thera); 8: Euboea (Evia); 9: Andros; 10: Paros; 11: Delos; 12: Naxos; 13: Amorgos; 14: Astypalaia; 15: Ikaria; 16: Kalymnos; 17: Tilos; 18: Rhodos; 19: Kasos; 20: Crete.
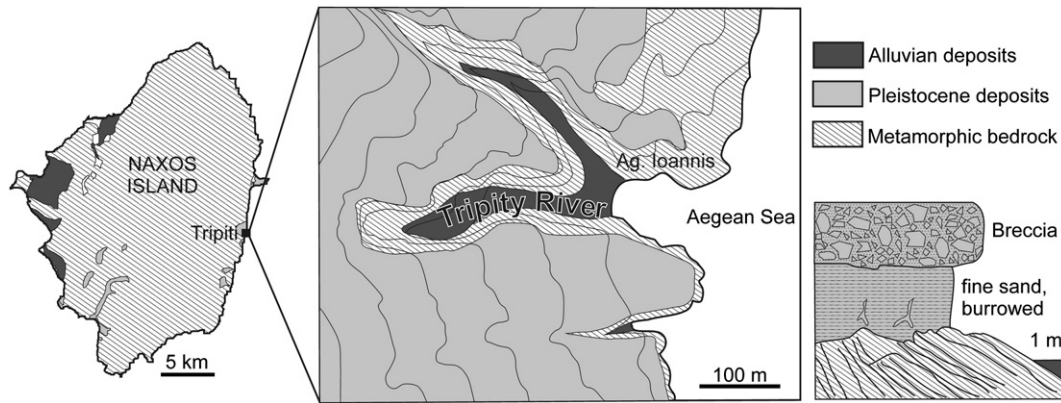
Fig. 2. Location of the Trypiti River and profile of the Pleistocene deposits near the fossil site. The thickness of the Pleistocene deposits ranges between 0.5 m and 5 m (Jansen, 1973). The outcrop consists of a reddish paleosol (Laterite), covered by an angular conglomerate, probably of riverine origin.

3.2. Comparative material

The elephant material from Naxos is compared with the following dwarf species: *Palaeoloxodon creutzburgi* (Crete, Late Pleistocene), *Palaeoloxodon tiliensis* (Tilos, Late Pleistocene), *P.* sp. (Rhodos, Pleistocene, probably Late Pleistocene in Symeonidis et al., 1974), *Palaeoloxodon* 'mnaidriensis' (San Teodoro, Sicily, Late Pleistocene), *Palaeoloxodon* 'melitensis' (Luparello, Sicily, Middle Pleistocene), *Palaeoloxodon falconeri* (Spinagallo, Sicily, Middle Pleistocene), and *Palaeoloxodon cypriotes* (Imbohary, Cyprus, Pleistocene). All are represented by dental material except for the species from Rhodos which is known by tarsal bones only.

3.3. Palaeogeographic setting

During periods of low sea level of the Pleistocene substantial parts of the now submerged Cycladic Plateau were exposed forming clusters of larger islands or, at periods of extensive sea-level drop, a single mega-island (Lambeck, 1996; Kapsimalis et al., 2009; Lykousis, 2009; see Sections 6.2 and 6.3 for detailed information on the palaeogeography) (Fig. 1). During such periods, Naxos was part of this large island here referred to as palaeo-Cyclades. The current islands Paros and Delos were part of the palaeo-Cyclades as well. The smaller Cycladic islands Milos, Kythnos, Serifos and Amorgos were not connected to the palaeo-Cyclades and may have formed islands on their own, harbouring their own faunas. These islands will not be further considered here as they bear no direct relation to the much larger palaeo-Cyclades of which Naxos forms an important part.

3.4. Size changes

Liscaljet (2012) recently divided diminutive proboscidean species, including those from the Aegean islands, into two size classes, based on shoulder height. Species with a shoulder height between 90 and 200 cm were listed as pygmy species, those with a shoulder height between 200 and 250 cm as dwarfed species based on the normal height of 250–350 cm for living elephants. However, the height of the endemic form depends not only on the degree of body size reduction,

Table 1

Linear measurements of *Palaeoloxodon* from Naxos (AMPG 999) in mm. For indices and ratios, see Table 2.

	Length	Width	Crown height
Left molar	122	42.7	102.6
Right molar	128	47.6	93.6
Average	125	45.2	98.1

but also on the ancestral height (which may also have exceeded 350 cm as is the case with *Palaeoloxodon antiquus*). Two similar-sized dwarf species may have followed (very) different trends of body size decrease. Furthermore, this approach splits insular proboscideans into two artificial groups. Instead, here size index Si is used, defined as estimated body mass of individuals from insular population divided by the estimated body mass of individuals of the mainland or ancestral form (see Lomolino et al., 2012, 2013). Body mass is based on the average of several individuals and calculated based on linear measurements of postcranial material where possible; if no postcranial material was available, molar dimension was used to estimate body mass (for details see caption to Table 3). The advantage of this approach is that in this way insular taxa can be compared between different families and even orders.

3.5. Measurements

Metric characters, taken from Herridge and Lister (2012) are as follows: molar width (W), molar length (L), molar height (H), enamel thickness (ET), plate count (PC), and hypsodonty index (HI: crown height/width × 100). Metric characters that differ from Herridge and Lister (2012) are lamellar frequency (LF), corresponding to DLI

Table 2

Indices and ratios of third molars of Mediterranean dwarf *Palaeoloxodon*, compared to their ancestor, *Palaeoloxodon antiquus*. Notes: ET is given in mm. Data for Naxos are from this study. For AMPG 999 the average of the two molars is given. 1) Mean values from Herridge and Lister (2012); *P. cypriotes* from the type-locality Imbohary, Cyprus, n = 4; *P. falconeri* from Luparello and Spinagallo Caves, Sicily, n = 17; *P. antiquus* from various UK and German sites, ca 500–120 ka; n = 26. 2) Herridge, 2010. Weighted mean for *P. falconeri* combined from Luparello and Spinagallo Caves. Spinagallo: PC (n = 4) 13, LF (n = 8) 9.7, and ET (n = 9) 1.7, for HI we used W (n = 8) 30.2 and CH (n = 5) 67.5 mm. Luparello: PC (n = 6) 11.8, LF (n = 11) 11.1, and ET (n = 10) 1.4, for HI we used W (n = 10) 31.5 and CH (n = 9) 77. *P. creutzburgi* (n = 2) from eastern Crete. *P. tiliensis* (n = 1) from Charkadio Cave. 3) Mean values from Herridge (2010), based on the same sample as in Herridge and Lister (2012); n = 14 for PC, n = 26 for LF, n = 21 for ET, and n = 11 for HI. 4) Data from Theodorou (1983) for T8209 (left; the only complete upper third molar): L 124 mm, W 47 mm, H 86 mm, ET 2.5–2.8 mm, and DLI ~9.5 Data from Vaufrey (1929). The specimen is incomplete (anterior part missing).

	PC	LF	HI	ET
AMPG 999 (upper)	10.5	7.1	217	2.5
P. cypriotes[1] (lower)	11.5	9.6	180	1.2
P. cypriotes[2] (upper)	11	11.8	196	1.3
P. creutzburgi[2] (lower)	–	6.8	–	1.7
P. falconeri[1] (lower)	12.5	9.4	197	1.4
P. falconeri[2] (upper)	12.3	10.5	237	1.5
P. antiquus[1] (lower)	18.5	4.7	221	2.0
P. antiquus[3] (upper)	18.3	6.2	210	1.9
P. tiliensis[2] (upper)	–	8.1	–	1.6
P. tiliensis[4] (upper)	11.5	c. 9	–	2.7
P. sp.[5] (Delos; upper)	>8	c. 5	–	–

Table 3

Body mass indices (Si) of Mediterranean dwarf elephant species with *P. antiquus* as ancestor. Most body mass estimations were based on postcranial elements and were calculated using the equations of Christiansen (2004). Three indices were based on dental elements (here indicated with an asterisk; for details see relevant species). *P. cypriotes*: no complete long bone belonging to this species is known. Based on the size and morphology of available partial femurs (Davies and Lister, 2001 and a partial femur in NBC) and the linear dimensions of its teeth we suggest that *P. cypriotes* had approximately the same size as *P. falconeri*. *P. leonardi*: based on its humerus length (89 cm), we estimate the body mass of the *P. leonardi* as 4329 kg. Rhodos *P.* sp.: no complete long bone is known. The mediolateral width of the distal diaphysis of the femur is 17 cm (Symeonidis et al., 1974). The left femur of the mounted *P.* 'mnaidriensis' in MPG has a distal diaphysis of 17 cm width and a total length of 76 cm. Based on these data we estimate a body mass of 1500 kg for the Rhodos elephant. Delos *P.* sp.: this elephant is known only from a partial M3. Its size is comparable to that of *P.* 'mnaidriensis' from Puntali, based on which we suggest that it had approximately the same body mass as that species. Naxos *P.* sp. nov: we assumed a simple geometric relationship between tooth length and body size. The index is calculated as the ratio of the cubed linear dimensions, following Lomolino (2005). Although this method likely overestimates body size of large-sized insular forms, it appears reliable in small-sized phylogenetic dwarfs (see for an extensive discussion on teeth and body size reduction of phylogenetic dwarfs in Lister (1996). Note: * = body size estimated on dental elements.

Species	Si	Palaeo-island	Source
Palaeoloxodon creutzburgi	0.38	Crete	Lomolino et al, (2013)
Palaeoloxodon 'cypriotes'	0.07	Cyprus	Lomolino et al. (2013)
Palaeoloxodon cypriotes	~0.02*	Cyprus	This study
Palaeoloxodon falconeri	0.02	Sicily	Lomolino et al. (2013)
Palaeoloxodon leonardi	0.54	Sicily	This study
Palaeoloxodon 'mnaidriensis'	0.17	Sicily	Lomolino et al. (2013)
Palaeoloxodon sp.	0.19	Rhodos	This study
Palaeoloxodon sp.	~0.17*	Delos	This study
Palaeoloxodon sp. nov.	~0.08*	Naxos	This study
Palaeoloxodon tiliensis	0.09	Tilos	Lomolino et al. (2013)

(Dezimeter–Lamellen-Interval, or number of plates per 10 cm) as used in German literature.

3.6. Institutional abbreviations

AMPG Museum of Palaeontology and Geology of the University of Athens, collection Vertebrates; IvAU Faculty of Geosciences, Department of Earth Sciences, Utrecht University, Utrecht, The Netherlands; GPM Gemellaro Museum, Palermo, Sicily, Italy; IPH Institut de Paléontologie Humaine, Paris, France. NBC: Naturalis Biodiversity Center, Leiden, The Netherlands.

4. Results

4.1. Identification

First of all, the elephant maxilla AMPG 999 from Naxos includes third molars and not second molars as Mitzopoulos (1961) assumed, based among others on the posterior tapering of both the crown and the root. The bone Mitzopoulos (1961) mistook for an alveolar rim for the subsequent molar in development likely is the palatum. Mitzopoulos (1961) though correctly noticed that the distal end of both molars does not show any pressure facet caused by a subsequent molar. The wrong diagnosis of the molar automatically influences his interpretation of relative size because third molars are always larger than second molars in elephants.

4.2. Genus attribution

4.2.1. Palaeoloxodon versus Elephas

In the literature, straight-tusked elephants are placed either in the genus *Elephas* or in the genus *Palaeoloxodon*. The cladistic analysis of Todd (2010) gives support to two separate genera within the *Elephas* group, an *Elephas* group including the living Asian elephant, and a *Palaeoloxodon* group. *Palaeoloxodon* was earlier shown to be a monophyletic clade on its own (Shoshani et al., 2005; Ferretti, 2008), which

is confirmed by morphological differences between the two genera (e.g. Inuzuka, 1977a, b; Shoshani and Marchant, 2001; Shoshani et al., 2005). In this contribution, Inuzuka and Takahashi (2004) and Shoshani and Tassy (2005) are followed in which *Palaeoloxodon* is treated as distinct from *Elephas*. The dwarf elephants (not the mammoths) of the Mediterranean may belong to either group in the analysis of Todd (2010), implying two separate dwarfing events. Until further analysis, *Palaeoloxodon antiquus* is considered ancestral to all Mediterranean dwarf elephants, with the exception of *Mammuthus creticus* (=*Elephas creticus* in Bate, 1905) and *Mammuthus lamarmorai* (=*Elephas lamarmorae* in Major, 1883), based on morphological grounds (for discussion and characters, see supporting information to Herridge and Lister, 2012). This new analysis should take secondarily derived characters and changes due to allometry into consideration (see for a discussion on convergent morphologies in unrelated insular taxa Van der Geer, 2014); in fact, this applies to the type species *Palaeoloxodon naumanni* as well, which is an insular species of Japan.

4.2.2. Mediterranean Palaeoloxodon

The conspecifity between *Palaeoloxodon* 'melitensis' from Luparello (Sicily) and from its type locality Zebbug (Malta) is considered here as unproven, and the species name is therefore placed between brackets for the Sicilian material. The reasoning is that in Luparello cave the layer with *P.* 'melitensis' underlies that with *Palaeoloxodon falconeri* (Imbesi, 1956), and could thus have been ancestral to the smallest species in this cave (Palombo, 2001; Herridge, 2010). The species name of the larger-sized dwarf species of Sicily is here put between quotes as well, as there is no proof that is conspecific with *Palaeoloxodon mnaidriensis* from the type locality Mnajdra Gap on Malta (Herridge, 2010; van der Geer et al., 2010). A revision of the Sicilian *P.* 'mnaidriensis' is in preparation (pers. comm. Victoria Herridge). To complicate matters even further, the difference in size between *P. mnaidriensis* and *P. melitensis* at one side and between *P. melitensis* and *P. falconeri* at the other side (all from Malta) may not be sufficient to warrant specific status of the middle-sized elephant, which would imply that either *P. melitensis* is a junior synonym of *P. falconeri* or *P. mnaidriensis* is a junior synonym of *P. melitensis*: *E. falconeri*, *E. melitensis* and *E. mnaidriensis* were described by Busk (1867), Falconer (1868), and Leith Adams (1870) respectively. A revision of the Sicilian and Maltese dwarf elephants is, however, beyond the scope of this research and therefore the current taxonomy is kept consistent with the literature.

Boekschoten and Sondaar (1972) and Davies and Lister (2001) mentioned the presence of two pygmy elephants in Cyprus: one is *Palaeoloxodon cypriotes* and the second is a larger, still unnamed, form. This form, known from the locality Xylophagou (Iliopoulos et al., 2011), might represent a second invasion or an earlier anagenenetic form of *P. cypriotes*. Pending a detailed study and revision of the Cypriot material, the larger form is referred here as *P.* 'cypriotes'.

4.2.3. The Naxos dwarf elephant

Possible candidate taxa for the Naxos specimen are *Palaeoloxodon*, *Elephas*, *Mammuthus* and *Loxodonta*. A taxonomically informative character in elephantids is the early-wear patterns of the enamel loop visible on the occlusal surface. *Elephas*, although present during the Middle and Late Pleistocene in the Levant (Lister et al., 2013) is no option because the initial wear pattern progresses from a row of small rings at the apex to three subequal ellipsoid forms (Lister et al., 2013), whereas this pattern in the Naxos molar consists of an elongated central ellipsoid flanked by two subcircular rings at the lateral and medial sides. This pattern is known as the typical *Palaeoloxodon* early wear pattern (Herridge and Lister, 2012). In *Mammuthus*, a sub-circular mesial ring is present between two elongated ellipsoids (more or less the opposite of *Palaeoloxodon*). The mesial expansion is either absent or in the form of rounded loops whereas it is triangular (pointed) in *Palaeoloxodon* and the Naxos molars. In addition, *Loxodonta* has the typical loxodont lozenge-shaped lamellar sinus, which is lacking in the Naxos molars.

Mammuthus further lacks the longitudinally grooved aspect of the ends of the enamel loops in lateral view as seen in the Naxos molar, *Palaeoloxodon* and *Elephas* which is considered an expression of strong enamel folding (Lister et al., 2013). The molars of *Mammuthus meridionalis* are low-crowned (HI = 115–175 in Van Essen, 2003), whereas the Naxos molars are high-crowned (HI = 217). Finally, in *Elephas* the enamel of the plates tends to be more intensively folded than in *Palaeoloxodon*. In sum, the occlusal wear pattern of the Naxos molars most closely resembles that seen in *Palaeoloxodon*.

Palaeoloxodon antiquus was the species present during the Late Pleistocene in Greece (Dermitzakis and Theodorou, 1980; Athanassiou, 2000; Doukas and Athanassiou, 2003) and is as such the most likely ancestor. The species was either already widespread during the Middle Pleistocene (Athanassiou, 2000), or occurred for the first time in Greece at Ambelia–Grevena around the end of the late Middle Pleistocene (Tsoukala et al., 2011).

4.3. Comparison with other insular Palaeoloxodon species

The Naxos elephant is readily distinguished from the mainland species by the small size of its molars (Figs. 3 and 4). The Naxos molars are just slightly larger than those of *Palaeoloxodon cypriotes* and *Palaeoloxodon falconeri* and all three are a fraction of the size of their respective ancestors. The Cretan dwarf species is the largest. The size of the Delos specimen relative to the Tilos species is not entirely certain because of the present unknown whereabouts of the fossil molar from Delos. However, based on the width of 64 mm and a length of at least 155 mm, the Delos specimen would plot within the 'mnaidriensis' group. The Rhodos species is not known by dental remains.

The lamellar frequency of the Naxos specimen is comparable to that of *Palaeoloxodon falconeri*, based on data given by Herridge and Lister (2012, Fig. 2). However, the number of lamellae in a 10 cm length of tooth (LF) is inversely related to crown width in mainland elephants (Lister et al., 2013) and was shown to be of limited taxonomic value in dwarf *Palaeoloxodon* taxa (Herridge and Lister, 2012; see also Table 2). This also applies to PC. Scoring this type of variable is thus nothing more than another approach to size. These data will therefore be lacking
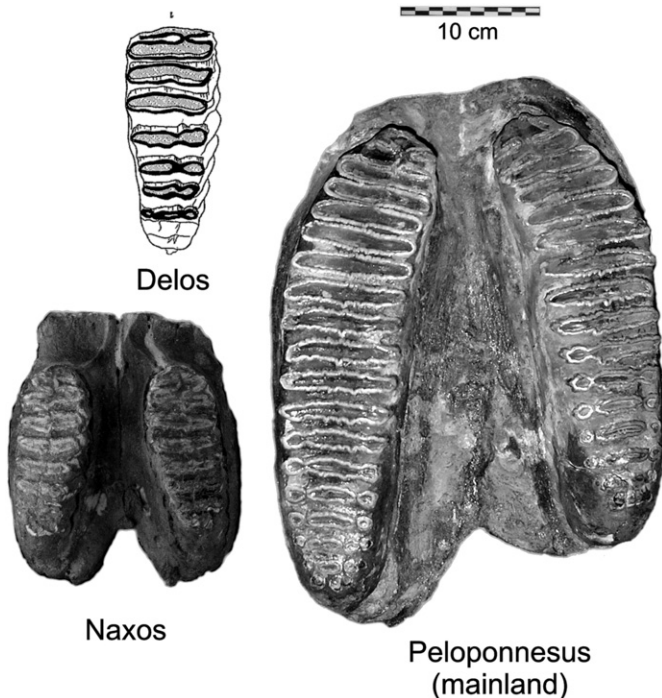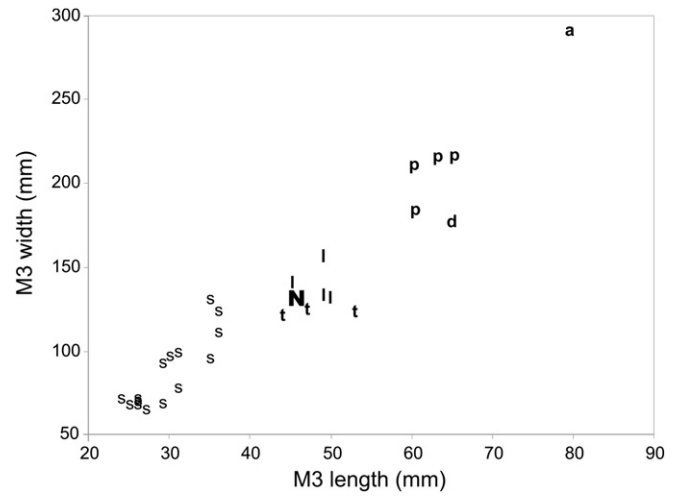

Fig. 4. Sizes of upper third molars (M3) of insular dwarf elephants. The length of M3, as depicted here, depends on the number of lamellae of each molar. As a consequence, the molars that had lost some of their anterior lamellae appear to be shorter and relatively broader than they should. This however, does not considerably affect the overall look of the diagram, as it can still provide a very good indication of the size of each species. Symbols: s: *P. falconeri* from Spinagalo, Sicily; l: *P. 'melitensis'* from Luparello, Sicily; N: *P. lomolinoi* nov. sp.; t: *P. tiliensis* from Tilos; p: *P. 'mnaidriensis'* from Puntali (own data from GPM); d: *P. mnaidriensis* from Ghar Dalam; a: mainland *P. antiquus*. Data sources: Ambrosetti (1968) for *P. falconeri*, Theodorou (1983) for *P. tiliensis*, Herridge (2010) for *P. mnaidriensis* (Ghar Dalam) and *P. antiquus*. Own data: *P. 'melitensis'*, Luparello (IPH), *P. 'mnaidriensis'*, Puntali (GPM).

for the here considered dwarf *Palaeoloxodon* taxa in scatter plots with molar size and body size index. The only taxonomically informative characters are limited to body size and perhaps hypsodonty index and enamel thickness. Enamel thickness seems to be increased in the Aegean taxa instead of decreased as in the Siculo-Maltese taxa.

When the Si of the Naxos specimen is compared to that of other Mediterranean dwarf elephants of the genus *Palaeoloxodon* (Table 3), the material from Naxos differs from *Palaeoloxodon creutzburgi*, *Palaeoloxodon 'mnaidriensis'* and *P.* sp. from Delos in its greater size reduction (= lower Si). The Naxos specimen further differs from *Palaeoloxodon cypriotes* and *Palaeoloxodon falconeri* (Spinagallo, Sicily) in its lesser size reduction (= higher Si). It is comparable in size reduction to *Palaeoloxodon tiliensis* and the larger individuals of *P. falconeri* (Luparello, Sicily).

4.4. A new species for the palaeo-Cyclades

The current view on the distribution of insular dwarf elephants is that every island harbours its own endemic species (Doukas and Athanassiou, 2003) as already suggested earlier (Sondaar, 1977; Dermitzakis and Sondaar, 1978; Theodorou, 1983; Theodorou et al., 2007). Species can thus not be shared by two islands unless these islands were connected to each other previously during periods of low sea-level and the period of isolation since the break-up of the islands was insufficient for speciation. The reasoning behind this is that dwarfed elephants are believed to have had a reduced their overseas long-distance dispersal abilities. Due to their size reduction, the maximum distance they could have crossed up and down is reduced accordingly, in comparison to mainland elephants. One-way long-distance chance dispersals of size-reduced elephantids may have taken place, giving rise to yet another speciation event, as probably in the case of *Stegodon florensis* if it is derived from *Stegodon* sp. B from southern Sulawesi (Van den Bergh et al., 2001) after crossing perhaps 100 km (Van den Bergh, 1999). The limitations of overseas return possibilities inevitably mean that even if two dwarf species are similar in size and morphology and are derived from the same ancestor but they evolved independently on two unrelated islands, they must be assigned to two

Fig. 3. Elephant maxillae from Naxos, Peloponnesus (continental *P. antiquus*, AMPG), and Delos (drawing from Vaufrey, 1929). All drawn to the same scale.

different species as any genetic contact was unlikely to have taken place. Based on similar body size of the dwarf elephants, the relevant islands for Naxos here are Tilos and Sicily, and the distance to be crossed greater than 150 km, which is well beyond the swimming capacity of modern Asian elephants (Johnson, 1978). For that reason a new species for the dwarf elephant of Naxos is erected here.

5. Systematic palaeontology

5.1. The dwarf elephant from Naxos

Order PROBOSCIDEA Illiger, 1811
Family ELEPHANTIDAE Gray, 1821
Genus *Palaeoloxodon* Matsumoto, 1924
Type species *Palaeoloxodon naumanni* (Makiyama, 1924)
Palaeoloxodon lomolinoi sp. nov.

Holotype: AMPG 999 (Fig. 5), an isolated maxilla preserving both third molars (M3). Curated at the Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens in Greece.

Synonymy: *Elephas melitensis* in Mitzopoulos, 1961: 334, textfig. 1; *Palaeoloxodon antiquus melitensis* in Mitzopoulos, 1961: 336; *P. antiquus* cf. *melitensis* in Mitzopoulos, 1961: 340; a dwarf elephant in Sondaar, 1971: 66; *P. antiquus melitensis* in Marinos and Symeonidis, 1976: 354; *P. antiquus melitensis* (lapsus calami) in Dermitzakis and Sondaar, 1978: 827; *Elephas antiquus melitensis* in Kotsakis, 1979: 36; elephant similar in size to *Elephas melitensis* in Shoshani and Tassy, 1996: 238; *Elephas* unnamed species B in Alcover et al., 1998: 19; elephant probably belonging to the palaeoloxodontine line in Palombo, 2001: 488; an endemic species smaller than *E. mnaidriensis* in Palombo, 2004: 366–367; *Elephas* sp. in Van der Geer et al., 2010: Plate 6.

Fig. 5. Occlusal and labial views of the holotype AMPG 999 of *Palaeoloxodon lomolinoi* sp. nov.

Type Locality: Trypiti river, Naxos, Greece.
Distribution and age: Late Pleistocene, Naxos, Greece.
Etymology: the species is named after Mark Lomolino, in honour of his contribution to the knowledge of island biogeography.
Referred specimens: Holotype only.
Measurements: see Tables 1 and 2.
Diagnosis: a dwarf palaeoloxontine elephant from Naxos.
Differential diagnosis: *Palaeoloxodon lomolinoi* is about ten percent the body mass of *Palaeoloxodon antiquus*, has a higher lamellar frequency and thicker enamel. It differs from *Palaeoloxodon creutzburgi*, *Palaeoloxodon 'mnaidriensis'* and *P.* sp. from Delos in its greater size reduction. It differs from *Palaeoloxodon cypriotes* and *Palaeoloxodon falconeri* (Spinagallo, Sicily) in its lesser size reduction. *Palaeoloxodon lomolinoi* has thicker enamel (ranging between 2 and 3 mm) than all other Mediterranean dwarf *Palaeoloxodon*, except for *Palaeoloxodon tiliensis*.

Description of the holotype: (adapted from Mitzopoulos, 1961) an exceptionally well-preserved partial upper jaw, consisting of the maxillar bones and the complete palatum of an adult individual. Both sides contain a fully erupted third molar in wear. The number of plates is 10.5 of which two are not in wear. The most anterior plate is oval. The following complete plate is merged with a worn central median pillar that lies between the two anterior plates to form a Y-shaped structure. The rest of the plates in wear have a rhomboid, lamellar form. The width decreases with plate number. The enamel loops are simple, 'cigar-shaped', scarcely folded with small mesial expansions. The occlusal surface of the plates at the first stage of wear is broken up into three connected oval islets, somewhat obscured due to the presence of matrix on the specimen. The enamel is thick. The occlusal surface is oblong with the proximal part wider than the distal part.

Remarks: originally, the material of *Palaeoloxodon lomolinoi* was attributed to the Maltese species *Palaeoloxodon antiquus melitensis* by Mitzopoulos (1961). However, since dwarf elephants are considered to have had reduced overseas dispersal abilities (see discussion above) and can thus not have reached the Cyclades from Sicily or Malta, the Naxos dwarf elephant can therefore not have been co-specific with any Siculo-Maltese dwarf species. *Palaeoloxodon lomolinoi* has about the same size as *Palaeoloxodon tiliensis* and *P. 'melitensis'* (Luparello, Sicily). *Palaeoloxodon lomolinoi* is smaller than *P.* sp. (Delos), which might be an older chronospecies. The individual age of the specimen seems rather high, as about 80% of the plates are in wear, translating to an age of above 50 Asian Elephant years (following Roth and Shoshani, 1988) assuming that wear proceeded with the same rate in insular *Palaeoloxodon* as in extant *Elephas*.

5.2. The rock mouse from Naxos

Order RODENTIA Bowdich, 1821
Family MURIDAE Illiger, 1815
Genus *Apodemus* Kaup, 1829
Type species *Apodemus agrarius* (Pallas, 1771)
Apodemus cf. *mystacinus* (Danford & Alston, 1877) (Fig. 6)

Holotype: MCZ 14887, male, skin and skull of a male. Curated at the Museum of Comparative Zoology of Harvard University of Cambridge in the USA.

Type locality: Turkey, Adana Province, Bulgar Dagh Mt, Zebil.

Referred material: Thirteen isolated upper first molars (NX1–NX9, NX11–NX14), eight isolated upper second molars (NX31, NX32, NX34–NX40), four isolated upper third molars (NX41–NX44), four isolated lower first molars (NX51–54), two mandibles with first and second molars (NX56, NX58) (Fig. 6). All specimens are stored at IvAU.

Synonymy: large *Apodemus* in Sondaar, 1971: 66; big *Apodemus* sp. in Kotsakis, 1979: 36.

Dimensions: See Table 4.

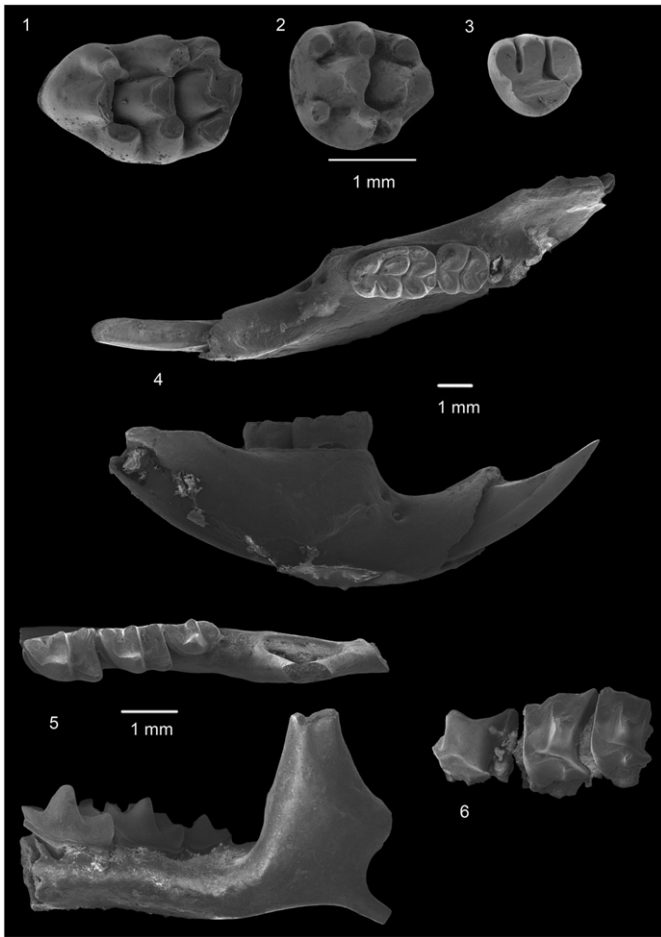*Distribution and age*: Late Pleistocene, Naxos, Greece.

Fig. 6. Small mammals from Naxos. *Apodemus* cf. *mystacinus*. 1: NX 2, left upper first molar (M1 sin.); 2: NX 37, right upper second molar (M2 dext.; inverse); 3: NX 41, left upper third molar (M3 sin.); 4: NX 56, mandible with first and second molars (m1, m2). *Crocidura* sp. 5: NX 137, left mandible with molar series (m1–m3 sin.); 6: NX 87, left maxillary with fourth premolar to second molar (P4–M2 sin.). All materials from IvAU.

Description: Upper dentition: on the M1, the t1 is positioned slightly more posterior than the t3. Because of the strong connection between t4 and t7, the posterior cusps form a continuous ridge from t6 to t9. A t12 is clearly present as a spur of the t8 in all specimens but one, which is relatively worn. In most M2, the t12 is a ridge-shaped extension of the t8, but its development is more variable than in the M1. One M2 has a clearly cusp-shaped t12, in two others it seems to be missing. The t1 is only slightly larger than the t3.

Lower dentition: the m1 is mainly characterised by its strong labial cingulum. A c1 is invariably present, as well as up to three accessory cusplets, which, however, can also be incorporated in a ridge. The two anterolophids are of similar size, the anterocentral cusp is small. The anterolingual cusp of the m2 is strongly developed. Some of the m2 have a very strong labial cingulum, but in most it is reduced to some slight patches. In two specimens, the cingulum bears to accessory cusplets.

Table 4
Measurements of the occlusal surface of the molars of *Apodemus* cf. *mystacinus* from Naxos (average between brackets), in mm.

	Length	Width	n
M1	2.28–2.53 (2.43)	1.54–1.68 (1.61)	13
M2	1.45–1.68 (1.55)	1.45–1.59 (1.53)	8
M3	1.03–1.21 (1.10)	1.05–1.14 (1.10)	4
m1	2.11–2.30 (2.25)	1.40–1.47 (1.42)	6
m2	1.41–1.46 (1.44)	1.39–1.40 (1.40)	2
Lower toothrow	5.76		

Remarks: Sondaar (1971) and Kotsakis (1979) already noted the presence of an *Apodemus* in the Naxos fauna. In the same sample remains of a crocidurine shrew (Fig. 6) and a bat are present, which will be published separately.

The Naxos *Apodemus* is a large species. In size, it agrees well with measurements of *Apodemus mystacinus* as given by Van de Weerd (1973), Mayhew (1978) and Niethammer (1978). Compared to the latter two, the m1 from Naxos seems relatively short. In that respect the material from Naxos metrically fits best with the sample form Varkiza 1, Greece (Middle or Late Pleistocene; Van de Weerd, 1973). The strong labial cingulum on the m1 and m2 also point to *A. mystacinus*, although the development of accessory cusplets is less than suggested by Niethammer (1978, Fig. 63). Moreover, Niethammer (1978) diagnosed the species as having at least on accessory cuspule on the m2, which is only present in part of the specimens in the Naxos assemblage. This could be a difference between subspecies, as the typical *mystacinus* and *Apodemus m. epimelas* do show some differences in the dentition. According to Storch (1975), the t12 is incorporated in the ridge formed by t9–t8–t7 in *A. m. mystacinus*, but is separate in *A. m. epimelas*. This implies that the Naxos *Apodemus* can be placed in the latter subspecies.

According to Masseti (2012), *Apodemus mystacinus* still occurs on Naxos. However, neither Niethammer (1978), nor Storch (2004) includes the island in the distribution of the species. Storch (2004) noted that the subspecies show a clear separation in the Aegean, *A. m. mystacinus* occurring on the eastern islands, whereas *Apodemus m. epimelas* is restricted to the west. Storch (2004) explained this difference by pointing out that *A. mystacinus* is a rock dweller, which would be well adapted to cross rocky land bridges during sea-level lows. Although, in contrast to Storch (2004), we do not want to rule out rafting as a mechanism for dispersal for this species, his argument fits well with finding the Greek subspecies on Naxos. After all, during sea-level lows the island would be far easier accessible from the west than from the east.

6. Discussion

6.1. Fossil insular elephants from the Southern Aegean Sea

The Cyclades does not form the only island complex in the Southern Aegean Sea with insular proboscideans. A fossil dwarf mammoth lived on Crete (*Mammuthus creticus*, early–Middle Pleistocene), and fossils of endemic palaeoloxodontine elephants have been found on Crete (*Palaeoloxodon creutzburgi*, Late Pleistocene), and the Dodecanese islands, namely Tilos (*Palaeoloxodon tiliensis*, Late Pleistocene), Rhodos (unnamed species; originally reported as *Palaeoloxodon antiquus mnaidriensis* by Marinos and Symeonidis, 1973), Astypalaia (unnamed dwarf elephant, reported as personal data in Doukas and Athanassiou, 2003) and Kasos (unnamed elephant, reported as personal data in Masseti, 2012) (for overviews see Doukas and Athanassiou, 2003; Masseti, 2009). Apart from these fossils, a number of elephant fossils from southern Aegean islands belong to mainland *P. antiquus*. These islands were connected to the mainland and include Kalymnos (Masseti, 2002, 2006; specimen figured in Masseti, 2009, Fig. 6), Kythera (Petrochilos, 1938; Dermitzakis et al., 1982), Ikaria (Masseti, 2006, 2009), which are not considered here. Gökceada (= Imbros, Masseti, 2009) is part of the northern Aegean Sea and was connected to Asia Minor.

With the exception of the Cretan mammoth, all the other Aegean proboscideans are palaeoloxodine elephants (pending a full description of the larger elephant from Xylophagou, Cyprus). There are two hypothetical phylogenies available for these elephants. The first is that they all result from independent colonisations from various mainlands and evolved in parallel into dwarf forms (convergent evolution). The second is that the islands of the Southern Aegean Sea acted as a speciation region for elephants. After all, archipelagos have been characterised as

'speciation machines' (sensu Rosenzweig, 1995; see also Whittaker and Fernández-Palacios, 2007). In this scenario a single mainland ancestor colonises an island of the archipelago from where it successively disperses to the other islands where further radiation takes place. Here the first scenario is adopted because in the case of the Southern Aegean Sea we deal with a set of islands that is surrounded by vast mainlands (Fig. 7). The distances between each (palaeo-)island and the respective nearest mainland are a fraction of the inter-island distance and colonisation for the mainland is thus more likely than from any other island. In addition, although the dispersal abilities of living elephants are well known (Johnson, 1978), the same unlikely applies to insular elephants. Due to reduced endurance as a result of their size reduction, it is likely to assume that they could cover a fraction of the distance their full-grown ancestors could cover. In addition, the loss of a strong pneumatisation of the dwarf elephant skull (Palombo, 2001; Van der Geer, 2014) and absolutely shorter trunk may have reduced their swimming capacities even further. In all likelihood, the various Southern Aegean dwarf species of *Palaeoloxodon* are the result of independent colonisation events from the mainland.

6.2. Geological and palaeogeographical setting

The Cyclades Plateau is part of the Attic–Cycladic complex, consisting mainly of metamorphic and igneous rocks (Hejl et al., 2002), and divides the northern Aegean Sea from the southern Aegean Sea (or Cretan Sea). The numerous outcropping islands on the plateau today are the result of its complex geomorphology (Kapsimalis et al., 2009). The Cyclades Plateau was a practically aseismic region during the Late Pleistocene and still is today (Papazachos, 1990). So for our purposes sea-level changes are the only relevant factor in assessing its palaeogeography, at least as far as the Late Pleistocene is concerned. The maximal depth of the Cyclades Plateau is less than 250 m. During periods of low sea level substantial parts of the now submerged Plateau were exposed forming clusters of larger islands or, at periods of more extensive sea-level drop, a single mega-island (Lambeck, 1996; Kapsimalis et al., 2009; Lykousis, 2009) of about 10,000 km^2 (Kapsimalis et al., 2009).

Lykousis (2009) suggests that during the Middle Pleistocene, larger areas were exposed subaerial, and, the Cyclades Plateau was connected to the mainland of Eurasia during major glaciations. Lykousis (2009), based on seismic data, argues that it was connected to both the Greek mainland and Asia Minor during oxygen isotopic stages 10 and 12 (480–350 kyrs BP) and stage 8 (300–250 kyrs BP) and that the area subsided progressively, implying that the connection remained intact during isotopic stage 9 but with less land exposed above sea level. During isotopic stage 6 (180–140 kyrs BP), the land mass was separated from Asia Minor but still connected to the mainland of Greece. Finally, the Plateau formed a single mega-island at oxygen isotopic stage 2 (30–18 kyrs BP) (Lykousis, 2009). These isotope stages correspond to glacial periods and low sea levels. In between, sea level was (much) higher and the emerged area (much) smaller. The breaking up of the single island into the present numerous islands started around the onset of the Holocene (ca 12 kyrs BP; Kapsimalis et al., 2009). The model of Lykousis (2009) is in conflict with the view that the seaways between Euboea–Andros and Kea–Sounion were already open during the early Pleistocene (Anastasakis et al., 2006), resulting in a significantly more insular condition of the Cycladic Plateau throughout the Pleistocene.

Since the current knowledge of the palaeogeography of the Cyclades cannot help us further, the maximum stratigraphic range of the fossil taxa from Naxos is here used as a starting point. *Apodemus mystacinus* is present in Europe and Asia Minor since the early Pleistocene (Masseti, 2012) while *Palaeoloxodon antiquus* was present during the Middle and Late Pleistocene (Athanassiou, 2000). This would imply a Middle or Late Pleistocene age for the Naxos fauna (this also fits the metrical values of the Naxos *Apodemus*, which indicate a Middle or Late Pleistocene age as well). Most of the palaeoloxodontine phylogenetic dwarfs are of Late Pleistocene age (e.g. Tilos, Crete, Rhodos and the large-sized elephants of Sicily and Malta), there are, however, some that have been attributed to the Middle Pleistocene (the smallest-sized elephants of Sicily and Malta).

6.3. Colonisation window and subsequent evolution

Kurtén (1968) suggested that during glacial stages of the Pleistocene the South European peninsulas served as refuges for *Palaeoloxodon antiquus*, which is adapted to the temperate climates of the interglacial stages. During such a colder stage sea-level drops are expected and the palaeo-Cyclades was not only much closer to the mainland but also much larger (Fig. 1). At excessive sea-level drops, the palaeo-Cyclades was connected to the mainland of Greece via Euboea (Anastasakis and
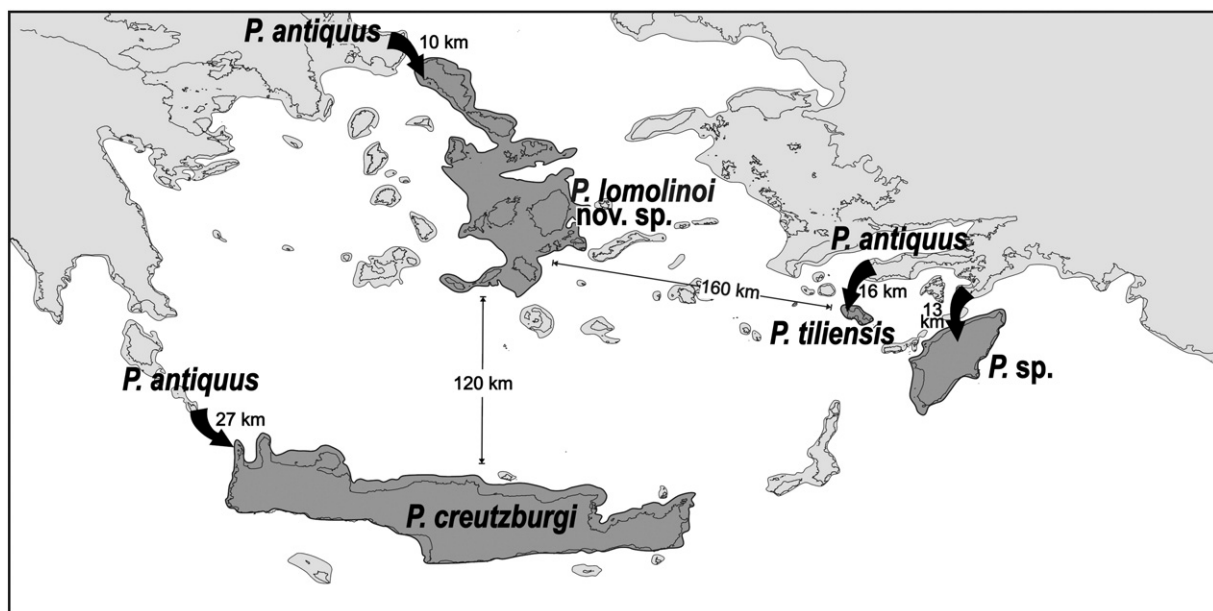

Fig. 7. Palaeogeographic map of the Southern Aegean when the sea level was 100 m below present day sea-level. The map also indicates the possible dispersal routes of four insular elephants and the overseas distances they would have had to cross. In all cases the mainland was significantly closer to each palaeo-island than the palaeo-islands from each other.

Dermitzakis, 1990). At such moments, *P. antiquus* could have easily reached the palaeo-Cyclades overland where it found sufficient area to survive as the submerged shelf areas of today formed flat plains then. After submerging of the land connection, colonisation was still possible but this time overseas by swimming as in the case of several other insular elephants (Van den Bergh, 1999; Van der Geer et al., 2010). Perhaps independently, the murid and the insectivore reached the palaeo-island supposedly by rafting. The nature of the ecological assemblage, consisting solely of an elephant, a mouse and a shrew, strongly favours overseas chance dispersal. When the climate became warmer again and sea level rose, the degree of isolation increased and may have either led or started a progressive body size reduction. Eventually the island may have become too small to sustain a population of large herbivores leading to the extinction of *Palaeoloxodon lomolinoi*. Other causes which could have led to the extinction of the dwarf elephant are climate change, volcanic activity e.g. of nearby Santorini (Thera), hunting pressure exerted by humans, disease or a combination of factors, all of which may be independent of sea-level changes. As to volcanic activity, Theodorou (1988) suggested that the Minoan eruption of Santorini was one of the factors that led the Tilos dwarf elephant to extinction. If this applies to Naxos as well, it's impossible to pinpoint a precise point in time, because the Santorini volcanic field has had twelve major and numerous minor eruptions over the last 200 ka (Druitt et al., 1989), the effect of which on Naxos is unknown (no ash layers were found). On the other hand, the Cyclades Plateau is unlike any other island in the Mediterranean. Sea-level changes can dramatically alter its size and topography. At low sea levels it forms a large island with extensive flat areas, but a modest sea-level rise leads to a fragmented landscape consisting of many smaller islands with rather rough terrain.

Several possible episodes of isolation, dispersal, evolution and extinction can be deduced from Lykousis' (2009) interpretation of seismic data, where extinction can have been caused by (re)connection to the mainland or by substantial submergence of habitat. Lykousis (2009) does not specify how much of the Plateau around Naxos was exposed during interglacials, so the most plausible colonisation window has to be narrowed down by elimination.

First of all, should the palaeogeographic reconstruction of Lykousis (2009) turn out to be incorrect and the palaeo-Cyclades was separated from the mainland throughout the entire Pleistocene, then *Palaeoloxodon lomolinoi* could have lived on Naxos during the colder stages of the Middle Pleistocene as well. A low sea level is important for two reasons. First, it minimises the distance between mainland and island, and thus increases the chances of a successful overseas crossing. Second, it increases the size of the palaeo-Cyclades by adding large territories with minimal inclination that form suitable habitats for elephants. This scenario would add isotope stages 16 (approx. 650 kyrs BP), 12 and 10 as possible colonisation and evolution window for *P. lomolinoi*.

In the case that the model of Lykousis (2009) is correct, the Middle Pleistocene glacials have to be excluded because of their land connections. Furthermore, isotopic stage 9 is excluded on the ground of its short duration (around 50 kyrs) during which the complete sequence of isolation, successful sweepstakes colonisation and subsequent evolution of dwarfism before land connection was re-established should have taken place. The data in Lykousis (2009) allow for at most a very short period, if at all, of isolation. Isotopic stage 7 is somewhat longer (about 70 kyrs) but in our opinion still unlikely short. In addition, Lykousis (2009) data indicate that the land connection with mainland Greece through Attika and Euboea remained intact throughout.

Taking all evidence together, the only relevant period for evolution of the Naxos fauna is a period when emerged landmasses formed a large island, the palaeo-Cyclades, and where submerged areas of today formed large plains and provided sufficient habitat to sustain an elephant population. This could be approx. 650 kyrs BP, 480 krys BP or between 140 and 30 kyrs BP. Available palynological data from the study area narrow the colonisation window significantly. The relevant deposits are quite rich in pollen and represent at least 20 taxa

(Dalongeville and Renault-Miskovsky, 1993). The deposits cannot be pinpointed in time but can most likely be attributed to the period between 116 and 11.5 kyrs BP (Würm) and represent the different stages of alternating open forest and arboreal steppes, or, in the case of one particular deposit, perhaps between 238 and 128 kyrs BP (Riss; Dalongeville and Renault-Miskovsky, 1993). A Late Pleistocene age, or perhaps a latest Middle Pleistocene age, is in line with the geological age of other *Palaeoloxodon* dwarfs from the Aegean and is not contradicted by the micromammal data.

The specimen from Delos might represent an earlier stage of isolation than the specimen from Naxos and in that case would constitute a chronospecies of *Palaeoloxodon lomolinoi*. To rule out the option of an earlier, independent colonisation followed by an independent evolutionary process further study of the Delos specimen and its context is needed. The species on Rhodos, Crete and Tilos on the other hand are doubtlessly the result of independent colonisations by *Palaeoloxodon antiquus* from different regions. Rhodos and Tilos were colonised from Asia Minor, Crete from Greece through Kythera and Antikythera, which were connected to each other and to the Peloponnesos.

The palaeo-Cyclades was not far removed from the mainland. A moderate degree of isolation is suggestive of a high colonisation rate, while a relatively large area can accommodate a high number of species (Lomolino, 2000). Yet, the recorded biodiversity of the palaeo-Cyclades is lower than that for Crete, an island with similar size and only slightly higher degree of isolation during periods with low sea level during the Late Pleistocene. Apart from a dwarf elephant, a large mouse and a shrew, Crete also harboured several deer species and an otter during the Late Pleistocene. This difference might simply be an artefact of the lack of fossils since there are thousands of fossils from Crete but only a handful from the Cyclades. A complete picture of the palaeobiodiversity and biostratigraphy of the palaeo-Cyclades is thus currently impossible to build and will perhaps never be. The available bits and pieces, however, give some clues about biogeography. First of all, the palaeo-Cyclades supported an elephant of about a quarter the body mass of that of Crete during the same period. This small relative size may be related to the absence of any competitor or predator as Lomolino et al. (2012) found that body size evolution of mammals on islands is contextual, and the absence or presence of competitors and predators is a main factor. However, this is by no means certain when taking the fragmentary fossil record of the palaeo-Cyclades into account. The smaller size may also be related to island area, but such a relation has never been proven for elephantids and is in conflict with the fact that Tilos, which is much smaller, harboured a similar-sized elephant. Secondly, the meagre fauna consisting of a dwarf elephant, shrews and a field mouse puts the island on a par with relatively remote islands like Middle Pleistocene Malta and Flores. As with the previous issue, this may prove untrue in case more taxa are found.

6.4. Remarks on palaeo-dietary ecology and habitat

Limited ecological information, at least for the Late Pleistocene, can be inferred from the fauna. The rock mouse is a species of primarily deciduous forests and Mediterranean woods but prefers drier habitats than most other *Apodemus* (Tchernov, 1986). It has been reported from rocky areas of dry, open environments (Mayhew, 1978; Montuire et al., 1994). Part of the palaeo-Cyclades was likely covered with deciduous forest and woodlands with, as can be inferred from the geology, barren rocky areas as well. As to the large herbivore spectrum of the fauna, the only component was *Palaeoloxodon lomolinoi* which might have deviated ecologically from its ancestor *Palaeoloxodon antiquus*. Palombo et al. (2005) and Palombo and Iacumin (2010) demonstrated dietary plasticity for the latter species. Its microwear patterns indicate wide dietary breadth and the ability to exploit feeding resources in a large diversity of habitats (Rivals et al., 2012). Apart from that, the European populations of this species show a trend towards an increased

amount of browse in its diet from the Middle Pleistocene (graze-dominated mixed feeder) to the Late Pleistocene (Eemian interglacial, MIS 5e; leaf browser) irrespective of latitude (Rivals et al., 2012). If the founder population of the palaeo-Cyclades belonged to a Late Pleistocene meta-population (see Section 6.3) and it would have been adapted predominantly to leaf browsing or browse-dominated mixed feeding. A higher amount of dietary plasticity is an advantage for a species on an island simply because of the ability of niche broadening without much need for adaptation. The slightly thicker enamel observed in molars of dwarf species such as *P. lomolinoi* might be related to diet but this relation has never been investigated systematically. Actually, this might very well be linked to increased dietary breadth rather than to niche narrowing and specialisation in parallel with the case of increased tooth crown height (hypsodonty) in ungulate lineages (Rivals et al., 2010).

Palynological data indicate a Late Pleistocene climate that was warmer than the present with a Mediterranean character and either drier or wetter than the present dependent on the stage (Dalongeville and Renault-Miskovsky, 1993). The arboreal component differs per deposit and varies between 40% (warm, wet) and 20% (warm, dry); in one case 12% in combination with a high percentage of aquatic plants, which is a local phenomenon.

The palaeo-Cyclades had a varied landscape with mountains and valleys. The present-day islands were the highlands, but in between there were low, large and relatively flat plains with an average slope of just 1.58° (Kapsimalis et al., 2009). Two major palaeo-plains can be recognised on the palaeo-Cyclades: a central plain located between the highlands of what are now Syros–Delos–Mykonos and Antiparos–Paros–Naxos, and a southern plain between the highlands of Antiparos–Paros–Naxos and Folegandros–Sikoos–Ios (Kapsimalis et al., 2009). These plains with their freshwater resources likely formed suitable habitats for elephants.

7. Conclusions

1. During the Late Pleistocene, Naxos and adjacent areas formed a large mega-island, referred to here as the palaeo-Cyclades.
2. Areas that are at present submerged formed extensive low-lying plains with lakes and rivers, providing suitable habitats for large herbivores.
3. Fossils of a dwarf elephant, formally named here *Palaeoloxodon lomolinoi*, a rock mouse (*Apodemus* cf. *mystacinus*), shrews and bats were found on Naxos in Late Pleistocene sediments.
4. The dwarf elephant from Naxos evolved miniature size due to long-term isolation. It had a body mass of about 10% of that of its mainland ancestor.
5. The various Aegean insular dwarf species each result from independent colonisations.

Acknowledgements

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