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Cranial evidence for the presence of a second endemic elephant species on Cyprus

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ABSTRACT

Cyprus, the largest Eastern Mediterranean island, hosted a highly impoverished endemic mammalian fauna during the Pleistocene to early Holocene times. This was a result of its extreme biogeographic isolation since its formation, which prevented the immigration of most terrestrial mammals, except for those with apparent sea channel crossing abilities. The main faunal elements are the extremely dwarfed hippo *Phanourios minor*, commonly found in many sites across the island, and the dwarf elephant *Palaeoloxodon cypriotes*. The latter is a very small-sized elephant species, comparable in size with the Siculo-Maltese *Palaeoloxodon falconeri*. Larger dental specimens found sporadically during the last century, raised the possibility that a second endemic elephant, larger than *P. cypriotes*, may have also existed in Cyprus. Here we describe a skull recently excavated in the coastal area of Xylophágou, SE Cyprus, which provides evidence that, indeed, two elephant species have existed on the island. The larger species, *Palaeoloxodon xylophagou* n. sp., is still strongly dwarfed and characterised by elongated, low and wide skull, diverging tusk alveoli and comparatively large molars. Dimensionally the dentition is distinctly larger than *P. cypriotes* and close to *Palaeoloxodon tiliensis*, though the skull size is intermediate between *P. tiliensis* and *P. falconeri*. Both Cypriot elephant species exhibit morphological affinities with *Palaeoloxodon antiquus*, which is their probable ancestor. Stratigraphic data suggest that *P. xylophagou* is older (late Middle Pleistocene), while *P. cypriotes* is more recent (latest Pleistocene to early Holocene) and may have descended from the former or – less probably – evolved as a result of a separate, more recent colonisation event.

1. Introduction

Mediterranean islands are famous in biogeography as a prime example of the "Island Rule", according to which an animal's size is affected as an adaptation to the peculiar ecological conditions of the insular environment (Van Valen, 1973). The proboscideans are perhaps the most iconic mammals illustrating this evolutionary process, owing to the extreme size-reduction observed in many insular species (Roth, 1992a; Caloi and Palombo, 1994; van den Bergh, 1999; Palombo, 2004, 2007, 2010; van den Bergh et al., 2008; van der Geer et al., 2010; Agenbroad, 2012). The extant elephants are among the very few terrestrial large mammals that are quite happy in the water and can swim over long distances (at least 48 km according to Johnson, 1980). Their peculiar morphological characters, such as the possession of a trunk and air-filled cranial sinuses, as well as the production of abundant gases in their digestive system, help in this respect by providing a snorkel-like respirator and additional buoyancy. As evidenced by numerous insular localities across most of the world's archipelagos, many extinct Proboscidea (most commonly Elephantidae) apparently had similar habits, being able to swim across sea channels to reach offshore islands. In most cases these dispersal events would be facilitated during cold climatic intervals, when the low sea levels

Abbreviations: AMPG, Museum of Palaeontology and Geology, University of Athens, Greece; BP, before present (i.e. AD 1950); GSDC, Geological Survey Department of Cyprus; ka, thousand years BP; ky, thousand years; NHML, Natural History Museum, London, United Kingdom.

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resulted in narrower sea channels and larger islands. Once isolated, insular elephants repeatedly underwent evolutionary change towards smaller body size, although the degree of size change varied.

The Mediterranean insular endemic elephants are found in Pleistocene to early Holocene cave or open-air sites on more than a dozen islands of the Central (Sardinia, Sicily, Malta) and Eastern Mediterranean (Náxos, Páros, Kýthnos, Sérifos, Délos, Mílos, Astypálaea, Kásos, Crete, Tílos, Rhodes, Cyprus) (Kotsakis et al., 1980; Dermitzakis and de Vos, 1987; Kotsakis, 1990; Caloi et al., 1996; Doukas and Athanassiou, 2003; Theodorou et al., 2007a; Palombo et al., 2012; Sen et al., 2014; van der Geer et al., 2014). With the exception of the Sardinian *Mammuthus lamarmorai* (Forsyth Major, 1883) and the Cretan *Mammuthus creticus* (Bate, 1907), Mediterranean insular dwarf elephants most likely derive from founding populations of the large-sized *Palaeoloxodon antiquus* (Falconer and Cautley, 1847). In many cases these insular forms underwent a drastic size decrease resulting in animals with a body mass in the order of 10^2 kg, which is a tiny fraction of the ca. 10^4 kg mainland species mass (Roth, 1990; Palombo and Giovinazzo, 2005; Herridge, 2010, pp. 310–321).

Fossil-bearing localities on Cyprus have usually yielded specimens referred to an extremely small-sized endemic elephant, *Palaeoloxodon cypriotes* (Bate, 1903). This endemic species together with the Sicilian *Palaeoloxodon falconeri* (Busk, 1867) are the smallest elephants ever evolved, having an adult height of about 1 m (Ambrosetti, 1968; Davies and Lister, 2001). However, there is also sporadic evidence for the presence of a larger elephant form on Cyprus (Vaufrey, 1929; Boekschoten and Sondaar, 1972; Reese, 1995; Iliopoulos et al., 2011). Here we report previously undescribed cranial material, excavated in the coastal area of Xylophágou, SE Cyprus, which corroborates previous sparse observations and documents the presence of an additional, larger-sized, but still dwarf, endemic elephant species on the island.

1.1. Methods

The osteological terminology used for the description of the cranial specimen that constitutes the main subject of this study, follows Van der Merwe et al. (1995). The dental measurements were taken according to the methodology proposed in the reference publication of Maglio (1973). All specimen measurements are in mm; the inaccurate ones are given in parentheses. The Cypriot toponyms were generally transliterated to the Latin alphabet following the Cypriot Government standards (Christodoulou and Konstantinidis, 1987) and may slightly differ from previously published ones.

2. Geological setting

Cyprus is the third largest island in the Mediterranean Sea (total area of 9251 km^2), situated between the major tectonic plates of Africa and Eurasia. The island's geological structure indicates a complex geologic history, whose main events may be summarised as the following: a) an initial emergence of the island's main mountainous area, the Tróodos Massif, during the Miocene, as a result of uplift of the Tethyan oceanic crust; b) the rise of the Pentadáktylos Range near the end of the Miocene; c) the uplift of the whole island, as a united land mass, about the beginning of the Pleistocene, resulting to its present form (Robertson, 1990). Because of this sequence of geological events, Cyprus constitutes a prime example of an oceanic island, an island that was never connected to the mainland since its formation (since the Miocene in Cyprus' case). Presently Cyprus is still separated from the adjacent Cilician and Levantine coasts of mainland Asia by very wide (>70 km) and deep (mostly >1000 m) sea channels.

The Xylophágou area (Fig. 1) is covered by terrestrial and shallow-marine or brackish sediments, indicating a proximity to the coastline during deposition. The fossiliferous layer, situated at about 6–7 m above sea level, consists of a 2 m-thick, well-cemented, medium-grained green sandstone, rich in microfossils (Fig. 2). The microfossil assemblage is dominated by the brackish ostracod *Cyprideis torosa*, with a significant contribution of the foraminiferan *Ammonia beccarii*, indicating that the fossil bones were deposited in a lagoonal environment (Prokopi, personal communication). The presence of *Candona* sp. in the upper part of the layer suggests a fresh water flow into the lagoon. Furthermore, the considerable numbers of Globigerinidae tests in the lower part of the layer possibly characterise high energy events that affected the lagoon. The fossiliferous layer is overlain by a 1–1.5 m-thick alternation of marls and thin marly limestones (Fig. 2) dominated by *C. torosa* and external molds of *Cerastoderma* sp. (Prokopi, personal communication), indicating again deposition in a lagoonal environment. The marl/limestone succession is superimposed uncomformably by thick, coarse-grained and poorly sorted red conglomerates (Fig. 2) with infrequent mollusc fragments.

Fig. 1. Geographic location (indicated by an asterisk) of the locality Xylophágou, SE Cyprus (34.9656°N, 33.8250°E; WGS84 datum). Satellite image source: Google.

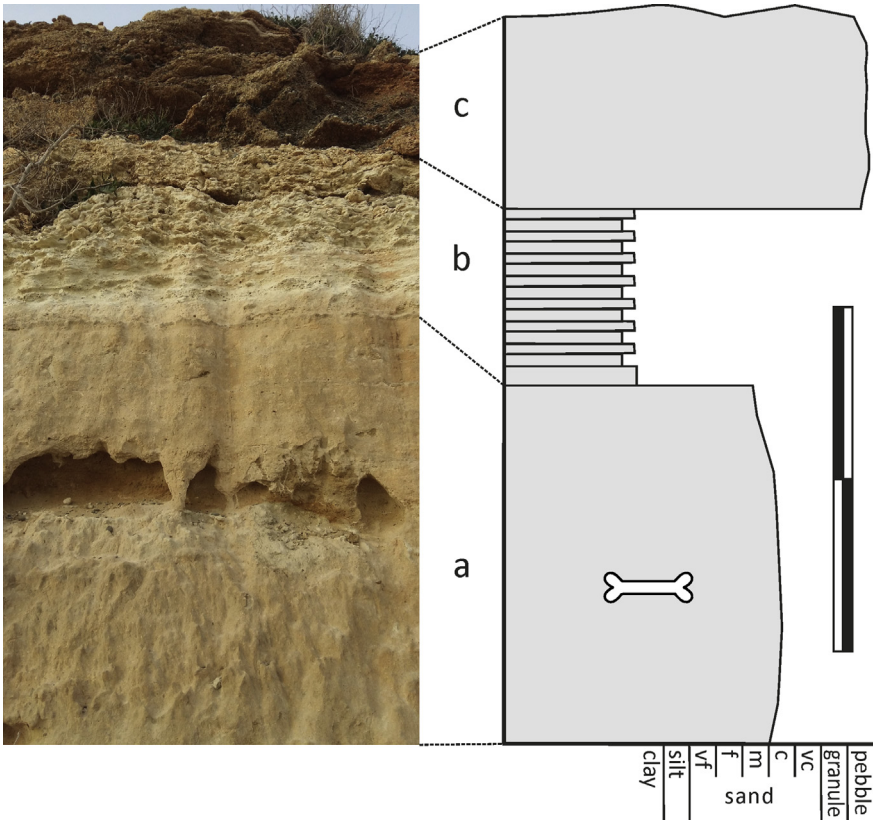

Fig. 2. Stratigraphic section at the Xylophágou coast, Cyprus. (a) green sandstone; (b) alternation of thin layers of marls and marly limestones; (c) coarse-grained red conglomerates. The photograph is proportionally different from the lithostratigraphic column because of perspective distortion. Abbreviations: vf, very fine; f, fine; m, middle; c, coarse; vc, very coarse. Scale in m.

Mammal fossils crop out in low concentrations along the present coastal zone, in a distance of more than 500 m. According to Poole and Robertson (1998) the fossiliferous level is stratigraphically correlatable to the F3 Fanglomerate Unit of the northern Tróodos margin, which, on the basis of lithostratigraphic correlations with radiometrically dated littoral marine terraces, is currently dated to the MIS 7, late Middle Pleistocene (Poole et al., 1990; Poole and Robertson, 1998). Based on the same radiometric data, Zomeni (2012, pp. 103–104) correlated the lower marine terrace in the Xylophágou coastal area, from sea level till an elevation of about 20 m, to the last interglacial (MIS 5e), thus implying an older age for the bedrock on which the terrace was formed.

3. The endemic fauna of Cyprus

As is the case with many Mediterranean islands that remained biogeographically isolated throughout the Pleistocene glacial/interglacial climatic cycles, Cyprus has witnessed at least one colonisation event of a few macro- and micro-mammalian populations, which were able to pass the sea barrier between the Eurasian mainland and the island by means of swimming, drifting on natural rafts, or flying. The subsequent rapid adaptive evolution of the colonisers to the insular environment (particularly characterised by reduced resource competition, as well as absence of large predators) has yielded a greatly impoverished, unbalanced endemic fauna of Pleistocene age, which is known from more than forty open-air and cave sites (Bate, 1904c; Boekschoten and Sondaar, 1972; Reese, 1995; van der Geer et al., 2010). According to the current knowledge, the endemic fauna of Cyprus comprised dwarfed large mammals —a hippo and at least one elephant species—, a genet (*Genetta plesictoides* Bate, 1903), as well as some poorly known small mammals: one or two species of murid rodents (*Mus* sp., *Mus cypriacus* Cucchi et al., 2006), more than one species of bats, and a soricid insectivore [*Crocidura suaveolens* (Pallas, 1811)] (Forsyth Major, 1902; Bate, 1903a, 1903b, 1903c, 1904a, 1904b, 1904c, 1905, 1906; Boekschoten and Sondaar, 1972; Reese, 1995; Cucchi et al., 2006; Theodorou et al., 2007b). The immigration chronology is not well established; it is generally accepted that the hippopotami and the elephants were the first to reach the island sometime during the Middle or Late Pleistocene, while the rest of the greatly impoverished fauna is considered a result of Late Pleistocene or even early Holocene colonisation event (Van der Geer et al., 2010). There is evidence, though, of coexistence among the taxa: elephants and hippopotami are found together in most sites (although hippopotamus remains predominate) (Reese, 1995), while the genet was found in association with hippopotamus in Agía Nápa rock-shelter, a site dated to the latest Pleistocene (Theodorou et al., 2007b). The same site also yielded an elephant tusk fragment, not directly associated with the other finds, as it comes from a disturbed layer (Stathopoulou et al., 2008), as well as stratified elephant and hippopotamus specimens from the same level (2008 excavation season, Theodorou, unpublished data). Endemic deer, a common fossil element in other Mediterranean Pleistocene insular faunas (and the Aegean in particular), have not been undoubtedly documented on Cyprus. *Dama*-sized dental and osteological material in an allegedly Late Pleistocene geological context at the Ormídeia–Xylophágou coast was described by Kassapis et al. (2005) as similar to *Dama mesopotamica* remains found in archaeological,

anthropogenic deposits. The authors do not conclude whether the finds belong indeed to a natural Pleistocene endemic population, or represent intrusive recent material belonging to animals brought to the island by humans not earlier than the Neolithic.

The dwarf hippopotamus *Phanourios minor* (Desmarest, 1822) is by far the most abundant species of the Cypriot endemic fauna, known from many thousands of specimens coming from more than 30 sites on the island (Forsyth Major, 1902; Bate, 1906; Boekschoten and Sondaar, 1972; Reese, 1995, 2001). This is an extremely small-bodied species (actually the smallest known insular hippo), exhibiting an array of peculiar morphological characters. These include a lophodont dentition, the loss of the fourth upper premolar, shortened distal limb segments and unguligrade locomotion (Boekschoten and Sondaar, 1972; Sondaar, 1977; Houtekamer and Sondaar, 1979). All are considered as adaptations to a rugged, mountainous environment, free from large predators, with considerably reduced herbivore competition.

3.1. The endemic elephants

The elephants are much less common, but still rather frequently found: they are known from more than twenty localities (Reese, 1995; Hadjisterkotis, 2012). Most finds consist of fragmentary material, usually molar fragments, or isolated molar plates. They are generally attributed to *Palaeoloxodon cypriotes* (Bate, 1903), an extremely dwarfed endemic species (Bate, 1903c, 1905). There is general consensus among authors that this insular form descended from a *P. antiquus* ancestral population that migrated to Cyprus sometime during the Middle–Late Pleistocene (Caloi et al., 1996; Palombo, 2004; Herridge, 2010; van der Geer et al., 2010). *P. cypriotes* is known mainly from dental material, the size of which is slightly smaller than that of the Siculo-Maltese species *P. falconeri* (Table 2; Davies and Lister, 2001; Herridge, 2010). The richest *P. cypriotes*-bearing sites are the type locality, Páno Dikomo-*Imbohary*, on the southern slopes of Pentadáktylos Range, and Akrotíri-*Aetókremnos* at the southernmost promontory of the island (Bate, 1903c, 1904a; 1904b, 1905; Reese, 1995, 2001).

Some additional but scanty remains of larger-bodied elephants, first found on Cyprus (Achna locality) in 1924, have raised doubts about their attribution to Bate's species (Vaufrey, 1929; Boekschoten and Sondaar, 1972; Reese, 1995; Davies and Lister, 2001; Herridge, 2010); however, they were inadequate for taxonomic evaluation, as their number and preservation state are poor. Over the years more fragmentary dental and postcranial material kept appearing on the SE side of the Mesaoría Basin (the lowland between the Tróodos and Pentadáktylos mountains), mainly as a result of private collectors' activities. This area was also investigated during a joint palaeontological survey by GSDC and AMPG since 2001. An excavation carried out in June 2005 on the coast near the town of Xylophágou (Fig. 1; Theodorou et al., 2005a, 2005b) yielded a partial elephant skull, which is described here. This important find offers new, solid evidence for the existence of an additional endemic elephant species, distinctly larger than *P. cypriotes*, on Cyprus.

4. Systematics

Order Proboscidea Illiger, 1811
Family Elephantidae Gray, 1821
Genus *Palaeoloxodon* Matsumoto, 1924
Palaeoloxodon xylophagou n. sp.

Synonymy

1929 *Elephas melitensis* – Vaufrey, pp. 108, 184, 209, Fig. 238 (M 12610, NHML)
1972 *Elephas* sp. – Boekschoten and Sondaar, 331–332, pl. VII, Fig. 5 (M 12611a, NHML)
1995 *Elephas* sp. – Reese, pp. 41, 132, 144–148
2005 *Elephas* sp. – Theodorou et al., p. 13
2011 *Elephas cypriotes* – Iliopoulos et al., p. 30

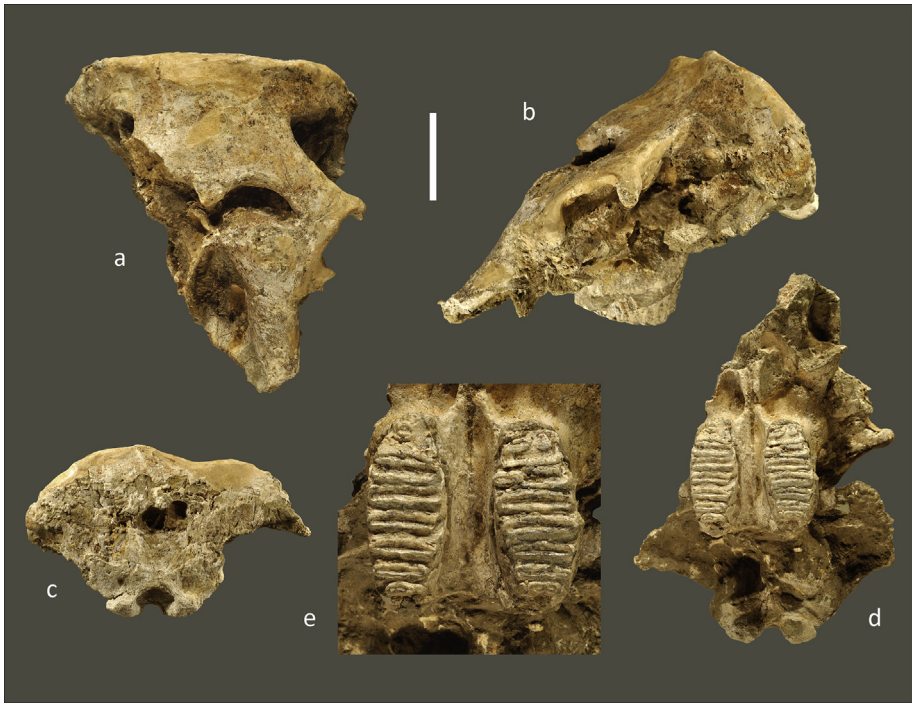

Fig. 3. *Palaeoloxodon xylophagou* n. sp., partial skull XY.05.1, Xylophágou, Cyprus, GSDC. (a) dorsorostral view; (b) left lateral view; (c) dorsocaudal view; (d) ventral view; (e) occlusal view of the dentition. Scale: 10 cm (a–d), 5 cm (e).

4.1. Type material

Holotype: XY.05.1, partial skull with the last molars (M3) (Fig. 3). GSDC collection; currently on display at AMPG. A cast is on display in the Thalassa Museum in Agía Nápa.

Referred material: molars M 12609, M 12610, M 12611a–c, M 12612a–b from Achna, Department of Palaeontology, NHML.

Etymology: Named after the homonymous town in SE Cyprus, in the region of which the new species' holotype and most of the fossils attributed to it were found.

Type locality: Xylophágou, SE Cyprus, 34.9656°N, 33.8250°E (WGS84 datum) (Fig. 1).

Stratigraphy: Stratigraphic level correlatable to the Fanglomerate Group F3 Unit of the Circum-Tróodos Sedimentary Succession (MIS 7, late Middle Pleistocene).

Geographic distribution: The island of Cyprus.

Diagnosis and differential diagnosis: A dwarf endemic species of the genus *Palaeoloxodon* with comparatively long, low and wide skull with respect to the mainland species proportions. Tusk alveoli diverging. Third molars large relative to the skull, with moderately folded, cigar-shaped enamel loops. Molar size distinctly larger than *P. cypriotes*, slightly smaller than *P. tiliensis*.

4.2. Description

4.2.1. Skull

The skull is partially preserved, lacking most of the right-side facial region including the right tusk alveolus, as well as both zygomatic arches (Fig. 3a, b). In general appearance it is rather low and rostrocaudally long for an elephant. The rostrum is slender. The preserved left tusk alveolus is subcircular in cross section and of small diameter (the maximal and minimal diameters are 38 and 31 mm respectively). This indicates that the tusks were also slender and thus the specimen is likely to be attributed to a female individual, in accordance with the tusk sexual dimorphism observed in other proboscidean species (Layser and Buss, 1985; Averianov, 1996; Smith and Fisher, 2013). This deduction is supported by the recent discovery of a large presumably male tusk (82 cm long, 65 mm in diameter) a few meters away from the skull, preliminarily presented by Iliopoulos et al. (2011), but unavailable for further study (see Section 6.1). The preserved alveolus in the studied skull forms an angle of about 145° with the molar alveolar level (Fig. 3b). Its position with respect to the basal region of the missing right alveolus indicates that both diverged from each other proximally, forming between them an angle of about 35° (Fig. 3a). The nasal opening is low and broad; a prominent median nasal process divides it into two crescent-shaped bilateral parts. The only preserved left orbit is large and rather low positioned, facing ventrolaterally. The forehead (formed by the fused frontal and parietal bones) is broad and almost flat, exhibiting only a slight rostrocaudal concavity between the nuchal line and the nasal opening, as well as a slight transversal convexity in the same region (Fig. 3a, b). Internally, it is pneumatised. Laterally, the dorsal and the lateral parts of the parietal bone are divided by a prominent temporal line. Dorsocaudally, the dorsal surface of the skull bends abruptly ventrally to the occipital face, forming an almost horizontal nuchal line. There is no excessive pneumatisation, thickening or rostral folding in this region. The occipital is low and wide; the occipital face is almost flat, except for the region of the fossa for the insertion of the nuchal ligament, which is markedly concave. The specimen's dimensions are given in Table 1.

Table 1
Dimensions (in mm) of the *Palaeoloxodon xylophagou* skull XY.05.1 from Xylophágou, SE Cyprus, in comparison to cranial specimens from other insular species: *P. falconeri*, female and male, from Spinagallo, Sicily (according to Ambrosetti, 1968, p. 361) and three specimens of *P. tiliensis* from Tílos (AMPG), of which T. 189/96 is probably male.

	P. xylophagou	*P. falconeri*		*P. tiliensis*		
	XY.05.1 (♀) Xylophágou	№ 4, № 7 (♀) Spinagallo	№ 5, № 6 (♂) Spinagallo	T. 189/96 Tílos	'Skull C' Tílos	T. 340/99 Tílos
Maximal length (parallel to the alveolar level)	>450	340	392	580	479	–
Maximal height (parallel to the face)	>410	285–290	–	505	–	–
Maximal height of the orbit	79	73–78	–	–	–	–
Width at the supraorbital processes	340[a]	204–212	–	–	–	–
Distance between the rostral end of the nasals and the nuchal line	191	–	–	–	–	–
Distance between the distal end of molars and the distal end of occipital condyles	195	135[b]	135[b]	252	290	–
Minimal frontal width (above the orbits, at the temporal lines)	186	–	–	–	–	–
Width at the level of the molar alveoli	134	78–88	91	156	154	152.4
Width at the level of the molars	125.5	–	–	143.0	143.0	–
Minimal width between the molars	27.5	–	–	44.5	28.7	31.6
Nasal width, left side only	105	–	–	–	–	–
Occipital width	≥283	–	–	–	–	–
Occipital height (opisthion–nuchal line)	184	160	170	(316)	–	–
Cranial height (normal to alveolar plane, including molars)	299	–	–	(421)	–	–
Occipital condyles width (at their lateral sides)	118.3	92	94–108	139	128	–
Foramen magnum height	34.0	–	–	60	57	–
Foramen magnum width	50.3	–	–	56	60	–

[a] Calculated by measuring left side only.
[b] Not exactly corresponding measurement.

The skull's preserved dentition consists of two molars, one on each side (Fig. 3d, e). Judging from their size and the maxillary morphology (particularly the strongly accenting alveolar margin at the distal part of the molars), they are interpreted as M3s. However, the maxillas are not preserved behind the molars, so they cannot be investigated for any forming or erupting more distal molars. The preserved molars consist of eight plates each; their

original number was greater, however, as some of them have been worn during life.

The molar crowns are high and rather narrow. They are clearly hypsodont, as observed at their distal ends (Fig. 3b), but their hypsodonty indices cannot be calculated, because their preservation in situ in the maxilla does not allow us to measure their height. The enamel is moderately folded. The enamel on the occlusal surface has subparallel mesial and distal sides producing 'cigar-shaped' loops, except for those of the slightly worn lamellae, the sides of which appear more convex (Fig. 3e). There are no clearly shaped median loxodont sinuses. The molar dimensions are given in Table 2.

Table 2
Third upper molar dimensions (in mm) of the *Palaeoloxodon xylophagou* skull XY.05.1 from Xylophágou, SE Cyprus, in comparison to corresponding metrical data of *P. cypriotes*, *P. falconeri*, *P. tiliensis*, *P. mnaidriensis* and *P. antiquus*. The measurement methodology follows Maglio (1973). Crown width includes cement; the parenthesis indicates the plate where the measurement was taken. *P. falconeri* dimensions according to Herridge (2010, tabs. 4.14, 4.16). *P. mnaidriensis* is meant in a restricted sense (following Herridge, 2010), excluding the 'large-sized' Sicilian and Maltese dwarf elephants. *P. antiquus* dimensions according to Herridge (2010, tab. 4.6).

	P. xylophagou (XY.05.1)		*P. cypriotes*	*P. falconeri*	*P. tiliensis*	*P. mnaidriensis*	*P. antiquus*
	Left	Right	Imbohary	Sicily	Tilos	Sicily, Malta	Various loc.
Plate number	>8	>8	11–12	13–15	9–12	13–14	16–20
Crown length	>123	>127	>86	86–120+	108–157	136–187	245–333
Crown width	48.0 (3rd)	47.4 (4th)	30.7–35.4	22–36	48.9–52.8	40–54	69–92
Lamellar frequency	6.7	6.0	10.8–12.4	7.6–13.3	6.6–9.7	7.1–10.3	5.4–7.4
Enamel thickness	2.1	2.2	1.1–1.5	1.3–1.9	1.8–2.9	1.1–2.0	1.6–2.4

5. Comparisons and discussion

We have putatively assigned XY.05.1 as a female morphotype of *P. xylophagou* based on its inferred slender tusk morphology and the presence of a larger tusk in the same deposit. We interpret this presence of two contemporaneous size-classes in a taxonomically conservative fashion: as a single, sexually dimorphic species. However, we recognize that sex attribution remains a hypothesis that needs to be confirmed by additional discoveries, and caution should be taken when making size comparisons between insular dwarf taxa. From the point of view of taxonomic and differential diagnosis, we have limited our size-based discrimination arguments to molar comparisons as (i) the type specimen of *P. cypriotes* is a lower m3, (ii) the paucity of cranial material within the *P. cypriotes* hypodigm precludes additional metric comparisons with XY.05.1, and (iii) elephant molars exhibit little-to-no sexual size dimorphism, negating any issues that might arise from a misdiagnosis of sex in XY.05.1.

When compared to the type material of *P. cypriotes*, the interpreted as third molars of the Xylophágou skull appear to be much larger: their width is 35–55% larger than the corresponding maximal and minimal dimensions of *P. cypriotes* (Table 2). An exact comparison of the molar length and height is not possible, as the measurable length depends on the wear stage and the consequent progressive loss of the mesial plates, while the height cannot be measured on non-isolated specimens. Even so, the XY.05.1 molar lengths are far greater than those of the *P. cypriotes* sample (Table 2), although a number of plates have been lost to wear in the studied specimen. Moreover, a lower third molar distal fragment from Achna (NHML M 12611c, referred here together with the other specimens from Achna to *P. xylophagou*) appears to be about 70% higher as the *P. cypriotes* lectotype M 8591 (NHML). The same size difference is observed when comparing the Xylophágou molars to the mostly fragmentary dental material of *P. cypriotes* from Akrotíri-*Aetókremnos*, where the maximal measurable occlusal width is less than 33 mm (Reese, 2001), much narrower than that of the studied molars. Thus for all tooth variables, barring plate count, *P. xylophagou* falls outside of the size-range of *P. cypriotes*. In this sense, it mirrors the situation in Sicily and Malta where *P. falconeri* and *P. mnaidriensis sensu stricto* (Adams, 1874) differ in size, but have overlapping plate count values (Herridge, 2010, tab. 2). Plate count, while being a key taxonomic character in mainland elephants is problematic for insular taxa. All insular dwarf species exhibit the parallel trait of having reduced plate number compared to the mainland species *P. antiquus*, as a retention of many plates in much smaller molars would result in extremely thin, thus functionally problematic, enamel bands (Lister and Joysey, 1992).

The interpretation of the XY.05.1 molars as M3s further means that our size-based differential diagnosis of *P. xylophagou* in relation to *P. cypriotes* is a conservative test: if indeed they are pre-M3 teeth, the true size difference between these taxa would have been underestimated, and our argument for taxonomic discrimination strengthened.

Apart from the size difference, however, there is no significant morphologic differentiation between the *P. xylophagou* and *P. cypriotes* dental samples. Both share high and relatively narrow molar crowns, with weakly wrinkled enamel forming cigar-shaped loops on the occlusal surface typical of *Palaeoloxodon* molars, and both also lack any appreciable median sinuses. Nevertheless, the metrical differentiation alone is considered significant for the specific separation of the XY.05.1, for the following reasons:

a) *Palaeoloxodon xylophagou* falls well outside of the size range of *P. cypriotes,* showing a similar degree of size difference as that observed in the Siculo-Maltese dwarf elephant species *P. falconeri* and *P. mnaidriensis sensu stricto.*
b) The metrical range reported for the mainland *P. antiquus*, sampled from various localities across Europe and various stratigraphic levels, is smaller (Table 2; see also Maglio, 1973, tab. 17; Herridge, 2010, tab. 4.6).
c) Although the elephants are in general highly sexually dimorphic, their molars exhibit only very weak dimorphism, resulting in male individuals having slightly larger molars (Roth, 1992b). As the studied skull is interpreted as belonging to a female individual, it would be expected to have comparatively small teeth, not much larger.

Compared to other samples of Mediterranean endemic elephants the Xylophágou specimen is larger than *P. falconeri* in cranial and dental dimensions, while its dentition is similar in size to *P. mnaidriensis sensu stricto* (Adams, 1874; after Herridge, 2010) from Malta and Sicily (Tables 1 and 2). *P. xylophagou*'s skull is smaller than that of *Palaeoloxodon tiliensis* (Theodorou, Symeonidis and Athopoulou, 2007), however both taxa have similar-sized third molars

(Tables 1 and 2) meaning that *P. xylophagou* has relatively large molars in comparison to *P. tiliensis*. *P. xylophagou*'s teeth and skull are considerably smaller than the large-sized species present on Malta and Sicily, from sites such as Puntali Cave, Za Minica, San Teodoro Cave and Ghar Dalam, erroneously referred to as '*P. mnaidriensis*' (Herridge, 2010; Herridge and Lister, unpublished results).

6. Taxonomic attribution

Palaeoloxodon has been frequently considered as a subgenus of *Elephas*, mainly due to shared dental characters, but it is increasingly regarded as a bona fide genus after the cranial morphological studies of Inuzuka (1977a, 1977b) and Inuzuka and Takahashi (2004) and the adoption and enhancement of their results by later authors (e.g. Shoshani and Tassy, 2005; Shoshani et al., 2007). We also follow this systematic scheme, accepting three genera within the Eurasian Elephantidae: *Elephas* Linnaeus, 1758, *Palaeoloxodon* Matsumoto, 1924 and *Mammuthus* Brookes, 1828 (though one of us, GT, prefers to refer all endemic insular elephants of the Eastern Mediterranean to *Elephas*, in the genus' broad sense that includes *Palaeoloxodon*).

The craniodental morphology of the studied specimen offers diagnostic characters for assessing the taxonomic and phylogenetic relationships of *P. xylophagou* to potentially ancestral populations of the common Pleistocene Eurasian genera *Palaeoloxodon* and *Mammuthus*. *Elephas* is also referred to in the Near Eastern Pleistocene (Albayrak and Lister, 2012; Lister et al., 2013), but its occurrence, systematics and morphology remain poorly understood. The absence of a domed cranial roof, as well as of parallel and closely spaced tusk alveoli in XY.05.1, precludes a connection to *Mammuthus*, whose cranial morphology is well known from numerous specimens (Osborn, 1942; Maglio, 1973; Lister, 1996a). Furthermore, XY.05.1 shares with *Palaeoloxodon* (*P. antiquus* in particular) the high and narrow molars, the rostrally diverging tusk alveoli, the flat or slightly concave frontal area and the very wide frontoparietal region (Osborn, 1942; Maglio, 1973). There is no well-developed rostrally-folding frontoparietal crest, as it is quite often observed in *P. antiquus* and the large-sized insular endemic '*P. mnaidriensis*' skulls from Puntali Cave, but the slight concavity of the frontal area may indicate a similar weakly-expressed condition. In comparison to already known skulls from other Mediterranean islands (Fig. 4) XY.05.1 appears rather lower, wider and less 'inflated' than the extremely paedomorphic *P. falconeri* from Spinagallo (see also Ambrosetti, 1968; pl. II; Palombo, 2001, figs. 1, 2), and proportionally lower and longer than the much larger and more *P. antiquus*-like skull of '*P. mnaidriensis*'. Allometric changes are a consequence of the dwarfing evolutionary process (Roth, 1992a; Palombo, 2001, 2004; Palombo and Giovinazzo, 2005) and mainly vary according to the degree of size diminution, constituting a typical case of evolutionary parallelism. Shape differences observed between *P. xylophagou* and *P. antiquus* may thus be explained by general insular dwarfing scaling trends, but this must be confirmed by further study. Another peculiar character of the studied skull is its rather small size in relation to its dentition: it is clearly smaller than the *P. tiliensis* skulls (Fig. 4), although its molar size falls among the minimal values of the *P. tiliensis* range. Given that XY.05.1 quite probably belongs to a female individual, this difference may be the result of pronounced sexual size dimorphism in the skull versus very little size dimorphism in the teeth. This is very common in Elephantidae, resulting in proportionally larger teeth in females (Haynes, 1991, chapter 2; Averianov, 1996). It is also possible that the relatively large teeth of *P. xylophagou* reflect time of isolation on Cyprus: insular mammals often have relatively large teeth reflective of ontogenetic scaling trends (Gould, 1975), but it has also been suggested that teeth and skeleton evolve at different rates in insular mammals, with the skeleton becoming reduced in size at a faster rate than the teeth (Lister, 1996b). Herridge (2010) further showed that for insular dwarfs, the smallest taxa exhibited the least discrepancy between postcranial and dental size reduction, leading her to postulate that the smallest taxa had also been isolated the longest, allowing time for dental size-reduction to 'catch up' with the body size. In this scenario, *P. xylophagou*'s small-sized skull with relatively large teeth would suggest a dwarfing process which had strong selection for rapid and extreme body-size change in comparison to *P. tiliensis*, which is interesting given the much larger land area of Cyprus. However, it could be also due to interspecific morphologic variations that reflect their distinct evolutionary paths and adaptations to non-identical insular environments. Insular dwarfing occurred independently multiple times in the Pleistocene, in multiple places in the Mediterranean and elsewhere, and to different degrees in response

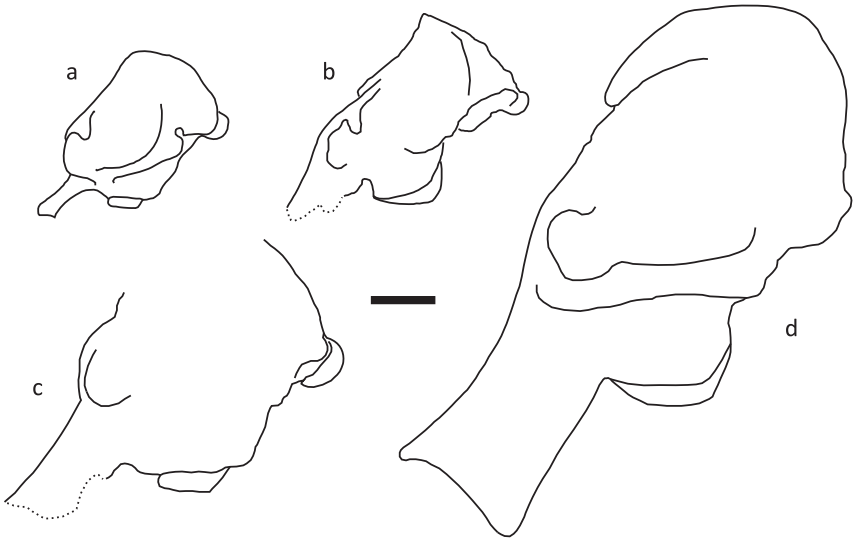

Fig. 4. Graphical comparison of Mediterranean endemic elephant cranial shapes in lateral view: (a) *Palaeoloxodon falconeri*, female skull № 4, Spinagallo Cave, Sicily (Ambrosetti, 1968, fig. 14, reversed); (b) *P. xylophagou* n. sp., partial female skull XY.05.1, Xylophágou, Cyprus, GSDC; (c) *P. tiliensis*, partial skull T. 189/96, Charkadió Cave, Tílos, AMPG; (d) '*P. mnaidriensis*', male skull MGP 1, Puntali Cave, Sicily (drawn from Ferretti, 2008, fig. 4B). Dotted lines denote the outline of preserved parts in incomplete specimens. Scale: 10 cm.

to each island's particular ecological conditions at colonisation time, thus resulting in potentially different morphotypes.

6.1. Attributable specimens to P. xylophagou

Other finds which are attributable to *P. xylophagou* according to existing descriptions include:

a) A molar from Kyrénia-*Athiaeféntis*, found in 1961 and anecdotically reported as having quite large dimensions (Reese, 1995, pp. 41–42).
b) Several large-sized bone and dental fragments occasionally cropping out at the beach at Ormídeia-*Vathiá Laxiá* (Reese, 1995, pp. 144–148).
c) Sporadic large-sized bones and a tusk from at least four additional sites along the Ormídeia–Xylophágou coast (Reese, 1995, p. 148; Poole and Robertson, 1998; Iliopoulos et al., 2011).

We were unable to examine and/or include these specimens in the present study, because they are either lost (a), or privately owned (b, c; in line with current ethics regarding taxonomic publications).

7. Biostratigraphy–biogeography

The reconstruction of the evolutionary history of the Cypriot endemic fauna as a whole and the endemic elephants in particular is hampered by the extremely impoverished nature of the fauna, which impedes the biostratigraphic correlations among the known localities, as well as by the lack of a well-established, fine-scale chronologic framework. *Phanourios minor* is ubiquitous and found in both *P. cypriotes* and *P. xylophagou*-bearing sites. There is also no apparent morphological or metrical change in the hippopotamus material, which could be used for biochronological reasons. A faunal chronology has then to be based on physicochemical dating methods, as well as on geologic and stratigraphic data.

Several dates have been produced using radiometric and chemical methods [Amino Acid Racemisation (AAR), Electron Spin Resonance (ESR) and Radiocarbon ^{14}C], but they refer to a few sites only. Moreover, they were usually published many years ago, using now outdated methodologies and should be regarded with caution (see Herridge, 2010, section 3.3, for a detailed discussion and an assessment of their reliability). Nevertheless, in some cases the reported ages are cross-checked using independent methods, thus increasing their reliability, while in any case they provide a gross estimation of a site's chronology. Practically all the direct dating of mammalian skeletal elements was carried out on *Phanourios* material, reflecting its great abundance with regard to other species.

Out of the more than twenty elephant-bearing sites on Cyprus only eight have associated radiometric ages. The best dated locality is Akrotíri-*Aetókremnos*. On the basis of 36 radiocarbon determinations, five of which are recent (following the ^{14}C Accelerator Mass Spectrometry method), Akrotíri-*Aetókremnos* is dated to 11,504–12,096 calibrated years BP with a 2σ uncertainty (Wigand and Simmons, in Simmons and associates, 1999; Simmons, 2014), that is at about the Pleistocene/Holocene boundary (currently set at 11.65 ka, Gradstein et al., 2012, chapter 30.7). An elephant molar plate fragment from the same site was dated using AAR at 13 ka ±20%. Other elephant-bearing localities that have been dated using ESR and AAR include Káto Dikomo-*Vokolóspilios*, Agía Eiríni-*Pervólia*, Agía Eiríni-*Dragontovounári*, Liverá-*Mándres Virilas*, Akanthoú-*Archángelos Michaíl*, Kisónerga-*Kleiotoúdes* and Agía Nápa (Reese, 1995; Theodorou et al., 2007b). Only Agía Eiríni-*Dragontovounári* and Akanthoú-*Archángelos Michaíl* have yielded finds determinable to the species level, that is *P. cypriotes* (see Reese, 1995). All seven have produced latest Pleistocene – early Holocene ages (about 6–20 ka BP). No older dates exist, so there is no indication on the lower biostratigraphic limit of *P. cypriotes*.

The large-sized elephant material, which is attributable to *P. xylophagou*, comes almost exclusively from the SE part of the island, at the area of Achna, Ormídeia and Xylophágou. There are no radiometric ages associated with these localities, but geological evidence suggest a significantly older age. Based on a preliminary study of the local stratigraphy Theodorou et al. (2005a) estimated that the fossiliferous layer in the Xylophágou locality is at least 75 ky old. In a broader geological aspect, the region belongs to the Fanglomerate Group of the Circum-Tróodos Sedimentary Succession, which consists of Pleistocene gravels, sands and silts (Poole and Robertson, 1991, 1998; GSDC, 1995). The Fanglomerate Group is widespread around the Tróodos massif and it is considered as a large-scale, tectonically controlled depositional event, directly related to the strong Quaternary uplift of the island (Robertson, 1977; Poole and Robertson, 1991, 1998; Harrison et al., 2013). According to Poole and Robertson (1998) the fossiliferous layer of the Xylophágou area is correlatable with the F3 Fanglomerate Unit of the northern Tróodos margin, which was deposited during the time period 192–185 ka (MIS 7, late Middle Pleistocene), based on Uranium-series dating (Poole et al., 1990; Poole and Robertson, 1991, 1998). If this correlation is true, then the *P. xylophagou* remains may date to around 190 ka. An early, pre-130 ka age would also be deduced even if the conglomerate that overlays uncomformably the fossiliferous sedimentary unit proved to belong to the most recent F4 Fanglomerate Unit, which has been dated to 130–116 ka (Poole et al., 1990). Such a correlation is rather unlikely, however, as, according to the same authors, the contemporary to F4 Tyrrhenian marine terrace is situated at less than 3 m above present sea level in the SE Cyprus coastal area, considerably lower than the sedimentary sequence at the Xylophágou coast.

Moreover, in a recent correlation of Poole's et al. (1990) radiometrically dated levels to the deposits along the Lárnaca Bay coast, Zomeni (2012, pp. 103–104) dated the formation of the lower marine terrace at Xylophágou to the last interglacial (MIS 5e). This means that the fossiliferous sequence, which was eroded by the sea during the terrace formation, is older, not contradicting Poole and Robertson's (1998) age estimation.

From the apparent stratigraphic differentiation between the two Cypriot elephant species, with *P. cypriotes* appearing to have an age in the order of 10 ka, and *P. xylophagou* in the order of 200 ka, two evolutionary and biogeographical hypotheses emerge:

A There is a single elephant migration event to Cyprus, presumably sometime in the Middle Pleistocene. *P. xylophagou* and *P. cypriotes* each represent 'snapshots' of a single evolutionary cline of phyletic size reduction, with *P. xylophagou* ancestral to the smaller-sized, stratigraphically younger *P. cypriotes.*
B There were at least two independent elephant colonisation events, involving two separate evolutionary processes of island dwarfing. The first resulted in the evolution of a medium-sized *P. xylophagou* and was followed by the extinction of this species after an unknown period of time. The second process led to the evolution of the smaller-sized *P. cypriotes.* Given there are no sites where *P. xylophagou* and *P. cypriotes* co-occur, the extinction of the former would have presumably occurred before the arrival of the latter taxon.

Hypothesis B is the least parsimonious, necessitating an additional migration event over a highly improbable (due to very long distance) 'sweepstake route'. Given the stratigraphical constraints imposed by the likely age of *P. xylophagou*, under this scenario the *P. cypriotes* migration may have taken place during the low sea level

of MIS 6 (c. 140 ka), or close to the last glacial maximum (MIS 2, c. 20 ka), which is approximately contemporary to the first appearance of this species in the Cypriot fossil record. Bathymetric data show that the sea level drop during these glacials would have indeed shortened the minimal distance of Cyprus from the mainland, though by a very modest 10–15%, because of the very deep sea bottom and the steepness of the coastal areas. In this case the shortest possible route (from the Cilician coast to the Karpasía Peninsula at the NE of the island) would be about 60 km, which is longer than the maximal recorded distance covered by a swimming extant elephant (48 km; Johnson, 1980). The low probability of immigration to Cyprus is further evidenced by the highly unbalanced and endemic nature of the Cypriot Pleistocene mammalian fauna. In addition, there is no evidence of faunal turnover in other Cypriot Pleistocene taxa. In contrast, multiple colonisation events by elephants on other Mediterranean islands (at least twice on both Sicily and Crete; Herridge, 2010) are supported by clear evidence of faunal turnover in other mammalian taxa.

A single phyletic dwarfing event in which *P. xylophagou* is the ancestor of *P. cypriotes*, Hypothesis A, is thus the most conservative interpretation of the current evidence available. However the existing faunal and chronologic data are too scanty and/or problematic for this scenario to be considered well supported. Current data also prevent a detailed discussion of the likely rate and mechanisms of dwarfism on the island: while there is evidence for the persistence of *P. cypriotes* on Cyprus until ca. 12 ka, only a few *P. cypriotes* specimens and sites are directly associated with radiometric dates, precluding a confident assessment of the first appearance date for this taxon. The island dwarfing is, at least potentially, a rapid evolutionary process, as illustrated by examples of dated colonisation events during the Holocene (Lister, 1989; Lomolino et al., 2013). It is not known, however, if this very high evolutionary rate applies to all island colonisers, or depends on the specific conditions of each colonisation. Moreover, it has been shown that some anatomical features (e.g. dental size and structure) may be more persistent and lag behind the rapid body dwarfing (Lister, 1996b; Lomolino et al., 2013). These less rapid adaptive changes may produce a significantly different morphology compared to the initial dwarfing event. There is no evidence for intermediate sizes between *P. xylophagou* and *P. cypriotes* in the available material, which could be argued to support the rapid evolution of small size and thus a large ghost range for *P. cypriotes*. Unfortunately the island-wide paucity of elephant samples could reflect a geological or taphonomic bias that resulted in an incomplete fossil record. Future systematic palaeontological sampling and dating of existing and additional localities will certainly help address these questions.

8. Conclusions

Although our knowledge on the Cypriot endemic elephants is limited by small sample sizes, the new specimen presented here provides important data on the cranial morphology of the larger form and offers good evidence on the existence of two elephant species on Cyprus: *P. xylophagou* of late Middle Pleistocene age, and *P. cypriotes* of latest Pleistocene to early Holocene age. Both are strongly dwarfed but the older is larger, close to the size of *P. tiliensis*, while the more recent is similar to the extremely small *P. falconeri*. Both species share morphological characters with *P. antiquus*, but the phylogenetic relations between them are not yet resolved.

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