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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.