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Insular adaptations in the astragalus-calcaneus of Sicilian and Maltese dwarf elephants

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ABSTRACT

The endemic Pleistocene dwarf elephants from Sicily and Malta display numerous anatomical changes with respect to their putative mainland ancestor and contemporary *Palaeoloxodon antiquus*, including significant differences in the functional morphology of the astragalus-calcaneus. Here we describe the functional morphology of dwarf elephants from the Siculo-Maltese palaeo-archipelago, with a particular emphasis on *Palaeoloxodon* ex gr. *P. falconeri* from Spinagallo Cave (Hyblean plateau, Sicily). Interspecific comparisons across a wide spectrum of body mass indicate that a decrease in the mass of dwarf elephants was accompanied by a shift from mass being transmitted between the tibia-astragalus to relatively more mass being transmitted by the tibia-calcaneus. This is most evident in the calcaneus of small-bodied *Palaeoloxodon* ex gr. *P. falconeri*, which have a large and continuous tibio-fibular facet suggesting increased flexion in the ankle-joint. Synostosis between the distal tibia-fibula and the calcaneus' wide articular facet for the fibula in this species limited medio-lateral displacement of the astragalus-calcaneus relative to the tibia, suggesting possible evidence of 'low-gear' locomotion related to the very hilly topography of Sicily. Furthermore, differences in the functional morphology of the calcaneus between the similar-sized *Palaeoloxodon* sp. from Luparello Fissure (Palermo, Sicily), and Benghisa Gap (southern Malta) are possibly ecophenotypic, as a result of differing insular environments, or alternatively warrant a taxonomic revision of the material from Luparello Fissure.

1. Introduction

Islands are well known for effecting significant size and shape changes in endemic species, and are justifiably often referred to as the laboratories of evolution (Whittaker and Fernandez-Palacios, 2006; van der Geer et al., 2010). Being excellent swimmers, proboscideans frequently colonized and became isolated on islands during the Pleistocene where they underwent significant changes in both body mass and anatomy (Ambrosetti, 1968; Roth, 1992, 1993; Caloi et al., 1996; van den Bergh, 1999; Agenbroad, 2001; Palombo, 2003, 2007; Ferretti, 2008; Herridge, 2010). However, the extent to which the highly derived morphologies evidenced in the appendicular skeleton of insular proboscideans reflect selection for locomotion in specific insular environments is poorly understood. In order to investigate the possible effects of insularity on proboscidean anatomy and locomotion in particular, we examined the anatomy of the Sicilian and Maltese dwarf elephant hindfoot, which differs significantly among insular *Palaeoloxodon* spp., as well as compared with their putative mainland ancestor and contemporary *Palaeoloxodon antiquus* (Falconer and Cautley, 1847).

The changes in the functional morphology of insular endemics are hypothesized to have been shaped by multiple factors, including the influence of selection for locomotion on rocky substrates (Caloi and Palombo, 1990, 1994, pp. 157) and in relatively inaccessible areas with steep relief (cf. Leinders and Sondaar, 1974, pp. 112). This particularly applies to animals with large home ranges that colonised islands with seasonal environments characterized by complex geomorphology where natural barriers separate food resources. Another factor, particularly among dwarf proboscideans likely includes a reduction in body mass, especially considering that large mass often constrains posture, morphology and locomotion (Hildebrandt, 1988; Biewener, 1989, 1990, 2003). Furthermore, in some unbalanced insular faunas the absence of top predators (such as on some Mediterranean islands and on the Siculo-Maltese palaeo-archipelago at the time of "*Elephas falconeri* Faunal complex") makes speed and manoeuvrability to escape predators redundant (van der Geer et al., 2010, p. 363; Quintana et al., 2011; see also Bonfiglio et al., 2002 for faunal assemblages).

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As a result, many Pleistocene insular endemic herbivores are characterized by morpho-functional adaptations in their limbs and feet specifically to increase stability and decrease the likelihood of injury through twisting ankles (see e.g. Sondaar, 1977; Caloi and Palombo, 1994, 1995; Köhler and Moyà-Solà, 2001; van der Geer et al., 2010, pp. 361–363), a pattern often referred to as 'low-gear locomotion' (Sondaar, 1977, pp. 683–686). Since dwarf elephants from the Siculo-Maltese palaeo-archipelago inhabited different physiographic contexts (Sicily is 86% hilly/mountainous while Malta's highest elevation is 253 m, see Benedetto and Giordano, 2008) they are therefore particularly suitable for investigating the factors shaping the locomotor evolution of endemic elephants. Insular elephants from these islands further include diverse body masses with respect to the ancestral mainland species, and also evolved in the presence/absence of predators (Bonfiglio et al., 2002; Palombo, 2007).

This study aims to contribute new data on the morphologically highly derived hindfoot, with a particular emphasis on the calcaneus and astragalus of the dwarf elephant from Spinagallo Cave, a site located on the escarpment of the Hyblean plateau of Sicily (Accordi and Colacicchi, 1962; Ambrosetti, 1968) with respect to its mainland ancestor and contemporary *P. antiquus*. This study further examines whether differences exist among co-generic endemic elephants of different size and mass that inhabited the islands of Sicily and Malta during the Middle and Late Pleistocene (e.g. Vaufrey, 1929; Imbesi, 1956; Ambrosetti, 1968; Caloi and Palombo, 1994; Caloi et al., 1996; Palombo, 1996, 2001, 2003, 2007; Raia et al., 2003; Ferretti, 2008; Herridge, 2010; van der Geer et al., 2010).

1.1. Systematics and taxonomy

Sicily was repeatedly colonized by *P. antiquus* during the Middle-Late Pleistocene, giving rise to multiple dwarf descendants. The systematics and taxonomy of Siculo-Maltese elephants are however the subject of on-going debate, particularly with regard the number of species and the nature of phyletic relationships between Sicilian and Maltese elephants (e.g. Vaufrey, 1929; Ambrosetti, 1968; Palombo, 2001; Herridge, 2010). These elephants have a wide range in size and mass, including individuals on Sicily within the size range of mainland *P. antiquus* (see Chilardi, 2001; Palombo, 2001, pp. 487–488), as well as *P. antiquus leonardi* (Aguirre, 1969), an allegedly endemic subspecies of slightly reduced size reported from Palermo. The presence of an as yet unnamed ca. 2 m-tall dwarf, *Palaeoloxodon* sp. was recently proposed for some Middle-Late Pleistocene deposits in Sicily (Herridge, 2010), and in addition the roughly 1,7 m-tall (Middle?) Pleistocene *Palaeoloxodon mnaidriensis* (Adams, 1874) is reported from Malta. The ca. 1 m-tall, 150–300 kg Middle Pleistocene *Palaeoloxodon falconeri* (Busk, 1867) is represented from both Sicily and Malta while *Palaeoloxodon melitensis* (= *Elephas melitensis* Falconer in Busk, 1867) is regarded as a junior synonym of *P. falconeri* Busk under the current taxonomy (see Ambrosetti, 1968, pp. 338–339; Herridge, 2010, pp. 193–194).

Pending a taxonomic revision of Siculo-Maltese remains, and notwithstanding issues of conspecificity between Malta and Sicily, we provisionally include the small Siculo-Maltese elephants in "*Palaeoloxodon* ex gr. *P. falconeri*" and the larger ones in "*Palaeoloxodon* ex gr. *P. mnaidriensis*", while *Palaeoloxodon* sp. is used for specimens whose attribution to either group is doubtful because of size or possible autapomorphies (see Palombo, 2001; Herridge, 2010). This nomenclature acknowledges that each group possibly includes multiple morphotypes or taxa, particularly since the chronological range of these species is poorly constrained and dwarfism may have occurred repeatedly on Sicily/Malta (Palombo, 2007; Herridge, 2010; Herridge et al., 2014).

2. Materials and methods

Table 1 lists the extant and fossil Elephantidae material studied. The sample includes the type-series of *P. falconeri* from Zebbug Fissure (Malta) and a range in body mass from ca. 150 kg *Palaeoloxodon* ex gr. *P. falconeri* to ca. 10-ton *P. antiquus* (for a discussion on body mass refer to Roth, 1990; Palombo, 2007; Lomolino et al., 2012; Larramendi, 2015). The insular *Palaeoloxodon* spp. fossils are derived from several Middle and Late Pleistocene cave and fissure deposits on Malta and Sicily (Fig. 1; see also Herridge, 2010, pp. 357–374) and were compared with extant species (*Loxodonta africana* (Blumenbach, 1797) and *Elephas maximus* (Linnaeus, 1758) and select specimens of *P. antiquus* from Germany (Neumark-Nord 1, Geiseltal, Sachsen-Anhalt) and Italy (Riano, Rome). The *P. antiquus* sample from Neumark-Nord 1 was collected from a lacustrine environment, and possibly dates to the late Middle (MIS 7) or early Late Pleistocene (MIS 5e) (see Palombo et al., 2010; Marano and Palombo, 2013 for a discussion) and likely postdates the *P. antiquus* remains collected from Riano, Italy (MIS 9) (Maccagno, 1962; Palombo, 2009). Additionally, type specimens of *Mammuthus lamarmorai* (Major, 1883), from Gonnesa, Sardinia were measured for comparison (see Palombo et al., 2012).

Table 1
Materials analysed in the present study. Collections abbreviations: Natural History Museum, London (NHMUK), Gemellaro Museum, Palermo (GMP), Museo di Paleontologia, Sapienza, University of Rome (MPRU), Institut de Paléontologie Humaine, Paris (IPH), Naturhistorisches Museum, Basel (NHMB), Landesmuseum für Vorgeschichte, Halle, Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt (LVH), Iziko SA Museum, Gardens, Cape Town (SAM) and the National Museums of Kenya, Nairobi (KNM).

Species	Provenance	Astragalus		Calcaneus	
		N	Specimens	N	Specimens
P. antiquus	Riano, Italy	0	MPRU	1	MPRU
	Neumark-Nord 1, Germany	5	LVH	7	MPRU
Palaeoloxodon ex gr. *P. mnaidriensis*	Puntali Cave, Sicily	1	NHMB-G.2344	3	NHMB-2343, GMP
	Mnaidra Gap, Malta	1	NHMUK-44453	–	–
Palaeoloxodon sp.	Zà Minica Cave, Sicily	1	GMP-ZM72	0	–
Palaeoloxodon sp.	Luparello Fissure, Sicily	6	IPH	5	GMP-GL103, IPH
'*P. melitensis*'	Mnaidra Gap, Malta	1	NHMUK-44452	0	–
	Benghisa Gap, Malta	–	–	2	NHMUK-44451 NHMUK-44456
Palaeoloxodon ex gr. *P. falconeri*	Spinagallo Cave, Sicily	51	MPRU, NHMB	50	MPRU, NHMB
	Luparello Fissure, Sicily	–	GMP	2	GMP-GL97, IPH
	Zebbug Fissure, Malta	1	NHMUK-49263	–	–
	Mnaidra Gap, Malta	1	NHMUK-44531	–	–
M. lamarmorai	Gonnesa, Sardinia	1	NHMB-Tyi207i	1	NHMB-Tyi207i
L. africana	Kenya, various places	–	–	13	KNM
	South Africa	2	SAM-M126	–	SAM-M126
E. maximus	Uncertain	1	SAM-ZM39031		SAM-ZM39031