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Extreme Body Size Variation in Pleistocene Dwarf Elephants from the Siculo-Maltese Palaeoarchipelago: Disentangling the Causes in Time and Space

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Abstract: The phenomenon of insular dwarfism in proboscideans is particularly well represented on the Siculo-Maltese Palaeoarchipelago, an island group on which a species complex of palaeoloxodont elephants evolved during the Middle-Late Pleistocene. This likely included three species from Malta, four from Sicily (and possibly its palaeo-islands), and one from Favignana Island, ranging in size from the 1 m-tall *Palaeoloxodon falconeri* to continental-sized 4m-tall *P. antiquus*. However, our understanding of the causes for extreme differences in body size among insular samples in such a small geographic region is still limited. Here, I document the full range in size of elephants from the palaeoarchipelago, and discuss the reasons for size differences on the three islands in time and space in relation to predation, competition, resource limitation, accelerated life history, and duration of isolation. Differences in size between larger and smaller Sicilian elephants from Luparello Fissure, as well as possibly also in *P. ex gr. P. mnaidriensis* from Puntali Cave, San Teodoro Cave, and Favignana Island, may relate to the duration of isolation, or alternatively environmental stressors associated with the Last Glacial Maximum in the case of the Favignana elephant. Additionally, small but significant differences in size observable in Middle Pleistocene *P. ex gr. P. falconeri* from different localities on Sicily, as well as in Maltese *P. 'melitensis'* may also relate to duration of isolation, highlighting the need for better geochronological data in order to better distinguish macro-ecological causes driving body size change from more subtle effects relating to duration of isolation.



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1. Introduction

Although the phenomenon of insular dwarfism is well-characterized globally in insular proboscideans from numerous islands and their archipelagos, recent evidence has shown there is no simple relationship between environment and body size in insular proboscideans. Furthermore, even elephants on the same island at different points in time may evidence large discrepancies in size [1]. No island archipelago illustrates this problem better than the Siculo-Maltese Palaeoarchipelago (Figures 1 and 2), a group of islands including Sicily, Malta and Favignana, which was repeatedly colonized during the Pleistocene by the straight-tusked elephant *Palaeoloxodon antiquus* (Falconer and Cautley, 1847), giving rise to a diverse species complex of dwarf palaeoloxodont elephants.

During this period, an extremely wide range in body sizes evolved in response to insularity, ranging almost continuously in size from 1 m-tall dwarfs to continental-sized elephants measuring ca. 4 m at the shoulders (Figure 2; Table 1). Thus far, the causes for size variation in insular proboscidean taxa belonging to the family Elephantidae have been compared in select samples from diverse geographic origins, shedding new light on the process of insular dwarfism [1,2]; p. 108–109 in [3], although the extreme size diversity seen in Siculo-Maltese elephants has never been comprehensively examined. Thanks to recently published data from the Siculo-Maltese archipelago and continental *P. antiquus* [4–8]), a

more complete understanding of the range of size variation in insular dwarfs and a fuller examination of its underlying causes is now possible.

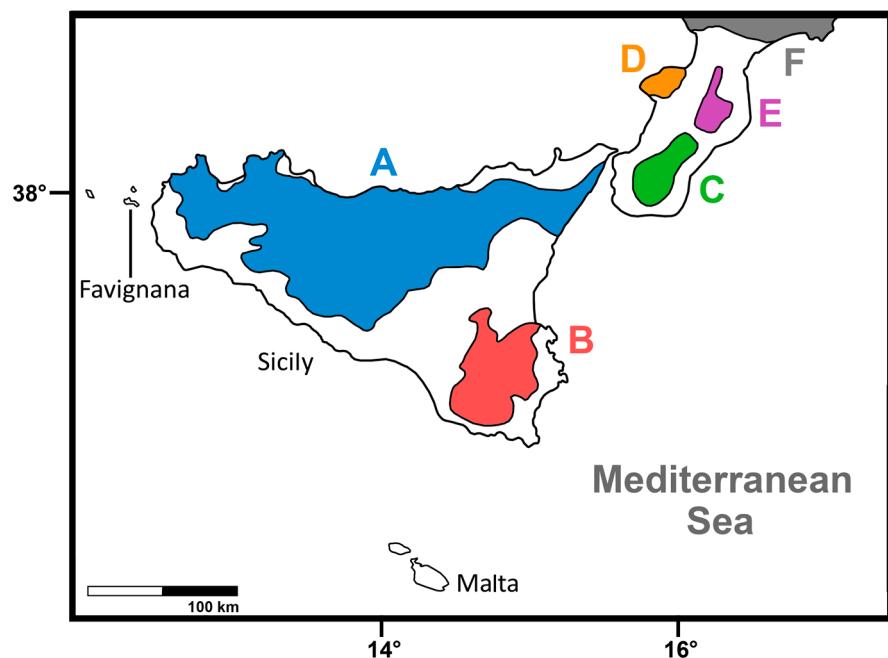


Figure 1. The Siculo-Maltese Palaeoarchipelago including present-day Sicily, Favignana and Malta. The palaeogeography of Calabria and Sicily during the Early Pleistocene is superimposed in colour (after [9]): (A) Northern-Central Sicily (B) Hyblean Plateau; (C) Aspromonte Massif (D) Cape Vaticano Massif (E) Serre Massif (F) Northern Calabria.

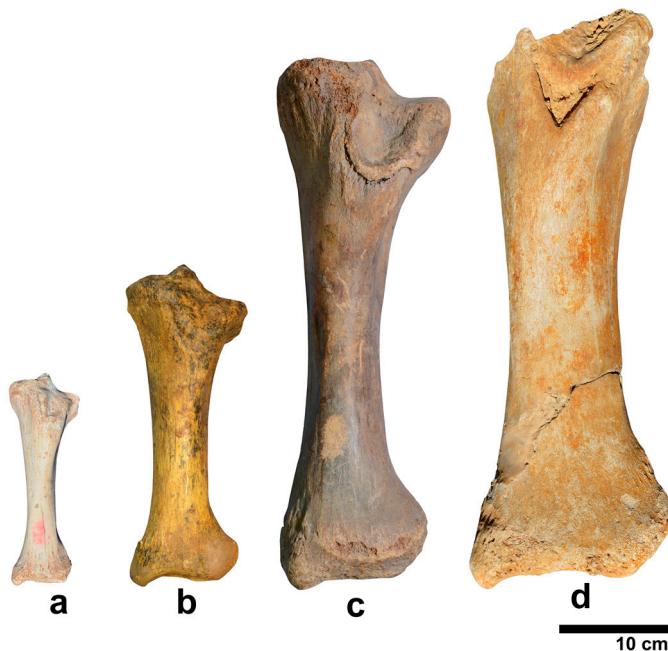


Figure 2. Tibiae of adult Sicilian *Palaeoloxodon* spp. in cranial aspect (a) *P. ex gr. P. falconeri* (Busk, 1867) from Spinagallo Cave (University of Catania-T64, dex) (b) *Palaeoloxodon* sp. From Luparello Fissure (Institut de Paléontologie Humaine, Paris-F2928, dex) (c) *P. ex gr. P. mnaidriensis* (Adams, 1874) from Puntali Cave (Gemellaro Museum, Palermo-GPM12, sin) (d) *P. antiquus* (Falconer and Cautley, 1847) of uncertain Sicilian provenance (University of Catania, dex).

Table 1. Elephantinae taxa sampled, their geographic provenance, approximate adult skeletal height, geochronological age and collections provenance. Shoulder heights are based on Scarborough [8]. Additional measurements from the literature [5–8] are included and acknowledged in the captions of Figures 3 and 4.

Taxon	Shoulder Height (m)	Provenance	Chronology	Collections
<i>Palaeoloxodon antiquus</i>	3.0–4.0	Neumark-Nord 1, Germany	late Middle or early Late Pleistocene	Landesmuseum für Vorgeschichte, Halle, Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt
		Riano, Italy	Middle Pleistocene	Museo di Paleontologia, Sapienza, University of Rome
		Blanzac, France	Pleistocene	Naturhistorisches Museum, Basel
<i>Palaeoloxodon ex gr. P. mnaidriensis</i>	2.0	Puntali Cave, Sicily	late Middle—early Late Pleistocene	Museo di paleontologia e geologia Gaetano Giorgio Gemmellaro, Università di Palermo; Naturhistorisches Museum, Basel
<i>Palaeoloxodon sp.</i>	~1.7	Grotta dell’Ucceria, Favignana	Late Pleistocene	Museo di paleontologia e geologia Gaetano Giorgio Gemmellaro, Università di Palermo
<i>Palaeoloxodon mnaidriensis</i>	~1.7	Mnaidra Gap, Malta	Pleistocene	Natural History Museum, London
<i>Palaeoloxodon ‘melitensis’</i>	-	Benghisa Gap, Malta	Middle Pleistocene	Natural History Museum, London
<i>Palaeoloxodon sp. 1</i>	~1.8	Luparello Fissure, Sicily	late Early or early Middle Pleistocene	Institut de Paléontologie Humaine, Paris; Museo di paleontologia e geologia Gaetano Giorgio Gemmellaro, Università di Palermo
<i>Palaeoloxodon falconeri</i>	1.0–1.2	Luparello Fissure, Sicily	Middle Pleistocene	Institut de Paléontologie Humaine, Paris; Museo di paleontologia e geologia Gaetano Giorgio Gemmellaro, Università di Palermo
		Spinagallo Cave, Sicily	Middle Pleistocene	Geological Museum, University of Catania; Museo di Paleontologia, Sapienza, University of Rome; Naturhistorisches Museum, Basel

1.1. Phylogeny and Palaeogeography

The systematics and taxonomy of Siculo-Maltese elephants are, however, the subject of on-going debate, due to uncertainty regarding the number of taxa and the nature of phyletic relationships between Siculo-Maltese elephants, including the elephant from Favignana Island (e.g. [4,8]). All Siculo-Maltese elephants are however descended from *P. antiquus*, which repeatedly colonized Sicily from the Middle-Late Pleistocene onwards, giving rise to multiple dwarf descendants. To begin with in this paper, I therefore provide a brief overview of the evolutionary history and phylogeny of Siculo-Maltese elephants, followed by a summary of the hypothesized causes of insular dwarfism in proboscideans:

During the Pleistocene, the Siculo-Maltese Palaeoarchipelago underwent significant changes in palaeogeography, which likely played a significant role in the evolutionary history of insular elephants: the earliest phyletic ancestors of the 1 m-tall dwarf elephant *Palaeoloxodon ex gr. P. falconeri* (Busk, 1867) appear to have been members of a ghost lineage (see below), likely on one or more of the palaeo-islands of Italy (Figure 1), whereas at the time the most extensive *P. ex gr. P. falconeri* deposit accumulated at Spinagallo Cave the palaeogeography of Sicily likely had more-or-less come to resemble its present shape [10].

In contrast to the small distance between Sicily and Calabria during the late Middle till Late Pleistocene, the distance between Sicily and Malta (at present 93 km) likely fluctuated more dramatically in response to glacio-eustatic sea level changes due to the presence of a shallow submarine bank (the Hyblean-Malta plateau) extending southwards from Sicily (Figure 3.3 in [4]; Figure 1b in [11]).

Thus it was possible for elephants and their coeval faunas to reach Malta using Sicily as a stepping-stone (*sensu* [12]) multiple times from the Middle Pleistocene onwards, most likely during glacial lowstands when a relatively narrow strait separated the two islands (see bathymetric reconstructions on pp. 56–60 in [4,13]. Palaeoloxodont elephants further colonized Favignana (now part of the Aegadian Archipelago) where an elephant survived until around the Last Glacial Maximum. Hence, Sicily, Favignana and Malta were isolated to a greater or lesser degree by rises and falls in Pleistocene sea levels, affording the opportunity for both anagenetic and cladogenetic speciation within the genus *Palaeoloxodon*: currently three taxa are recognized from Malta, *Palaeoloxodon falconeri* (Busk, 1867), *Palaeoloxodon mnaidriensis* (Adams, 1874) and *Palaeoloxodon* sp. from Għar Dalam Cave [4]), although the geochronological range of most Maltese material remains poorly constrained. On Sicily *P. antiquus*, *P. ex gr. P. mnaidriensis* (possibly not part of the Maltese hypodigm, see [4]), *Palaeoloxodon* sp. from Luparello Fissure, and *P. ex gr. P. falconeri* were present, as well as scant *Palaeoloxodon* sp. remains from Favignana Island.

1.2. The Causes of Dwarfism in Insular Proboscideans

Changes in body mass are very common among insular vertebrates [14], with small mammalian taxa typically evolving giant forms, and large taxa evolving dwarfed forms, a phenomenon known as the ‘island rule’ (see [15]). Body mass changes resulting in dwarfism are also well-known in a diverse range of proboscideans [3] and different insular Mediterranean settings [16,17] and though the causes are widely debated, are ascribed to a combination of several factors, among them (i) release from predation pressure, (ii) a decrease in inter and intra-guild competition, (iii) resource limitation, (iv) selection for an accelerated life-history, (v) optimal body size, and (vi) duration of isolation (see [2]; pp. 108–109 in [3,8,18]). Isolation, while also a potential factor, appears to act more indirectly on body size through its effect on the presence/absence of predators and competitors [1], and is therefore not specifically included in the following discussion.

(i) Release from predation pressure—The presence/absence of predators on islands is hypothesized to have influenced the degree of body mass reduction in insular endemics [1]; p. 108 in [3,19] due to ecological release resulting in more pronounced changes in body size on islands lacking mammalian competitors or predators [20,21]. In Sicilian elephants this is likely illustrated by the disparity between the Middle Pleistocene ca. 1 m-tall *P. ex gr. P. falconeri* which inhabited Sicily (or its palaeo-islands) and Malta, whereas the Middle-Late Pleistocene ca. 2 m-tall *P. ex gr. P. mnaidriensis* maintained a larger body size in the presence of predators.

(ii) A decrease in inter- and intra-guild competition—The influence of competition on body size has an important effect on insular taxa, according to the model of Lomolino [20], and the observations of [18]. In Siculo-Maltese insular elephants, it has been suggested that they maintained a larger size in the presence of deer and hippo, likely because smaller intra-guild competitors prevented elephants from reducing in size [3]; see also p. 1447 in [22] and references therein. In contrast, a more recent survey of insular proboscideans including a larger and more geographically diverse sample argued there was much greater size reduction in the presence of competitors, and ecological release from predators and competitors was found to be more important on smaller islands. Another example of size increase because of competition was observed in the Cretan shrew *Crocidura zimmermanni* which increased in size following the arrival of two continental shrews, although this possibly resulted because ecological displacement caused it to adapt to higher regions where greater surface area is better suited to colder temperatures (p. 1447 in [22]).

(iii) Resource limitation—Due to islands being confined areas with finite resources, endemic insular taxa are often faced with resource shortages, favouring the evolution of dwarfs that require less food or water in order to survive and reproduce. Studies of extant elephants indicate that they consume large amounts of biomass (p. 212 in [23]) and frequently move around, sometimes migrating long distances to avoid depleting any one area as they track changes in the local seasonal abundance in food and water [24,25]; p. 534 in [26]. Daily movement distances averaging 27.5 km are reported in *Loxodonta africana* from arid environments, with elephants moving up to 38 km over a 12-h period ([27], see also Table 1 in [28] and references therein for other environments), and African elephants also sometimes migrate several hundred kilometres annually [29–31].

When an inability to migrate long distances on small islands is coupled with seasonal shortages such as likely in the context of a highly seasonal Mediterranean-type climate (which was likely already established around 3.2 Ma in the western Mediterranean, see [32,33], resource limitation is likely to have been a significant factor resulting in a decrease in body mass through time. Additionally, it is conceivable that adaptation on palaeo-islands between what was then southernmost peninsular Italy and the northern palaeo-island of Sicily (Figure 1) may have contributed to reduced size during an early phase of insular endemism (p. 347 in [4]; see also p. 34 in [9]), although fossil evidence for this evolutionary scenario is still lacking.

(iv) Accelerated life-history—In the more recent literature, attention has also been drawn to the fact that selection on life-history traits may have the effect of changing body size merely because of their correlation, rather than primarily acting on body size *eo ipso* [3,34–38]. This view is based on the observation that smaller body mass is typically associated with large litters, rapid maturation, short gestation periods, early reproduction and high population densities [39].

Evidence of an accelerated life history in *P. ex gr. P. falconeri* is allegedly seen in the age-mortality profile of the assemblage from Spinagallo Cave [35] which predominantly consists of immature individuals (at 59%—contrast the mortality profiles in [40] vs. [41–43], and dental remains also potentially suggest higher juvenile mortality in *P. ex gr. P. falconeri* than in the larger *P. ex gr. P. mnaidriensis* (see [44]), as is typical in more r-selected species [45]. Furthermore, the apparent bilateral tusklessness in *P. ex gr. P. falconeri* females (pp. 295–296 in [40]) has also been cited as evidence of a more r-selected life-history as this implies increased investment in reproduction relative to growth and somatic maintenance (p. 303 in [35,37], see also [46]).

Using a mathematical equation which describes the allometric relationship between body mass and physiological time, it has also been proposed that *P. ex gr. P. falconeri* attained sexual maturity much earlier (at 3–4 years), much earlier than in extant elephants, although see evidence against this in [47] and discussion below, also bearing in mind that mass estimates for *P. ex gr. P. falconeri* have since been revised upwards (ranging between 165–300 kg, see p. 104 in [37,48]).

(vi) Optimal body size—The body size and fitness of a particular taxon is a trade-off between energy acquisition and the various requirements of growth and reproduction, including the various thermoregulatory, metabolic, ecological and other factors [49,50]. Under different ecological conditions, different sizes may be favoured (including dwarfism and gigantism on islands), something which is known as optimal body size theory. This has been hypothesized to be around either 0.1 kg [49], 1 kg [50], or different size-optima for different taxa and their underlying bauplans [51]. Accordingly, body size may change when a taxon colonizes an island if it either permits the taxon to attain an optimal body size not attainable in the mainland niche, or if it encounters new restraints requiring body size change. There are however theoretical and observational limits to the theory, which may apply to varying degrees in different situations (see, e.g. [52]).

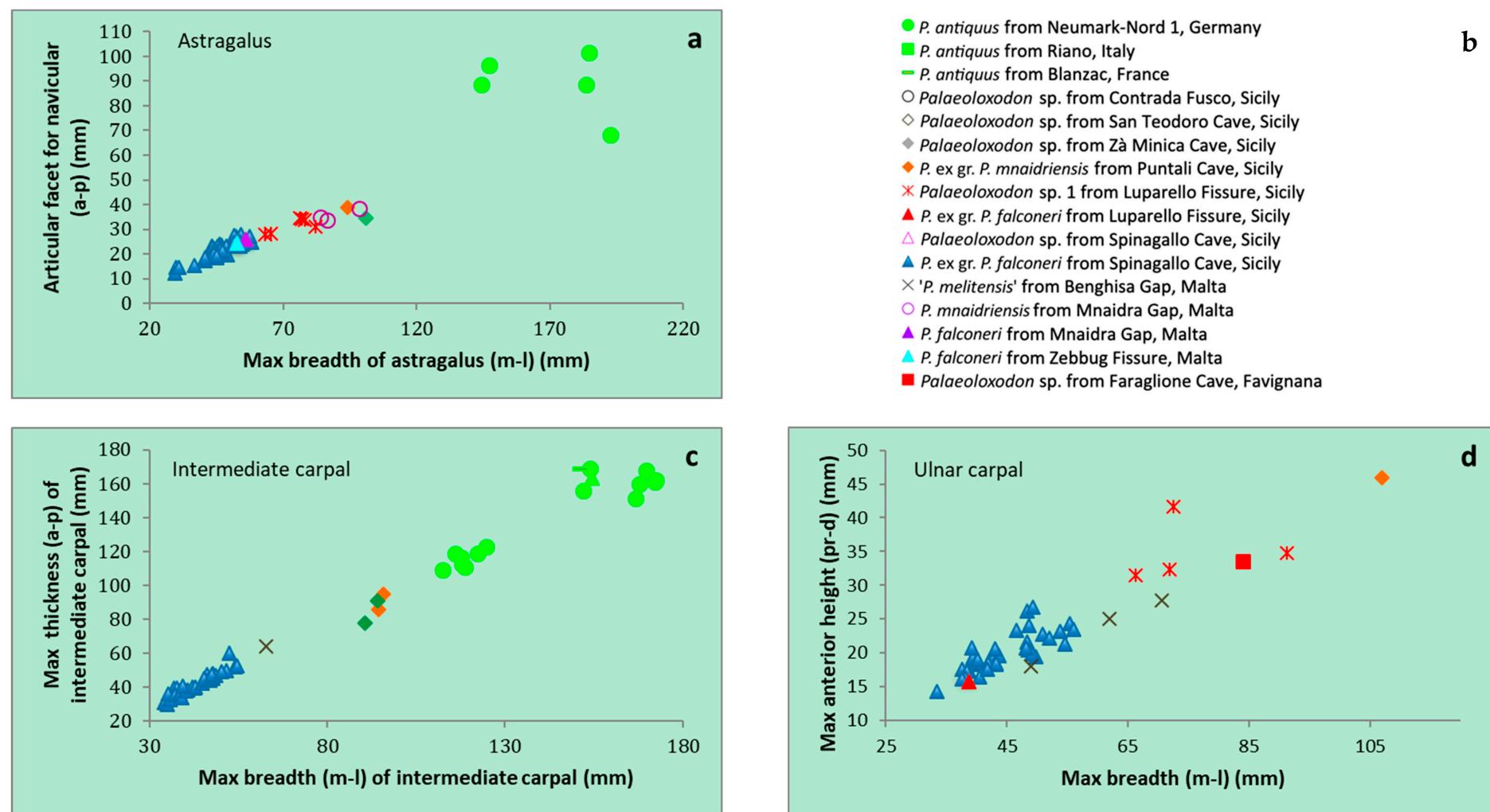


Figure 3. Scatterplot of the dimensions of the foot bones (a) Max breadth of astragalus (m-l) vs. articular facet for navicular (a-p). (b) Figure legend. (c) Intermediate carpal max breadth (m-l) vs. max thickness (a-p). (d) Ulnar carpal max breadth vs. max anterior height. Data sources: *P. antiquus* from Palombo et al., unpublished. All remaining data are original.

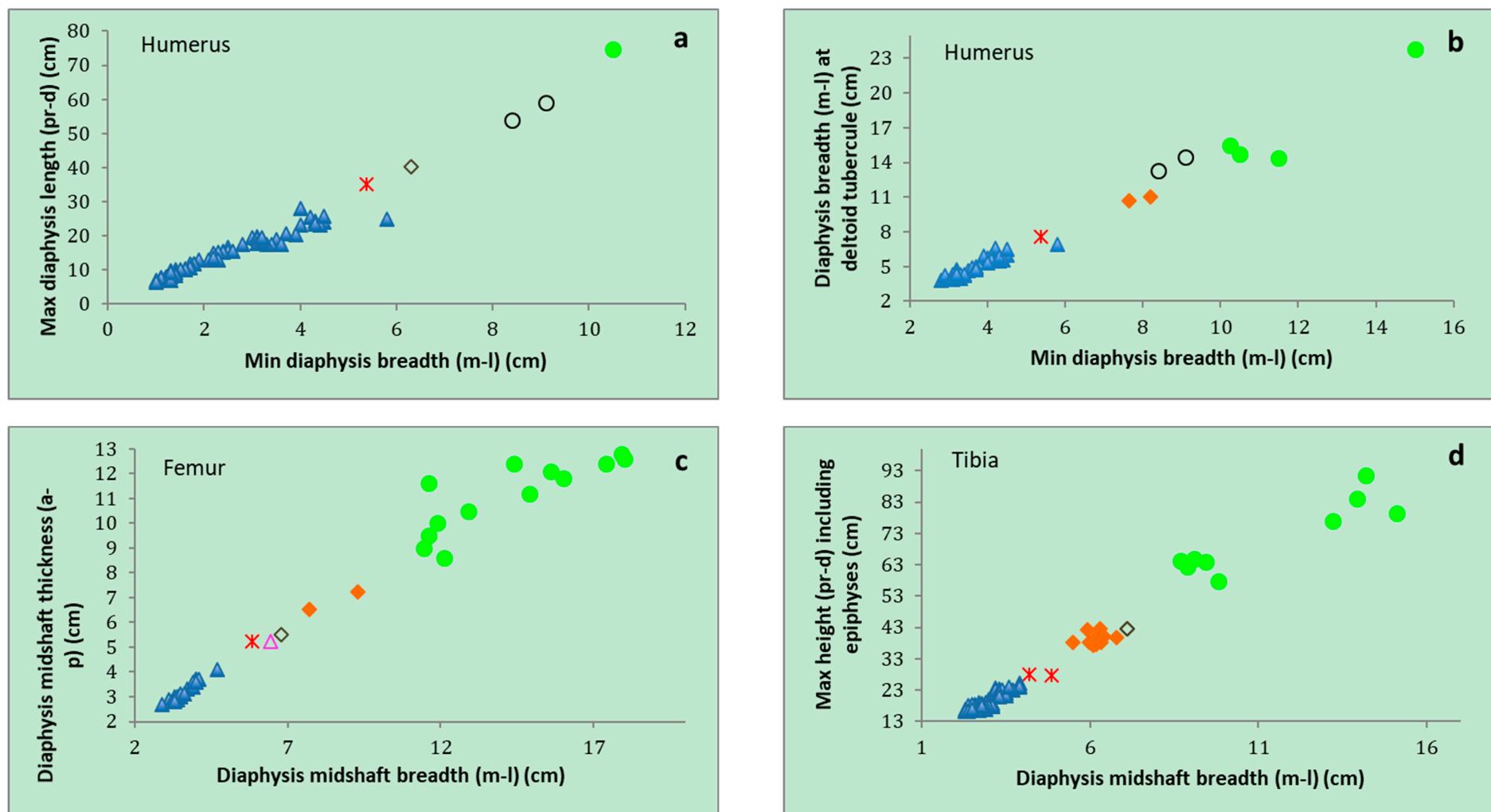


Figure 4. Dimensions of the long bones (a) Humeral min diaphysis breadth (m-l) vs. min diaphysis height (pr-d); (b) Humeral min diaphysis breadth (m-l) vs. diaphysis breadth (m-l) at deltoid tubercle; (c) Femoral diaphysis midshaft breadth (m-l) vs. diaphysis midshaft thickness (a-p); (d) Tibial diaphysis midshaft breadth (m-l) vs. max height (pr-d) including epiphyses. Data sources: *P. antiquus* from Palombo et al., unpublished; for Contrada Fusco and San Teodoro Cave (Table 2 in [5]). Measurements of *P. ex gr. P. falconeri* are from [40]. All remaining data are original. Refer to Figure 3b for figure legend.

(vii) Duration of isolation—Assuming directional selection for increasingly reduced body size over time, one would expect proboscideans that were isolated for longer periods (particularly on islands without predators) to be smaller than those isolated for a shorter duration in time. A further consideration with regard to the degree of dwarfism in insular proboscideans is therefore the duration of isolation, which is known to have differed greatly on different islands ([1], pp. 56–58, 355 in [4,21,53,54]).

When considering the roles of all of the above factors in influencing or permitting size changes in elephants, it is important to remember that the island rule is an emergent trend, and the degree of dwarfism in vertebrates is influenced by a combination of selective forces, depending on the specific context of each island [14,20]. Interestingly, insular body size of large mammals in general is not positively correlated with island area [20], but proboscidean body size is weakly correlated [1], again emphasizing the need for caution when it comes to making generalizations regarding size changes in insular vertebrates [55–57].

2. Materials and Methods

The nomenclature for elephants used here follows the tentative taxonomic framework and phylogeny of Appendix A in [8]. The open nomenclature terminology *ex gr.* (*ex grege*) is used where Maltese taxonomy was later applied to Sicilian material, reflecting the uncertainty in conspecificity between islands (see Appendix A in [8] for details). On Sicily, remains from Spinagallo Cave were dated between 366 and 233 ka (OSL, U-series, see preliminary abstract of [58]). Although the absolute chronology of Pleistocene Malta is also poorly resolved, it has been suggested that Maltese *P. falconeri* is not younger than the Sicilian Stage (Lower Middle Pleistocene, see [59]). The Puntali Cave *P. ex gr. P. mnaidriensis* assemblage from Sicily dates to the late Middle-early Late Pleistocene [60]; the Luparello Fissure, Sicily assemblage likely to the late Early or early Middle Pleistocene [8]. Due to the fact that most of the sites from which samples included in the present study were excavated before rigorous excavation methodologies were commonplace, the stratigraphic provenance of fossils are often only vaguely known, an issue I return to in more detail in the following discussion.

The size of the proboscidean taxa compared varies greatly: *P. ex gr. P. falconeri* shoulder height in the flesh is estimated at ca. 95 cm in bulls, and 80 cm in cows, with estimated body mass ca. 280–300 and 165 kg, respectively (p. 104 in [37]) or perhaps slightly less [61]. The mainland comparator, *P. antiquus* from Neumark-Nord 1, Germany is a rich sample deriving from lacustrine deposits evidencing interglacial climatic conditions [61,62]. The age of the main Neumark-Nord 1 fossiliferous deposits are controversial, either being ascribed to MIS 7 (243–191 ka), or alternatively MIS 5e (128–116 ka, see p. 81 in [63] and references therein). The site has produced the richest *P. antiquus* assemblage from any single locality to date, with the added advantage of the stratigraphic provenance of each fossil being known (pp. 201–218 in [64]). In *P. antiquus* (volumetric) mass estimates in two European individuals indicated a mass of circa 11 and 15 tons, respectively [48].

All measurements were taken with calipers and/or an osteometric board, and measured as the maximum medio-lateral (m-l) breadth and maximum proximo-distal (pr-d) length, and all measurement locations are illustrated in [8]. For the humerus, femur and tibia, measurements from the literature were included for Contrada Fusco and San Teodoro Cave (Table 2 in [5]). For the long bones, measurements of *P. ex gr. P. falconeri* were included from [40]. Due to time constraints and accessibility limitations because of the collection being in storage, the NN1 assemblage was only sub-sampled by the author. However, data were also obtained in 2008–2009 by Maria Rita Palombo (Sapienza, University of Rome), assisted by Federica Marano (Sapienza, University of Rome) and Ebru Albayrak (M.T.A. Natural History Museum, Ankara), and are here included (referred to as Palombo et al., unpublished; see also [65]). Although this adds an element of inter-observer variability, any uncertainties regarding how measurements were obtained were queried directly with Maria Rita Palombo, and in some cases a sub-sample of measurements was compared in order to verify consistency between observers.

Although only appendicular elements were sampled here, comparing size in insular proboscideans using elements of the appendicular skeleton potentially has some advantages in avoiding allometric changes in proportions which may have occurred in the teeth, as relative megalodonty is a known phenomenon in insular vertebrates (pp. 224; 311 in [66]; see also [53]). Differences in appendicular elements measured may however be less comparable in terms of ontogenetic stage (Figure 5.2 in [4]) relative to the dentition, which may potentially be classified more precisely according to dental stage (p. 45 of [8]) Table 2.

Table 2. Factors which likely influenced the evolution of reduced size in Pleistocene Siculo-Maltese *Palaeoloxodon* spp. For Faunal Complex associations and chronology refer to [8,9,67] and references therein [68]. * See palaeogeography in Figure 1. Note that some *Palaeoloxodon* lineages/taxa were isolated on multiple Siculo-Maltese islands. # Assuming an arrival of 690 ka or earlier (p. 31 in [8] and references therein). The duration of isolation of *P. ex gr. P. mnaidriensis* from Puntali Cave is unknown, but see also [68].

Taxon	Island	Figures	Locality	Age	Predators	Competitors	Duration of Isolation (ka)
<i>P. antiquus</i>	Sicily	Figure 1	Unknown	Pleistocene	?	?	?
<i>P. ex gr. P. mnaidriensis</i>	Sicily	Figure 3a,c and Figure 4b–d	Puntali Cave	late Middle-early Late Pleistocene	<i>Panthera leo</i> , <i>Crocuta crocuta</i> , <i> spelaea</i> , <i>Canis lupus</i> , <i>Ursus cf. arctos</i>	<i>Hippopotamus pentlandi</i> , <i>Cervus elaphus siciliae</i> , <i>Dama carburangelensis</i> , <i>Bos primigenius siciliae</i> , <i>Bison priscus siciliae</i>	?
<i>Palaeoloxodon</i> sp.	Sicily	Figure 4a,b	Contrada Fusco	MIS5? (130–80 ka)	Likely all taxa in cell above	Likely all taxa in cell above	Likely relatively brief (tens of ka)
<i>Palaeoloxodon</i> sp.	Sicily	Figure 4a,c,d	San Teodoro Cave	Younger than 32 ± 4 ka	Likely all taxa in cell above	Likely all taxa in cell above; also <i>Equus hydruntinus</i>	Likely > 50 ka
<i>Palaeoloxodon</i> sp.	Favignana	Figure 3d	Grotta dell'Ucceria	20.350–19.840 cal. BP	None?	? <i>Dama carburangelensis</i>	Likely ca. 10 ka longer than at San Teodoro
<i>Palaeoloxodon</i> sp. 1	Northern-Central Sicily * and/or Sicily	Figure 3a,d	Luparello Fissure	Late Early or early Middle Pleistocene	None	None	# Likely > 340 ka
<i>P. falconeri</i>	Sicily	Figure 3a,c,d and Figure 4a–d	Spinagallo Cave	Middle Pleistocene (ca. 350–230 ka)	None	None	# Likely > 460 ka
<i>P. mnaidriensis</i>	Malta	Figure 3a	Mnaidra Gap	?Middle Pleistocene	None	None?	?
<i>P. 'melitensis'</i>	Malta	Figure 3c,d	Benghisa Gap	Pleistocene	None?	None?	?

3. Results

Measurements were obtained from Sicily, Malta, Favignana, as well as a large sample from mainland Germany (Figures 3 and 4), representing an extensive range in size. A nearly completely overlapping distribution in size is evident, from the 1 m-tall dwarf elephant *P. ex gr. P. falconeri* to continental *P. antiquus*, and similar differences in size are evident in the foot and long bones (Figures 3 and 4). None of the insular samples fall within the range of variation of the continental sample from Neumark-Nord 1, which exceeds the size of all insular samples, although the dimensions of the humerus from Contrada Fusco approaches the size of continental *P. antiquus* from Germany (Figure 4a,b).

It is also noteworthy that two humeri from Contrada Fusco, Sicily are significantly larger than con-specific samples from San Teodoro Cave (Figure 4a). When considering Sicilian humeri, tibiae and femora together (Figure 4b–d), sizes overlap between Puntali and San Teodoro Cave samples, although some specimens from San Teodoro are larger (Figure 4b,d). Femoral dimensions are very similar between elephants from Spinagallo Cave, Luparello Fissure and San Teodoro Caves (Figure 3c), although dwarfism in these samples resulted from at least two separate colonizations of Sicily.

4. Discussion

Here, I discuss the size diversity observed in the different Siculo-Maltese taxa in relation to (i) release from predation pressure, (ii) a decrease in inter and intra-guild competition, (iii) resource limitation, (iv) selection for an accelerated life-history, (v) so-called optimal body size, and (vi) duration of isolation. Particular emphasis is given to measurements obtained from *Palaeoloxodon* sp. from Favignana Island and San Teodoro Cave, Sicily which have recently been added to the dataset of Siculo-Maltese material.

4.1. *Palaeoloxodon falconeri*

The most extreme size reduction in Sicilian elephants is evident in *P. ex gr. P. falconeri* (Figures 3 and 4). Similarly extreme size reduction evolved in proboscideans on Cyprus [69], and in the Cretan dwarf mammoth [70]. In all the aforementioned proboscideans extreme size reduction evolved in the absence of predators and competitors (Table 1 in [9]; pp. 122–124 in [67]) and likely also over prolonged periods of time. The islands in question also had large surface areas (see [71]), and were all strongly isolated (Figure 1.1 in [72]), including Sicily, which despite its close proximity to peninsular Italy, is effectively isolated by the presence of strong marine currents (the inspiration for the myth of *Scylla and Charybdis*, see [73]). Somewhat paradoxically, the fact that Sicily was a large island may actually have indirectly been a contributing factor in the evolution of extreme size reduction, because it allowed *P. ex gr. P. falconeri* to persist longer than on smaller islands where extinction rates are typically higher [12]. Since islands are prone to frequent species-turnover and associated extinction events, it is possible that Sicily as a large island was able to sustain a larger population of elephants, its greater surface area lessening the chances of extinction and allowing *P. ex gr. P. falconeri* to evolve an optimal body size in the absence of predators and competitors.

With regard to the alleged role of accelerated life-history playing a role in size reduction, alleged evidence has been argued in the form of the high juvenile mortality observed in the Spinagallo Cave assemblage [35]. According to [35], the Spinagallo assemblage age-structure is representative of a living population, and there is no evidence of any significant age-skewing taphonomic bias in the assemblage (pp. 295–296 in [35]), despite a high frequency of bones of a similar size previously being interpreted as attrition in young males (p. 325 in [40]), a period during adolescence when these leave the close-knit social group of the herd, and are thus more vulnerable to mortality. Moreover, recent evidence based on palaeohistology clearly indicates that *P. ex gr. P. falconeri* matured much more slowly than might be predicted from allometric equations alone [47], negating the alleged role of accelerated life-history in its body mass reduction.

4.2. Possible Late Phyletic Ancestors of *P. ex gr. P. falconeri*

Intriguingly, remains considered somewhat atypically large for *P. ex gr. P. falconeri* have been found at least three Sicilian localities: (i) Luparello Fissure; (ii) Spinagallo Cave; (iii) Alcamo Quarry; as well as at (iv) Benghisa Gap on Malta.

(i) The Luparello Fissure assemblage—This assemblage includes a wide range in size (Figure 3d), including specimens within the typical range of *P. ex gr. P. falconeri*, as well as specimens marginally larger, to much larger than the numerically large sample of late Middle Pleistocene origin from Spinagallo Cave (Figures 8, 13 and 14 in [74]; Figure 3.16, 3.17b,d, 3.22 and 3.26 in [8]).

(ii) Remains from the lower stratum of the lower cavern of Spinagallo Cave—The *P. ex gr. P. falconeri* sample from Spinagallo Cave displays an extensive range in absolute size (in adult specimens with fused epiphyses, Figure 4), variation which has been attributed to ontogeny and sexual dimorphism ([4], p. 329ff in [40]). However, the excavators clearly described excavating larger remains deriving from the lower stratum of the lower cavern (pp. 221–222 in [75]; see also p. 209 in [8], p. 487 in [76]), something which has largely been ignored by subsequent researchers; partly no doubt, because of the misguided taxonomy applied by the excavators which assigned larger specimens to '*Elephas melitensis*'. However, the fact that larger remains were allegedly derived lower strata may still be a *bona fide* observation significant in terms of a progressive reduction in size through time (p. 209 in [8]).

(iii) Remains from Alcamo Quarry travertine—The remains from Alcamo Quarry are sometimes large relative to remains of *P. ex gr. P. falconeri* from Spinagallo Cave (Palombo, pers. comm. 2014; see metric study on the Spinagallo Cave assemblage in [40]), although metric data on limb bones are lacking from Alcamo. An *in situ* tusk measures 5 cm in diameter, falling within the upper size range of the maximum tusk diameter of *P. ex gr. P. falconeri* from Spinagallo Cave (Figure 5.1 in [8]; see Figure 16 in [40]). If there are *bona fide* size differences between Alcamo Quarry and Spinagallo Cave this may relate to geochronological age differences, as a tentative U-Th range of ca. 514–551 ka was recently obtained from the former site (p. 251 [8]), earlier than the ages for Spinagallo Cave (between 366 and 233 ka (OSL, U-series, see preliminary abstract of [58]).

(iv) *P. 'melitensis'* from Benghisa Gap, Malta—These include samples belonging to large individuals which fall outside the range of variation of *P. ex gr. P. falconeri* from Spinagallo Cave (Figure 3d). Assuming the previous suggestion that *P. ex gr. P. falconeri* initially reduced in size on Sicily or its northern palaeo-island is correct, and only later dispersed to Malta when glacio-eustatic conditions were favourable (see [74]; p. 206 in [8]; and palaeogeographical reconstructions in Figure 3.3 in [4,77–79]), there are at least three possible explanations as to why *P. 'melitensis'* was larger: (a) the larger ancestors of this taxon evolved as a metapopulation which included Malta, (b) *P. 'melitensis'* derives from a separate, independent dwarfing event, or (c) a founding effect resulted in unusually large *P. ex gr. P. falconeri* individuals colonizing Malta. The final suggestion (c) might be argued on the basis that larger elephants are more likely to be able to swim the strait between Sicily and Malta than their smaller relatives.

4.3. Probable Early Phyletic Ancestors of *P. ex gr. P. falconeri*

Early or Middle Pleistocene fossil elephants distinctly larger than the 1 m-tall *P. ex gr. P. falconeri* have been found at least two localities on Sicily; in the north-west at Luparello Fissure (Figures 2b, 3 and 4; see also [4,8,74], and the Comiso limnic deposits of the Vittoria Plain in the south-east (p. 202 in [80]; p. 175 in [81]; Figure 3 in [82]). Stratigraphic, metric and morphological evidence suggest that large *Palaeoloxodon* sp. 1 from Luparello Fissure is the ancestral chronospecies of *P. ex gr. P. falconeri*, though its age remains poorly constrained [8,74].

At present, the phylogenetic relationship between the large remains from Luparello Fissure and Comiso is uncertain, but one of the following phylogenetic scenarios may be postulated: (a) a metapopulation on the two palaeo-islands of Northern-Central Sicily and the Hyblean Plateau as per Figure 1; (b) two similarly sized species on the aforementioned palaeo-islands; or (c) one species on a single island with a similar geography to present-day Sicily. Which one of these three scenarios may apply is currently not possible to distinguish, because chronological, metric and morphological comparisons between the Luparello Fissure and Comiso fossils are still lacking. A late Early Pleistocene age has been ascribed to Sicilian strata allegedly containing *P. ex gr. P. falconeri* in the Comiso area of the Vittoria Plain, though without anatomical description (p. 919 in [11]).

4.4. Earliest Insular Palaeoloxodont Ghost Lineage

The straight-tusked elephant existed within continental Europe from ca. 900–34 ka [83,84], although it is unclear when the taxon first arrived on Sicily. It is however worth noting the absence of large elephants dating to the late Early, or early Middle Pleistocene of Sicily, despite the fact that *P. ex gr. P. falconeri* was descended from a founding population of *P. antiquus* [4] which must have colonized the island during this period. Although the earliest arrival of elephants on Sicily is currently unreported in the fossil record, their arrival presumably postdates the earliest evidence of *P. antiquus* in Europe, likely dating to approximately 0.9 Ma [84], by which time the species may already have been present on the Italian peninsula [85]. Considering that the oldest radiometrically dated *Palaeoloxodon* sp. remains from Sicily currently date to ca. 0.5 Ma (Appendix B in [8]), this likely leaves a very noticeable gap in the fossil record of several hundred thousand years.

There are several ways in which this gap in the Sicilian proboscidean fossil record might be explained: (i) The *P. antiquus* founding population was geographically restricted to a palaeoisland, possibly on the Aspromonte Massif, Cape Vaticano Massif, or Serre Massif (Figure 1). (ii) Rates of evolution are known to be greatly accelerated on islands, so that fossils of large insular *P. antiquus* are less likely to be represented: dwarfism may evolve rapidly in a so-called tachytelic stage (spanning the order of millennia), followed by a second stage of slower, but ultimately much more pronounced size change [22,53,86,87]; see also quantitative dwarfing models of [68,88–90]). It is also pertinent to note that on numerous other islands with abundant endemic palaeoloxodont fossil records, the ancestral *P. antiquus* has also often not been retrieved (Table 1.2 in [8,91]).

4.5. *P. ex gr. P. mnaidriensis* from Puntali Cave, Sicily

The 2 m-tall *P. ex gr. P. mnaidriensis* evolved in the presence of non-endemic or slightly endemic predators and competitors belonging to two successive faunal complexes, dating to the late Middle-Late Pleistocene (Maccagnone and San Teodoro FCs *sensu* [67] and *E. mnaidriensis* and San Teodoro FCs *sensu* [81]). Predators, though not necessarily all coeval with each other, included lion (*Panthera leo*), wolf (*Canis lupus*) and hyena (*Crocuta crocuta spelaea*), the latter which left bone gnaw-marks indicating it scavenged or preyed on elephants (p. 59 in [5]), suggesting large body size still held an important advantage for evading predators, and in part explaining its large size relative to other Sicilian dwarfs (Figures 3 and 4).

Additionally, competition plays an important role in influencing body size evolution as animals maintain different diets by maintaining or evolving to different sizes to avoid competitive exclusion (*sensu* [92]; see also [1,21]). Continental *P. antiquus* was generally associated with temperate, wooded, or mixed vegetational conditions [93,94], and capable of facultative feeding, with browsing, grazing and mixed feeding behaviour being observed [95]. *P. ex gr. P. mnaidriensis* evolved in the presence of competitors: deer (*Cervus elaphus*, *Dama carburangelensis*), and bovids (*Bos primigenius*, *Bison priscus sicilae*). Furthermore, niche occupancy may often shift significantly on islands in the absence of similar-sized ecological competitors [3], and it has been suggested that *P. ex gr. P. mnaidriensis* was a mixed-feeder, which shifted towards the vacant niche more typical of mainland horses (grazers) and rhinoceroses (mixed feeders) (p. 347 in [18]).

4.6. The Possibility of a Late Middle Pleistocene Colonization of Sicily by *P. antiquus*

An alleged possible third colonization of Sicily by *P. antiquus* during the late Middle Pleistocene has also been hypothesized based on the presence of large individuals (Figure 3a,b) from Contrada Fusco in eastern Sicily (p. 124 in [96]). The presence of medium and much rarer large-sized remains from the site have however also been suggested to represent sexual dimorphism [97].

Electron spin resonance dating of tooth enamel from Contrada Fusco produces an average age of 146.8 ± 28.7 ka (the average age of three strata, see [97,98]), which, in combination with the interglacial nature of the palaeoenvironment suggests it may be

referable to MIS 5 (130–80 ka, see [97]). *P. ex gr. P. mnaidriensis* remains from Puntali Cave are likely younger than 180 ka (p. 92 in [60]), and an mtDNA sample produced an estimated period of divergence from continental *P. antiquus* of between 147–50 ka [68], while the age of elephants recently excavated from San Teodoro is closer to 32 ka [99].

Whether or not this alleged third colonization might have taken place while *P. ex gr. P. mnaidriensis* was still present on Sicily is unclear, and unlike the previous two colonizations the alleged subsequent colonization probably never resulted in the evolution of an endemic taxon. It would therefore potentially be informative to compare mtDNA in elephants from Contrada Fusco and San Teodoro Caves in order to determine if the elephants belonged to the same haplogroup/descended from a common founding population.

4.7. *Palaeoloxodon* sp. from Favignana Island

Of particular note are the dimensions observed in the Favignana elephant foot bones (Figure 3d), which substantially exceed those measured in the large assemblage of the smallest dwarf *P. ex gr. P. falconeri* from Spinagallo Cave, while also being smaller than *P. ex gr. P. mnaidriensis* from Puntali Cave, suggesting an equivalent shoulder height of roughly 1.5 m [100]. The ulnar carpal (the only postcranial element for which it is currently possible to make comparisons with published dimensions) evidences dimensions similar to a specimen from San Teodoro Cave found in a layer overlaying a flowstone U-Th dated to ca. 32 ka [5]. In comparison, a calibrated radiocarbon age of 20.350–19.840 BP was obtained from a tooth belonging to the Favignana elephant, suggesting that the Favignana elephant was the most recent endemic insular *Palaeoloxodon* from the Western Mediterranean.

Several alternative hypotheses may be invoked to explain the small size of the Favignana elephant relative to *P. ex gr. P. mnaidriensis* from Puntali Cave, Sicily: (a) The size of Sicilian *P. ex gr. P. mnaidriensis* decreased somewhat during the Late Pleistocene, so that the Favignana elephant is descended from a *P. ex gr. P. mnaidriensis* population that inhabited Sicily during the last Glacial (MIS4–MIS 3), and was moderately reduced in size relative to earlier Sicilian populations. (b) The Favignana elephant population underwent a reduction in size relative to its Sicilian ancestor due to endemism specific to Favignana.

The relatively recent age of the middle-sized elephant from San Teodoro Cave (post-dating ca. 32 ka [5] in comparison to the older age from Puntali Cave, see p. 92 in [60] compared with the young age of the *Palaeoloxodon* sp. (20.350–19.840 cal. BP) and relatively small gap in age, spanning less than ca. 20 ka may support derivation from a relatively small, late representative of *P. ex gr. P. mnaidriensis*. Favignana was joined to Sicily proper for most of the Late Pleistocene by an isthmus, the extent of which depended on sea-level fluctuations, and was last separated from Sicily about 7.4 ka, when Favignana became an island [100]. The radiocarbon age (dating to the time of the Last Glacial Maximum) therefore makes endemism specific to Favignana Island unlikely to be the cause of its reduced size.

(c) Finally, given the extreme climatic conditions which prevailed at the time of the LGM, it might be hypothesized that the Favignana elephant's small size might be related to unfavourable environmental conditions, such as a shortage in food quantity or quality or other environmental factors. LGM air temperatures were around 7–8 °C colder on Sicily [101], with southern peninsular Italy experiencing seasonal drought [102]. Fossil pollen indicates that steppe conditions dominated on Sicily during the pre-Late Glacial [103], perhaps not particularly favourable conditions for an insular elephant descended from a species typically associated with interglacial fauna, mild humid/temperate climates and wooded or mixed vegetation (reflected in the German colloquial for *P. antiquus* ‘Europäische Waldelefant’—literally the ‘European forest-elephant’ (see [61,62,83,94])). However, proboscideans are generally flexible herbivores, and dietary change in insular herbivores is common [66].

4.8. The Problems of Disentangling Ontogenetic Stage, Phylogeny and Sexual Size Dimorphism

Distinguishing between intraspecific size variability and interspecific size variation in insular elephants often poses challenges, because a substantial range in sexual size dimorphism also contributes significantly to size variability in insular proboscidean fossil samples, often leading to mistaking intraspecific sexual size dimorphism for interspecific size differences, especially when sample-sizes are small. In extant African elephants, which are better characterized than fossil assemblages, males are up to 40% taller than females, humeri and femora being up to 25% longer (in individuals over fifteen years old), while differences in limb bones over 40% for *Loxodonta africana* were occasionally observed [43,97]. Thus, the larger males and smaller females of sexually size-dimorphic insular elephants have on several occasions been misdiagnosed as belonging to separate species, as happened for example with the Charkadio Cave assemblage on Tilos (e.g. [91] vs. [104]). The opposite is also a cause for confusion, with multiple species being conflated with single, sexually dimorphic species (as has for example happened with remains from Luparello Fissure, Sicily, see p. in 87 [66] vs. [8]). Particularly when samples are small, incomplete, and the range of variation in an insular taxon has not been adequately ascertained, greater caution is required.

Ontogenetic stage can however be discerned from other size-influencing factors such as sex to varying degrees from indicators such as dental stage, epiphyseal fusion stage, absolute size, and tissue maturation and allometry, although insular species including proboscideans may evidence different allometries relative to their ancestors, often due to paedomorphism (see references in pp. 16ff in [8]). However, the extent to which ontogenetic stage contributes to size variation in fossil assemblages is often difficult to distinguish in practice from independent factors, in part because anagenesis may also contribute to a wide range in size variation, especially in historic collections where there is a lack of stratigraphic control. Anagenesis is also likely more prevalent in time-averaged assemblages from poorly controlled excavations than is often assumed, and likely explains a significant amount of size variation in elephants from the Siculo-Maltese Palaeoarchipelago often not featured in discussions of body size adaptation.

5. Conclusions

Although still poorly resolved in terms of systematics and taxonomy, repeated colonizations of the Siculo-Maltese Palaeoarchipelago during the Pleistocene were followed by speciation, resulting in a palaeoloxodont species complex, with a wide range in environmental and ecological conditions in time and space being responsible for differences in body size. While the current framework of macro-ecological interactions explains much of this variation in size in insular Siculo-Maltese elephants, it does not completely account for some observations under consideration.

Some differences in size among both Middle and Late Pleistocene elephants almost certainly relate to the duration of isolation (including the phyletic ancestors of *P. falconeri* likely represented at Luparello Fissure; whereas smaller size differences in *P. falconeri* samples from Spinagallo, Alcamo, and Malta are more ambiguous). Additionally, the *P. ex gr. P. mnaidriensis* San Teodoro Cave sample includes remains larger than those from Puntali Cave, perhaps due to differences in duration of isolation. Similarly, the elephant from Favignana was likely smaller than *P. ex gr. P. mnaidriensis* from Puntali Cave due to duration of isolation, or alternatively because of harsh climatic conditions associated with the time of the LGM.

These observations underscore the need for researchers to pay more thorough attention to differences in size related to duration of isolation, as well as the need for more robust geochronologies, especially when sample sizes are small. Until a more thorough review of the geochronology of Siculo-Maltese sites is undertaken through new excavations and absolute dating, more precise explanations for differences in size will likely remain causally obscure, in light of the complexities of their palaeogeographical, environmental and ecological contexts.

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