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Extreme insular dwarfism evolved in a mammoth

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The insular dwarfism seen in Pleistocene elephants has come to epitomize the island rule; yet our understanding of this phenomenon is hampered by poor taxonomy. For Mediterranean dwarf elephants, where the most extreme cases of insular dwarfism are observed, a key systematic question remains unresolved: are all taxa phyletic dwarfs of a single mainland species *Palaeoloxodon antiquus* (straight-tusked elephant), or are some referable to *Mammuthus* (mammoths)? Ancient DNA and geochronological evidence have been used to support a *Mammuthus* origin for the Cretan ‘*Palaeoloxodon*’ *creticus*, but these studies have been shown to be flawed. On the basis of existing collections and recent field discoveries, we present new, morphological evidence for the taxonomic status of ‘*P. creticus*’, and show that it is indeed a mammoth, most probably derived from Early Pleistocene *Mammuthus meridionalis* or possibly Late Pliocene *Mammuthus rumanus*. We also show that *Mammuthus creticus* is smaller than other known insular dwarf mammoths, and is similar in size to the smallest dwarf *Palaeoloxodon* species from Sicily and Malta, making it the smallest mammoth species known to have existed. These findings indicate that extreme insular dwarfism has evolved to a similar degree independently in two elephant lineages.

Keywords: *Mammuthus creticus*; island rule; *Palaeoloxodon*; dwarf elephant; insular dwarfism; taxonomy

1. INTRODUCTION

Dwarfism is a well-known evolutionary response of large mammals to insular environments, forming part of the ‘island rule’, whereby large mammals evolve smaller size, and small mammals larger size, on islands [1]. Mediterranean Pleistocene dwarf elephants, such as the Siculo-Maltese species *Palaeoloxodon falconeri*, represent some of the most extreme examples of insular dwarfism and have come to epitomize this phenomenon. However, poor taxonomy has hampered research into the causes and mechanisms of insular body size change in elephants and, by extension, broader topics such as the island rule.

The generic affinity of Mediterranean dwarf elephants is the subject of ongoing debate (see the electronic supplementary material). With the exception of the Sardinian *Mammuthus lamarmorai*, Mediterranean island elephants were thought to be phyletic dwarfs of a single mainland taxon, *Palaeoloxodon antiquus*, the straight-tusked elephant [2]. A study by Poulakakis *et al.* [3] challenged this consensus, presenting ancient DNA (aDNA) evidence for *Mammuthus* (mammoth) affinity of a rib bone fragment from Cape Malekas in Crete, the type locality for *Palaeoloxodon creticus* [4]. On the basis of this aDNA evidence and the purported geological age of this specimen (earlier than 800 ka), Poulakakis *et al.* recommended that Cretan *P. creticus* be revised to *Mammuthus*, and further suggested that Sicilian and Maltese taxa might also be referable to this genus. Their study was immediately challenged [5,6], and its credibility questioned owing to ‘serious theoretical and methodological flaws’ ([6], p. 56; see the electronic supplementary material). Poulakakis *et al.* defended their

findings, but acknowledged the need for independent corroboration of their work ([7], p. 61); such corroboration is still outstanding.

Thus, the identification of ‘*P. creticus*’ as a mammoth currently rests on the assertion that material from Cape Malekas pre-dates the arrival of *Palaeoloxodon* in Europe, precluding derivation from that taxon [8,9]. Temporal arguments are not sufficient to merit taxonomic revision, but the chronology is in any case open to question. The antiquity of Cape Malekas is far from certain, being based on a hypothesized biostratigraphical relationship with material from the Katharo Plateau (East Crete), which was in turn dated using a discredited amino acid racemization (AAR) methodology [10,11]. Even if the oldest Katharo Plateau AAR date is given credence (738 ka \pm 20% [10]), the first appearance of *P. antiquus* in Europe dates to around the Brunhes–Matuyama boundary (*ca* 780 ka) [12]; thus it cannot be ruled out as a potential ancestor, given that insular dwarfing can occur rapidly [13].

The generic attribution of the Cape Malekas elephants therefore remains uncertain. Despite well-preserved type material displaying a number of taxonomically informative characters, there has been no systematic attempt to assess their morphological affinity, although Bate [4] and Mol *et al.* [8] noted the low-crowned, *Mammuthus meridionalis*-like nature of the teeth. Here, we use an alpha-taxonomic approach to perform the first such analysis, comparing the Cape Malekas elephant material, including newly discovered *in situ* specimens, with Late Pliocene to Middle Pleistocene mainland European *Palaeoloxodon* and *Mammuthus*. We further compare the Malekas material with other insular dwarf elephants to take account of the allometric effects of insular dwarfism on taxonomically informative characters.

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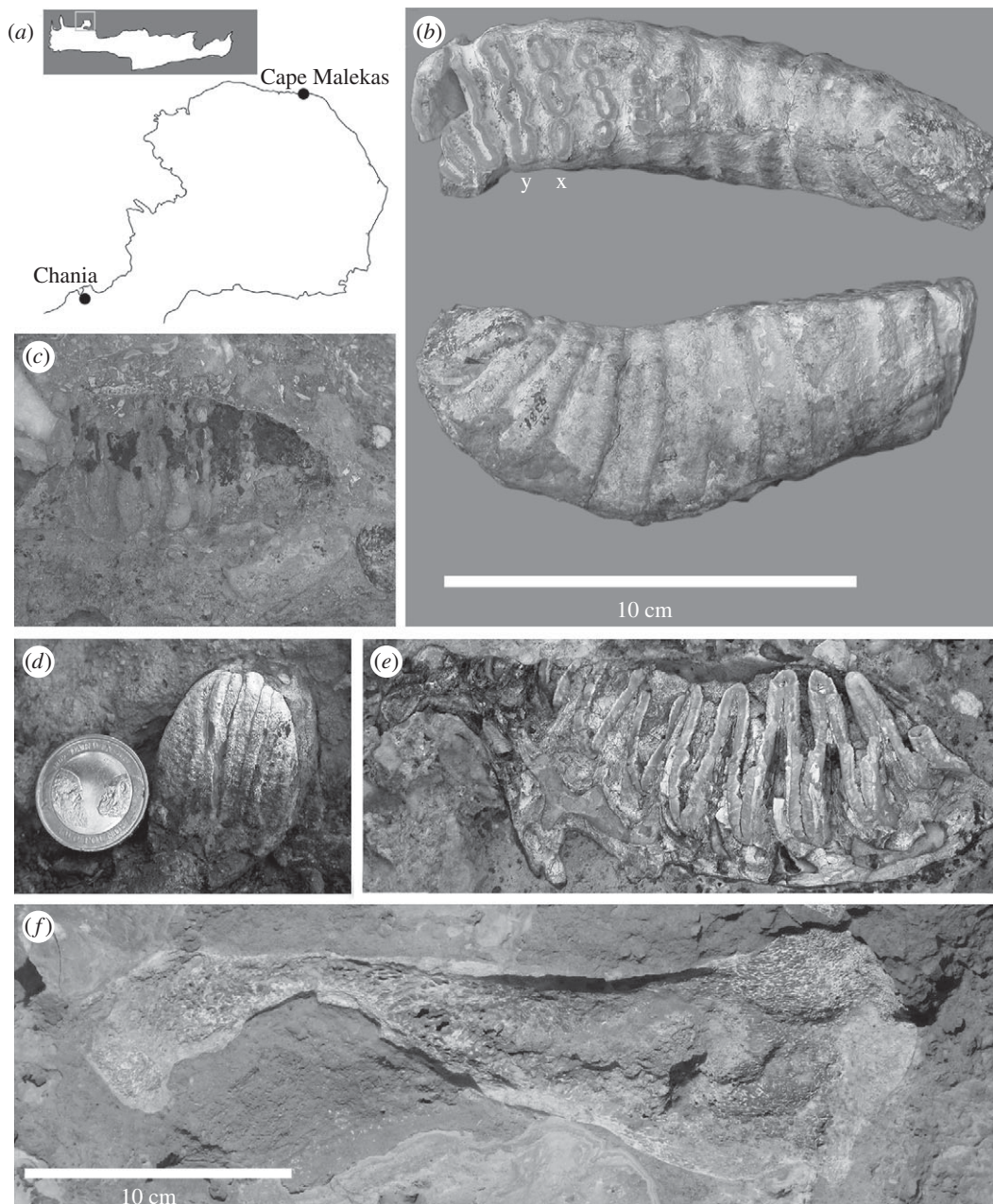


Figure 1. (a) Location of Cape Malekas, Crete. (b) Lectotype of *M. creticus* [4] (NHM M9381) showing *Mammuthus*-like early wear (x) and enamel figure (y). (c–f) *In situ* fossil from Cape Malekas: (c) natural mould of the occlusal surface of a probable upper molar; (d) posterior view of lower molar embedded in sediment; (e) probable lower M2 in cross section; (f) adult humerus in longitudinal section. Images (c–e) are to same scale.

2. MATERIAL AND METHODS

(a) Sample

We consider *P. antiquus* and *M. meridionalis* (the proposed ancestral taxa of *P. creticus*), and extend our analyses to two further species: *Mammuthus rumanus* and *Mammuthus trogontherii*. These species were present in Europe during the Late Pliocene (*M. rumanus*), Early Pleistocene (*M. meridionalis*) or Middle Pleistocene (*M. trogontherii* and *P. antiquus*). We limit our Cretan elephant sample to those specimens collected by Dorothea Bate, housed in the Natural History Museum (London), which are clearly labelled and registered with the locality ‘Cape Maleka’. This sample lacks cranial and post-cranial material [4], and thus taxonomic assessment must be based on the well-preserved molars (which include the lectotype of *P. creticus* fixed by Osborn [14], a lower third molar (M₃), NHM M9381; figure 1b).

In elephants, the M3 is the final tooth in the dental series. It has a distinctive curved and posteriorly tapering morphology ensuring metric comparisons are made between homologous elements in different-sized taxa. Non-metric occlusal characters are applicable to the entire dental ontogenetic series (dp2–M3) [14–16], and thus pre-M3 *creticus* teeth were scored in addition to M₃s (total sample $n = 6$). Taxonomic or size-informative data (see below) were collected for M₃s of the following taxa (locality information; source collection—abbreviations defined in the electronic supplementary material; total sample size): *P. creticus* (Cape Malekas; NHM; $n = 3$); *P. antiquus* (various sites, UK and Germany, ca 500–120 ka; NHM, SMNS; $n = 26$); *M. trogontherii* (Süssenborn, Germany, ca 600 ka; SMNS, SRSQP; $n = 28$); *M. meridionalis* (Upper Valdarno, Italy, ca 2.0–1.8 Ma; NMB, MPM, MGPF; $n = 26$). *Mammuthus*

rumanus data were collected from the literature [17–19] (various sites, UK and eastern Europe, 3.5–3.0 Ma; $n = 4$). Data were also collected for M_3 s of the two smallest Mediterranean dwarf *Palaeoloxodon* species, *Palaeoloxodon falconeri* (Luparello and Spinagallo Caves, Sicily; UCat, GM; $n = 17$) and *Palaeoloxodon cypristes* (Imbohary, Cyprus; NHM; $n = 4$). Data are available from the authors on request (*Palaeoloxodon* data from V.L.H.; *Mammuthus* data from A.M.L.). We restricted the *P. falconeri* sample to Sicilian localities, given ongoing debate over the conspecificity of Maltese and Sicilian elephants [20,21]. In addition, total bone length (TL: from most proximal end of lateral tuberosity to most distal end of lateral condyle) and diaphyseal length (DL: between proximal and distal epiphyseal lines, taken on anterior surface) were collected for adult humeri of *P. falconeri* from Spinagallo Cave, Sicily (UCat; $n = 7$), *Palaeoloxodon tiliensis*, a medium-sized (approx. 810 kg) dwarf *Palaeoloxodon* from Charkadio Cave, Tilos [22] (UoA; $n = 6$) and *M. lamarmorai* from Sardinia (MSNF). ‘Adult’ is here defined as those bones with fused distal epiphyses. Additional literature data and unpublished *M. exilis* data collected by Larry Agenbroad were used to supplement our insular mammoth dataset (table 1).

(b) Taxonomically informative characters

An alpha-taxonomic approach akin to that of Higham *et al.* [26] is justified here because (i) there are only two elephant genera (*Mammuthus* and *Palaeoloxodon*) on the European mainland during the Pleistocene, comprising a few very well-known species; (ii) it is biogeographically almost certain that one of these species was the ancestor of the Cretan dwarf species; (iii) the scoreable/measurable traits on the existing Cretan specimens are well-characterized and widely used to discriminate *Mammuthus* from *Palaeoloxodon* in mainland material. With these provisos, the absence of *Palaeoloxodon* apomorphies, and the presence of plesiomorphic character states observed in *Mammuthus* but not in *Palaeoloxodon*, can be used as evidence for *Mammuthus* affinity, and vice versa.

Three non-metric characters of the occlusal surface are accepted for discriminating *Palaeoloxodon* from *Mammuthus* [15]: the shape of the enamel loop visible on the occlusal surface; the early-wear pattern of that loop; and the existence and shape of any enamel ‘expansions’ in the mesial region of the enamel figure (‘mesial expansions’). Enamel-loop shape is scored in mid-wear as: 0, parallel-sided enamel figures that sometimes expand to form a sub-circular mesial region (diagnostic for *Mammuthus*); or 1, lozenge- or cigar-shaped (diagnostic for *Palaeoloxodon*). Early-wear pattern is scored as: 0, equal-sized enamel rings, or a sub-circular mesial ring between two elongated rings (diagnostic for *Mammuthus*); or 1, a long central loop between two much shorter loops, the ‘short–long–short’ pattern (diagnostic for *Palaeoloxodon*). Mesial expansions are coded as: 0, absent or vestigial (characteristic of derived *Mammuthus* species and seen in *P. antiquus*); 1, rounded loops (the plesiomorphic state for the Elephantidae—occurs in early *Mammuthus*, but not in *Palaeoloxodon*); or 2, pointed or ‘triangular’ (common in *Palaeoloxodon*). Mesial expansion character state 1 is therefore diagnostic for *Mammuthus* in this context, while state 0 is consistent with *Mammuthus* but cannot rule out *Palaeoloxodon* in the absence of other characters.

Metric characters followed standard protocols [15,27], except molar width (W), enamel thickness (ET) and lamellar frequency (LF; see the electronic supplementary material for details). M_3 plate count (PC), hypsodonty index (HI: crown height/width $\times 100$), relative length index (RLI: length/

width $\times 100$), ET and LF are useful for species-level identification in full-size elephants (see electronic supplementary material, S2) and are thus potentially informative on Cretan to mainland elephant taxon affinity within a genus. The potential impact of allometric change on these characters in dwarf taxa is poorly understood. For example, LF is expected to be of limited taxonomic value in dwarf taxa: full-sized elephants have been shown to exhibit intraspecific size-related trends in M_3 teeth [28], and through the molar ontogenetic series (dP2- M_3) [29]. Only W, length (L) and crown height (CH) are assumed *a priori* to be size characters and thus discounted as taxonomically useful (these can be used in size comparisons between the Cape Malekas elephants and other dwarf elephant taxa). The taxonomic value of PC, HI, RLI, ET and LF was assessed with reference to evolutionary patterns in *Palaeoloxodon* dwarfs (see §3).

Significant difference of *creticus* mean values from (i) mainland taxa and (ii) other dwarf elephant taxa was tested using ANOVA across species-groups, followed by a Tukey–Kramer honestly significant difference (HSD) test, a post hoc mean-comparison method that corrects for experiment-wide error resulting from multiple pair-wise comparisons [30]. Sample sizes are small (and thus the power of the statistical test to detect differences is relatively low, and prone to type II error), but this equates to a conservative test of morphological dissimilarity. Range data were used to identify morphological similarity, and minimize the type II error rate: if there is no significant difference in mean values, *creticus* data must also fall within that taxon’s range to be considered morphologically similar.

3. RESULTS AND DISCUSSION

(a) New field data

In 2011, one of us (V.L.H.), with George Iliopoulos, University of Patras, located a fossiliferous deposit on Cape Malekas consistent with the description of the type locality of *P. creticus* by Bate [4,31]. Coastal cliff retreat on Cape Malekas has exposed fossil specimens in a well-cemented clastic deposit approximately 20–30 m above the present sea level, which appears to have no internal stratigraphy. Sediments are mostly fine-grained sands that fill fissures of a previously active karst system. Multiple disarticulated bone and tooth fragments are found within the matrix, which, in some localities, is capped by horizontal flowstone of up to 10 cm thickness. This deposit is the most fossil-rich of several 2–3 m wide ‘tongues’ of clastic sediment found in close proximity to one another, at roughly the same altitude, in the Cape Malekas region.

A lower molar fragment (field number, fn: MAL_11_01; figure 1d), a probable M_2 (fn: MAL_11_02; visible in longitudinal section, figure 1e) and an adult humerus in longitudinal section (fn: MAL_11_04; figure 1f) were measured *in situ* (removal was not possible without risking damage to the specimens). The natural mould of the occlusal surface of a molar, probably an upper (fn: MAL_11_03; figure 1c), was also discovered, and can be unequivocally identified as the mould of the molar figured by Van der Geer *et al.* ([32], p.53), collected in the Malekas region by Paul Sondaar in 1973 (Jon de Vos 2011, personal communication).

MAL_11_02 has a PC of $\infty 10x$; it is worn down almost to the root at the front, but a large root interpreted as the anterior root is visible (figure 1e), suggesting that only the anterior talon has been lost, and giving a

Table 1. *Mammuthus creticus* M₃ and *in situ* Cape Malekas cf. *M. creticus* pre-M3 specimens (see text), compared with upper and lower M₃s of insular dwarf and mainland elephants. *Mammuthus creticus* was compared separately with (i) *P. falconeri* and *P. cypristes* (3-taxon HSD), (ii) *M. rumanus*, *M. meridionalis* and *M. trogontherii* (four-taxon HSD), and (iii) all included full-sized elephants (five-taxon HSD). *Mammuthus primigenius* data from Vartanyan *et al.* [23] and Velre *et al.* [24]. *M. exilis* M3 data provided by L. Agenbroad (superseding the data of Agenbroad [25], which contain errors; L. Agenbroad 2011, personal communication). Asterisks indicates mean values that are significantly different from mean *M. creticus* M₃ (Tukey–Kramer HSD, $p < 0.05$). Literature data for insular mammoths could not be compared statistically.

species/specimen	upper/lower	plate count						width (mm)						crown height (mm)						length (mm)					
		<i>n</i>		mean		min		max		<i>n</i>		mean		min		max		<i>n</i>		mean		min		max	
MAL_11_01	lower	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
MAL_11_02	lower	1	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>M. creticus</i>	lower	2	12	12	12	12	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>M. exilis</i>	lower	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>M. primigenius</i> WI	lower	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>M. primigenius</i> SP	lower	1	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>M. lamarmorai</i>	upper	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>P. cypristes</i>	lower	2	11.5	11	11	12	12	24.3	28.9*	4	28.9*	24.3	33.4	52.7	59.7	59.7	3	111	94	127	—	—	—	—	
<i>P. falconeri</i>	lower	10	12.5	11	11	13	13	19.3	27.8*	24	27.8*	19.3	35.4	39.1	66.2	66.2	7	111	85	144	—	—	—	—	
<i>M. rumanus</i>	lower	4	9.8	9	9	10	10	75	92*	3	92*	75	106	90	142	142	3	264*	226	306	—	—	—	—	
<i>M. meridionalis</i>	lower	13	12.9	10	10	15	15	77	96.8*	27	96.8*	77	119	92	135	135	16	278*	250	335	—	—	—	—	
<i>M. trogontherii</i>	lower	17	19*	17	17	21	21	83	97.7*	26	97.7*	83	118	134	160	160	17	342*	299	393	—	—	—	—	
<i>P. antiquus</i>	lower	13	18.5*	18	18	20	20	60	77*	24	77*	60	90.5	148	175	175	5	378*	341	391	—	—	—	—	

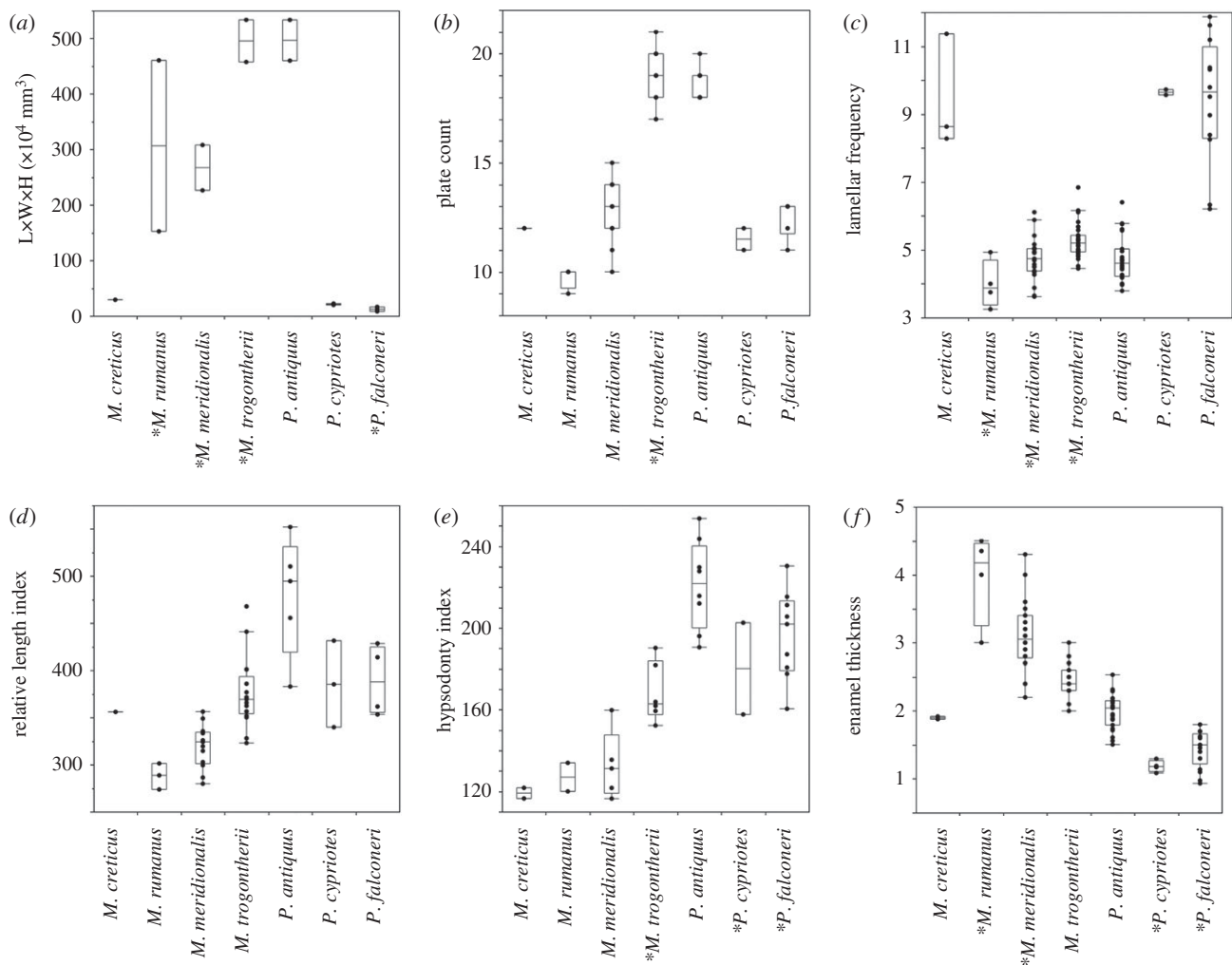


Figure 2. (a–f) Size and shape comparisons with *M. creticus* lower M3s. L (length) \times W (width) \times H (height) provides an estimate of tooth volume, capturing overall tooth size. Two 3-taxon Tukey HSD tests were carried out (i) between *M. creticus*, *M. meridionalis* and *M. trogontherii*, for taxonomic purposes, and (ii) between *M. creticus*, *P. cypristes* and *P. falconeri*, for size and shape comparison within insular dwarfs. Asterisks indicate taxa that are significantly different to *M. creticus* at $p < 0.05$.

reconstructed M₂ PC of $\times 10x$. Molar widths and heights overlap considerably in M2 and M3 teeth in an elephant species; measurements on both *in situ* molars (including unworn crown heights) are consistent with Cape Malekas M₃s (including type material) collected by D. M. A. Bate, and are thus probably conspecifics (table 1).

(b) Genus attribution

Cape Malekas teeth from the Bate collection, including the *creticus* type specimen NHM M9381 (figure 1b), were scored as follows (data in the electronic supplementary material): mid-wear enamel-loop shape ‘0’ = 4/4 (i.e. four out of four specimens that could be scored for this character show character state ‘0’), ‘1’ = 0/4 (note however that M9377 also shows character state ‘1’ in late wear; see the electronic supplementary material); early-wear pattern ‘0’ = 3/3, ‘1’ = 0/3; the shape of mesial expansions ‘0’ = 3/4, ‘1’ = 1/4, ‘2’ = 0/4. *Palaeoloxodon falconeri* and *P. cypristes* M₃s, conversely, show an enamel-loop shape typical of *P. antiquus* (16/16 and 4/4 scored as ‘1’, respectively), and mesial expansions that are either diagnostic for *P. antiquus* (*P. falconeri*: 16/16 scored as ‘2’), or consistent with it (*P. cypristes*: 4/4 scored as ‘0’). All scoreable *P. falconeri* M₃s also show an early-wear pattern diagnostic for *P. antiquus*

(10/10 scored as ‘1’); no *P. cypristes* teeth were at the appropriate wear stage to be scored for this characteristic. The *creticus* hypodigm thus displays occlusal surface traits that are diagnostic for mainland *Mammuthus*. Furthermore, the presence of rounded or ‘looped’ mesial expansion on M9378a suggests affinity with early *Mammuthus* taxa, *M. rumanus* or *M. meridionalis*, rather than the more derived *M. trogontherii* (see electronic supplementary material, S4). The Cape Malekas elephants are thus identified as mammoths, and are henceforth referred to the genus *Mammuthus*.

(c) Affinity with mainland species

Differences between *Mammuthus creticus* and full-sized mammoth species may result from allometric changes associated with dwarfism, as observed in *P. falconeri* skull shape [33,34], or reflect adaptation to small body size and/or insular feeding niche. Although we cannot tease apart these effects given the paucity of evidence, the *Palaeoloxodon* dwarfing model provides a useful analogue. We identified traits that (i) do not retain a taxonomic signal within *Palaeoloxodon* dwarfs and (ii) are shared between *Palaeoloxodon* dwarfs and *M. creticus*, and which thus may indicate size-related and/or adaptive convergence.

Table 2. Morphological similarity (not significantly different, and falls within the range) and dissimilarity (significantly different, and falls outside the range) of *M. rumanus*, *M. meridionalis* and *M. trogontherii* compared with *M. creticus*. Means are compared using a four-taxon Tukey's HSD, $p < 0.05$. *Mammuthus creticus* falls outside the range of, but is not significantly different from, *M. trogontherii* for ET, and *M. rumanus* for PC and RLI; given the small sample size and likelihood of type II error, this cannot be seen, on current data, as a robust indicator of either similarity or dissimilarity. Asterisks indicate character similarity between *M. creticus* and *Palaeoloxodon* dwarfs. Square brackets indicate characters that do not retain a taxonomic signal in *Palaeoloxodon* dwarfs.

<i>M. rumanus</i>		<i>M. meridionalis</i>		<i>M. trogontherii</i>	
similar	dissimilar	similar	dissimilar	similar	dissimilar
HI	[ET] [LF*]	[PC*] RLI* HI	[ET] [LF*]	RLI*	[PC*] [LF*] HI

Table 3. Dwarf elephant humerus lengths, and body size estimation. *In situ* Cape Malekas humerus, MAL_11_04, shaft lengths were not significantly different from *M. lamarmorai*, *P. falconeri* or *P. tiliensis* (Tukey–Kramer HSD, $p > 0.05$; see text for further discussion). *Mammuthus exilis* humerus data from Roth [39] could not be compared statistically. Body mass estimation from Christiansen [40]: $\log \text{body mass (kg)} = -4.15 + 2.64 \times \log \text{humerus TL (mm)}$. Shoulder height estimation from Lister & Stuart [41]: $\text{shoulder height (mm)} = 183.631 + 2.8744 \times \text{humerus TL (mm)}$.

species/specimen	<i>n</i>	total length (mm)			<i>n</i>	diaphysis length (mm)			body mass (kg)			shoulder height (m)		
		mean	min	max		mean	min	max	mean	min	max	mean	min	max
MAL_11_04	1	330	—	—	1	270	—	—	310	—	—	1.13	—	—
<i>M. exilis</i>	—	—	—	—	2	405	377	433	—	—	—	—	—	—
<i>M. lamarmorai</i>	1	462	—	—	1	355	—	—	752	—	—	1.51	—	—
<i>P. falconeri</i>	5	299	231	352	7	222	173	260	238	121	367	1.04	0.85	1.19
<i>P. tiliensis</i>	6	475	409	528	6	372	323	416	809	546	1069	1.55	1.36	1.70

Palaeoloxodon cypristes and *P. falconeri* are both significantly different from *P. antiquus* for mean M_3 PC, LF and ET (HSD test of all three taxa, $p < 0.05$; see the electronic supplementary material for full statistical tables), but not for RLI or HI. Hence, PC, LF and ET are not robust indicators of taxonomic affinity for *Palaeoloxodon* dwarf taxa, and thus may not be for *Mammuthus*. *Mammuthus creticus* is also similar in PC, RLI and LF to the similarly sized *P. falconeri* and *P. cypristes* (figure 2), further undermining the taxonomic usefulness of PC and LF. The strong size-dependency of LF in full-sized elephants [28,29] predicts this for any dwarf elephant, and significant differences in mean LF also exist between *M. creticus* and all full-sized mammoth taxa. Size effects on other characters are less well understood, but this approach suggests that PC should be interpreted with care and that HI is the most taxonomically useful character (table 2).

PC in *M. creticus* matches *meridionalis* ancestry without character change (mean M_3 PC = 12 and 12.9, respectively), but following the *Palaeoloxodon* model, could have been achieved by reduction from the *M. trogontherii* state (mean M_3 PC = 19). *Mammuthus creticus* falls above the *M. rumanus* range for both PC and RLI, but samples are small and the differences are not statistically significant (figure 2). The strongest evidence against *M. trogontherii* ancestry comes from the low HI, which would require a further character change from this high-crowned taxon not predicted by the *Palaeoloxodon* model. *Mammuthus creticus* is instead similar in HI to both *M. rumanus* and *M. meridionalis*, indicating an affinity with the low-crowned 'early' mammoths that is consistent with occlusal surface

data. Although statistical support for *M. meridionalis*–*M. creticus* similarity is statistically more robust, with an implied colonization between 2.5 and 0.8 Ma, we cannot reject *creticus* affinity with *M. rumanus*. The latter could imply a Late Pliocene origin for *M. creticus* (known range of *M. rumanus* ca 3.5–2.5 Ma [17]), significantly earlier than previously thought.

(d) Comparison with other insular dwarf elephants

Insular mammoths are known from Sardinia (*M. lamarmorai* [35]) and the Californian Channel Islands (*Mammuthus exilis* [25,36]), as well as Wrangel Island (northeast Siberia) and St Paul (Pribilof Islands, Alaska; *Mammuthus primigenius* [23,24]). MAL_11_04 provides us with the first data for *M. creticus* skeletal dimensions and is particularly valuable, given that teeth can be problematic for body size estimation, especially in insular dwarfs [37,38]. Although measurement protocol cannot be exactly equivalent for *in situ* and disarticulated museum specimens, inclusion of this specimen extends our exploration of body size differences in dwarf elephants.

Mammuthus creticus falls below the observed ranges for *M. exilis* and Wrangel Island *M. primigenius* M_3 s, and for *M. exilis* adult humerus shaft lengths (tables 1 and 3). Only one *M. lamarmorai* M^3 and one adult humerus are available for comparison with *M. creticus*. Body mass estimates based on humerus length indicate that at 310 kg, *M. creticus* was less than half the size of the approximately 750 kg *M. lamarmorai* (table 3). Although this degree of difference is observed in sexual size dimorphism of living elephants [42], elephant teeth are similar in absolute size

in both sexes [43]. The *M. lamarmorai* M_3 width is almost twice that of the *M. creticus* mean M_3 value, and this is inconsistent with teeth being drawn from two populations of similar-sized, sexually dimorphic elephants (even allowing that, within an individual, M_3 s are somewhat wider than M_3 s). *Mammuthus creticus* is thus smaller than all other known insular mammoths, based on both dental and post-cranial evidence.

Mammuthus creticus molars are wider than, but similar in length and crown height to, those of *P. falconeri* and *P. cypriotes* (table 1), resulting in a tooth that is larger overall, though significantly different only from *P. falconeri* (figure 2a). The *M. creticus* adult humerus falls within, or just above, the upper range of *P. falconeri* for TL and DL, respectively, and well below the range of *P. tiliensis* (the next largest dwarf *Palaeoloxodon* species after *P. falconeri* and *P. cypriotes* [22]) for both DL and TL (table 3). This suggests a body size closer to *P. falconeri* (shoulder height: approximately 1 m; mass: approximately 240 kg) than *P. tiliensis* (1.5 m; approximately 810 kg), which is similar in size to *M. exilis* and *M. lamarmorai* (table 3). Thus, with an estimated shoulder height of 1.13 m, *M. creticus* is not only the smallest known mammoth species, but shows a degree of insular dwarfism approaching that of the smallest known elephant, *P. falconeri*.

Both the smallest (*P. falconeri*, *P. cypriotes*, *M. creticus*) and the largest (Sicilian *Palaeoloxodon mmaidriensis*, *Palaeoloxodon creutzburgi*) dwarf elephants occurred on the largest Mediterranean islands, belying a simple link between island area and degree of dwarfism. However, this reflects current, not palaeo-, island area, and while there are significant difficulties in such reconstructions (not least a lack of robust geochronology), palaeogeography is an essential element in determining the environmental drivers of island dwarfism. An early Pleistocene (*M. meridionalis*) ancestry for *M. creticus* would imply an island area similar to that of present-day Crete. However, a Late Pliocene origin (from *M. rumanus*) would suggest that the small-sized *M. creticus* evolved on a smaller island than previously thought, because the Cretan region is thought to have comprised a series of palaeoislands until 3 Ma [44]. Bonfiglio *et al.* [45] have similarly suggested that pre-Middle Pleistocene (the estimated age of *P. falconeri* [46]) Sicily was composed of two smaller palaeoislands within a Calabrian Arc archipelago.

4. CONCLUSION

This study provides morphological evidence of *Mammuthus* affinity for *M. creticus*, independent of the disputed aDNA and geochronological evidence. Early-wear pattern and enamel figure morphology in *M. creticus* are diagnostic for *Mammuthus*, while mesial expansion shape, relative crown height and PC suggest taxonomic affinity with either *M. rumanus* or *M. meridionalis*. *Mammuthus meridionalis* was extinct in Europe by 800 ka, or possibly 700 ka [41], placing an upper bound on the arrival of *M. creticus*'s ancestor on Crete. However, as we cannot rule out *M. rumanus* as a possible progenitor, the lower bound for isolation on Crete could potentially occur as far back as 3.5 Ma, significantly earlier than previously thought. *Mammuthus creticus* is similar in size to the smallest dwarf elephant species, *P. falconeri*, and smaller than all other known mammoth species. Our taxonomic reassessment and morphological comparisons show that extreme insular dwarfism occurred in *Mammuthus*, not

just in *Palaeoloxodon*, and that *M. creticus* is the smallest mammoth ever to have evolved.

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