



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

## A new elephant fossil from the late Pleistocene of Alghero: The puzzling question of Sardinian dwarf elephants



*Un nouveau reste d'éléphant du Pléistocène supérieur d'Alghero et la question des éléphants « nains » de Sardaigne*

Maria Rita Palombo<sup>a,b,\*</sup>, Marco Zedda<sup>c</sup>, Rita Teresa Melis<sup>d</sup>

<sup>a</sup> Sapienza University of Rome, Department of Earth Sciences, p.le Aldo Moro 5, 00185 Roma, Italy

<sup>b</sup> CNR-IGAG, Via Salaria km 29,300-Montelibretti, 00015 Monterotondo (Roma), Italy

<sup>c</sup> University of Sassari, Department of Veterinary Medicine, via Vienna 2, 07100 Sassari, Italy

<sup>d</sup> University of Cagliari, Department of Chemical and Geological Sciences, via Trentino, 51, 09127 Cagliari, Italy

### ARTICLE INFO

#### Article history:

Received 30 November 2016

Accepted after revision 3 May 2017

Available online 1 August 2017

Handled by Lars vanden Hoek Ostende

#### Keywords:

*Mammuthus*  
Sardinia  
Dispersal  
Chronology  
Pleistocene

#### Mots clés :

*Mammuthus*  
Sardaigne  
Colonisation  
Chronologie  
Pléistocène

### ABSTRACT

Endemic elephants, variously reduced in size, have been reported from a number of Mediterranean islands. Most of these originated from the mainland species *Palaeoloxodon antiquus*. A few dwarf mammoth remains are recorded from Crete and Sardinia. In Sardinia, a largely incomplete skeleton and a few mammoth teeth have been reported from localities believed to range in age from the late middle to the late Pleistocene. The chronology of colonisation by the ancestral species, the actual persistence through time of *Mammuthus lamarmorai* on the island, and the morphological and dimensional range of the species are, however, poorly known. This research aims to describe a distal portion of a left tibia of a dwarf elephant found in the Alghero area (NW Sardinia), showing some morphological traits and dimensions consistent with those of the endemic Sardinian mammoth (*Mammuthus lamarmorai*). The main unanswered questions about chronology, colonisation and population dynamics of endemic Sardinian elephants are highlighted and briefly discussed.

© 2017 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

### RÉSUMÉ

Des éléphants endémiques de taille diversement réduite ont été signalés dans plusieurs îles méditerranéennes. L'espèce continentale *Palaeoloxodon antiquus* est l'ancêtre de la plupart de ces éléphants insulaires, alors que quelques restes de mammoth nains ont été rapportés de Crète et de Sardaigne. En Sardaigne, ils ont été signalés dans des localités dont l'âge va de la fin du Pléistocène moyen au Pléistocène tardif. La chronologie de la colonisation par l'espèce ancestrale, la persistance de *Mammuthus lamarmorai* sur l'île et la variabilité morphologique et dimensionnelle de l'espèce sont, cependant, peu

\* Corresponding author. Dip. Scienze della Terra, Sapienza, Università di Roma, P.le Aldo Moro 5, 00185 Roma, Italy.  
E-mail address: [mariarita.palombo@uniroma1.it](mailto:mariarita.palombo@uniroma1.it) (M.R. Palombo).

connues. Cette recherche a pour but de décrire une portion distale d'un tibia d'éléphant nain provenant de dépôts éoliens de la région d'Alghero (Nord-Ouest de la Sardaigne), dont certains traits morphologiques et dimensions sont compatibles avec ceux du mammoth endémique de Sardaigne (*Mammuthus lamarmorai*). Les questions les plus débattues sur la chronologie, la colonisation et la dynamique des populations d'éléphants de Sardaigne sont mises en évidence et brièvement discutées.

© 2017 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

## 1. Introduction

During the middle Pleistocene to the earliest Holocene times, Sardinia, the second largest Mediterranean island, hosted an impoverished, unbalanced endemic mammalian fauna. During the late early and middle Pleistocene, the biogeographic isolation of Sardinia allowed the arrival on the island by over-sea dispersal of only some small mammals and a few terrestrial large mammals with some swimming abilities. Extant elephants are among the few large terrestrial mammals that are able to swim over quite long distances (48 km or more according to Johnson, 1980), because of their peculiar morphology, body structure and physiology (i.e. the vacuolar structure of some cranial bones, the lung capacity, their plant diet that produces abundant gases in their digestive system that augment buoyancy, and the possession of a trunk functioning as a snorkel). These features enhance their ability to swim and reduce their respiratory effort during swimming. Fossil representatives of Stegodontidae (*Stegodon*) and Elephantidae (*Palaeoloxodon* and *Mammuthus*) probably had the same ability, as documented by the number of insular endemic species recorded across most of the world, from Indonesia to the California Channel islands.

Endemic elephants, variously reduced in size, have been reported from a number of Mediterranean islands. Most of the species originated from the mainland species *Palaeoloxodon antiquus* (e.g., dwarf straight-tusked elephants from Siculo-Maltese archipelago, Crete, Tilos, Rhodos, palaeo-Cyclades, Cyprus) (see, e.g., Ambrosetti, 1968; Athanassiou et al., 2015; Ferretti, 2008; Herridge, 2010; Herridge and Lister, 2012; Mangano and Bonfiglio, 2012; Masseti, 2006; Palombo, 2004, 2010; Poulakakis et al., 2002; Theodorou et al., 2007; Sen et al., 2014; Van der Geer et al., 2010, 2014). Conversely, in the Mediterranean islands, few dwarf mammoth remains have been reported, and those only in the oldest Pleistocene fauna of Crete (*Mammuthus creticus*), and in the youngest Pleistocene fauna of Sardinia (*Mammuthus lamarmorai*) (Herridge and Lister, 2012; Palombo et al., 2012).

This research describes a distal portion of a dwarf elephant tibia found in the 1980s along the coast south of the village of Alghero (NW Sardinia), and briefly discusses and highlights the main unanswered questions about chronology, colonisation and population dynamics of endemic Sardinian elephants.

## 2. The Quaternary deposit along the Alghero coast

The coast of the Alghero area (Fig. 1) is characterised by small cliff-bounded bays with sandy or gravel pocket beaches. Along the coast, from the Porto Conte

bay to about 30 km south of Alghero, Quaternary deposits, mainly consisting of shallow-marine to coastal aeolian deposits formed during major climatic changes and sea-level variations, overlap Mesozoic and Cenozoic bedrock. A chronology of Pleistocene sandy beach and aeolian dune deposits, based on OSL method, provided ages ranging from MIS 6 to MIS 3 (Andreucci et al., 2010; Sechi, 2013).

The bottom of the Pleistocene succession (Fig. 2a) is characterised by planar cross-bedded or locally through-bedded deposits, regarded as coastal aeolian dunes, and referred to MIS 6 (Andreucci et al., 2010). The sand grains consist mostly of marine bioclastic material (red algae, molluscs, echinoids, benthic foraminifera and bryozoans), with a minor amount of quartz and feldspar (Andreucci et al., 2010). The MIS6 dunes are overlain by shallow-marine sediments rich in shell remains, palaeosoils and aeolian Aeoliansands referred to MIS 5.5. The upper deposits of the Pleistocene succession deposited on a regressive surface of erosion caused by a fall of the sea-level during which a rapid exposure of shelf allowed the deposition of aeolian sediments (Andreucci et al., 2010). These sands, OSL dated to MIS 4, show the same composition as the aeolian deposits at the bottom of the succession.

### 2.1. Sediments embedding the elephant remain

The elephant bone is embedded in well-cemented sandy sediment. The sediments are characterised by well-rounded bioclasts of red algae, molluscs, echinoids, and benthic foraminifera. Quartz, feldspar and lithic metamorphic grains occur (Fig. 2b). The composition is similar to sandy MIS 6 or MIS 4 coastal dunes cropping out in the Pleistocene succession along the coast. However, the presence of altered lithic grains and rare red pedorelict (Fig. 2c) indicates palaeosoils as a probable source. As the palaeosoils are present in the MIS 3 and MIS 5.5 deposits (Andreucci et al., 2010), it is reasonable to suppose that sediments embedding the elephant tibia belong to the sandy sediments of coastal dunes deposited during MIS 3/4. This datum provides for the first time a hint of the potential persistence of endemic elephants in Sardinia till about 57–29 ka BP.

## 3. The Alghero elephant

In the 1980s, Ennio Sanna, professor in veterinary pathological anatomy at Sassari University, who used to practice paragliding in the Alghero area, noted a sandstone block in which a quite large bone was embedded while landing on a beach in the southern coast not far from the village of Alghero. The block was brought to the laboratory of Archaeozoology in the section of Anatomy of the



**Fig. 1.** A map of Sardinia showing localities where elephant remains were discovered: 1: Tramariglio; 2: Alghero; 3: Campo Giavesu; 4: San Giovanni di Sinis; 5: Guardia Pisano (Morimenta).

**Fig. 1.** Carte de Sardaigne, montrant les localités où les restes d'éléphant ont été découverts.

Department of Veterinary Medicine (University of Sassari), where it is kept.

The fossil consists of the distal portion of a left tibia of an adult dwarf elephant (Fig. 3). The size of the large tibia fragment (Table 1) seems to be roughly consistent with that of *M. lamarmorai* skeleton found at Guardia Pisano (Gonnesa basin, SW Sardinia) (Palombo et al., 2012), although no direct comparison is possible because the latter lacks tibias.

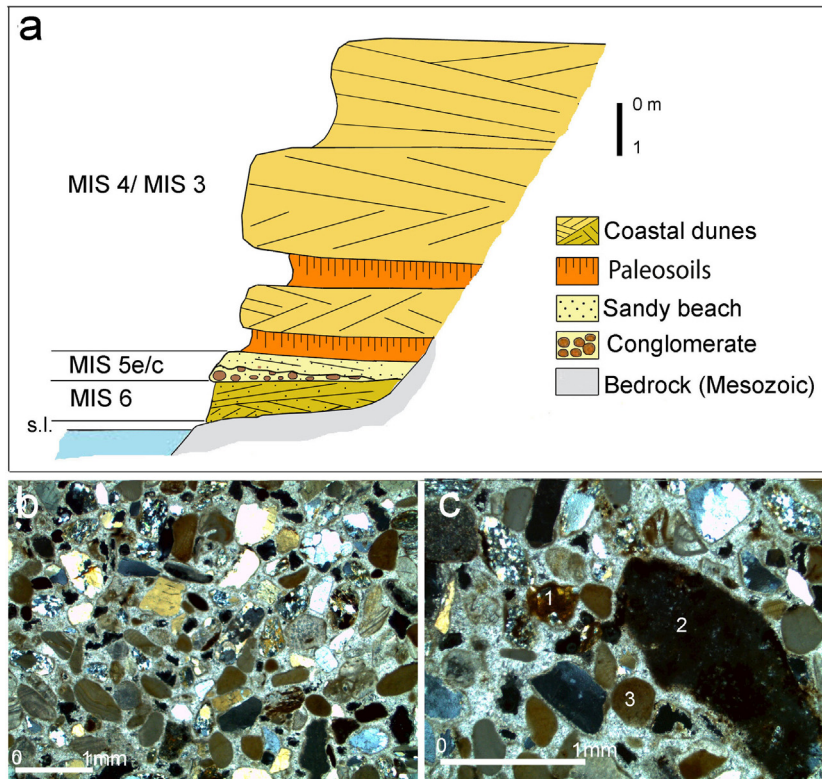
The Alghero tibia (Fig. 3) is rather robust, as suggested by the medio-lateral width of the diaphysis above the distal epiphysis. The shape of the articular surface for the astragalus, still partially incrustated by the hard sandy matrix, seems to have a trapezoid shape, the anterior outline is nearly straight, gently curved at the medial malleolus, which is not robust and weakly protruded downwards. The supra-articular antero-lateral outline, corresponding to the tibio-fibula joint, is nearly straight, 25 mm long, and forms with the antero supra-articular medio-lateral plane an angle of about 65°. The fibular notch, wide and shallow, forms a rough concave surface on the lateral side of the tibia. On the medial-posterior side, the groove for tendons of the tibialis posterior and flexor digitorum longus muscles are rather deep and well marked.

Compared to the tibiae of dwarf elephants of similar size, the overall shape of the anterior side of the Alghero specimen shows a quite peculiar shape. On one hand, the lateral outline of the joint with the fibula and the shape of the medial malleolus show some similarities with *Mammuthus exilis* from the Channel Islands (California)

(Agenbroad, 2002, 2003, 2009), although the inferior outline of the distal epiphysis is less concave in *M. exilis* than in the Alghero specimen. On the other hand, the distal portion of the Alghero tibia differs from that of *Palaeoloxodon ex gr. P. mnaidriensis* from Puntali cave (Sicily) (Ferretti, 2008), in which the inferior outline of the distal epiphysis is more sinuous with a more robust, rounded medial malleolus, features that are respectively more and less pronounced in *Palaeoloxodon tiliensis* (Theodorou et al., 2007) and *P. antiquus* (Fig. 4).

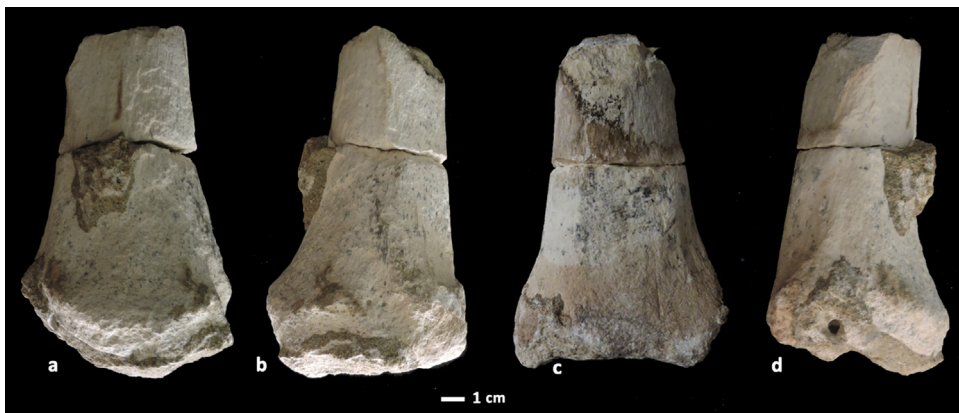
It is, however, worth noting that tibiae of Elephantidae, especially the distal part, show a high intra- and inter-species variation in morphology and sometimes proportions. The shapes of bones in insular large mammals, in particular that of joints, may, moreover, change considerably during the dwarfing process as size and body proportions change, as well as the appearance of apomorphic, ecomorphological features depending on landscape, environmental characteristics, and difference in gait based on speed, terrain, the need to manoeuvre, and energetic efficiency (see, e.g., Rozzi and Palombo, 2013; Scarborough et al., 2016; Van der Geer, 2014 and references in those papers).

The morphology of the specimen from Alghero on the one hand differs from the morphology of continental and insular palaeoloxodonts and on the other shows some similarities with that of dwarf mammoths. Therefore, taking into account that the size of the Alghero specimen is consistent with that of the Sardinian mammoth, we



**Fig. 2.** a: stratigraphic sketch of Pleistocene deposits along the coast at south of Alghero (based on data from Andreucci et al., 2010 and personal observations); b: thin section of sediments embedding the elephant tibia characterised by well-rounded bioclasts of red algae, molluscs, echinoids, benthic foraminifera, grains of quartz, feldspar and lithic metamorphic (XPL,  $\times 2.5$ ); c: rounded red pedorelict (1), altered lithic grain (2), red algae bioclasts (3) in sediments embedding the elephant remain (XPL,  $\times 4$ ).

**Fig. 2.** a : schéma stratigraphique des dépôts pléistocènes le long de la côte au sud d'Alghero (d'après les données d'Andreucci et al. (2010) et des observations personnelles) ; b : section mince de sédiments enrobant le tibia d'éléphant, caractérisés par des bioclastes bien arrondis d'algues rouges, des mollusques, des échinoides, des foraminifères benthiques, des grains de quartz, de feldspath et d'éléments lithiques métamorphiques (XPL,  $\times 2,5$ ) ; c : pédorelict rouge arrondie (1), grain lithique altéré (2), bioclastes d'algue rouge (3) reste dans les sédiments enrobant les restes d'éléphant (XPL,  $\times 4$ ).



**Fig. 3.** *Mammuthus* cf. *M. lamarmorai* from Alghero: distal part of the left tibia in lateral (a), anterior (b), medial (c), and posterior (d) views.

**Fig. 3.** *Mammuthus* cf. *M. lamarmorai* d'Alghero : partie distale du tibia gauche en vues latérale (a), antérieure (b), médiale (c) et postérieure (d).

tentatively refer the tibia to *Mammuthus* cf. *M. lamarmorai*. Although we are aware that the morphology of the limb bone and articular surface has to be considered with caution as compelling evidence for a correct taxonomic identification of large insular mammals, in this case, our

proposed identification of the Alghero elephant seems to be the most reasonable based on the available data. . .

An attempt to infer the body mass of the Alghero elephant, estimating it from the outermost circumference of the tibial diaphysis (although it is not perfectly preserved

**Table 1**

Comparison among tibia dimensions of Alghero specimen, *Mammuthus exilis* (Channel Islands, California) (data from Agenbroad, 2009), *Palaeoloxodon tiliensis* (Charkadio cave, Tilos, Greece) (data from Theodorou, 1983), *Palaeoloxodon ex gr. P. mnaidriensis* (Puntali cave, Sicily, Italy) (data from Ferretti, 2008).

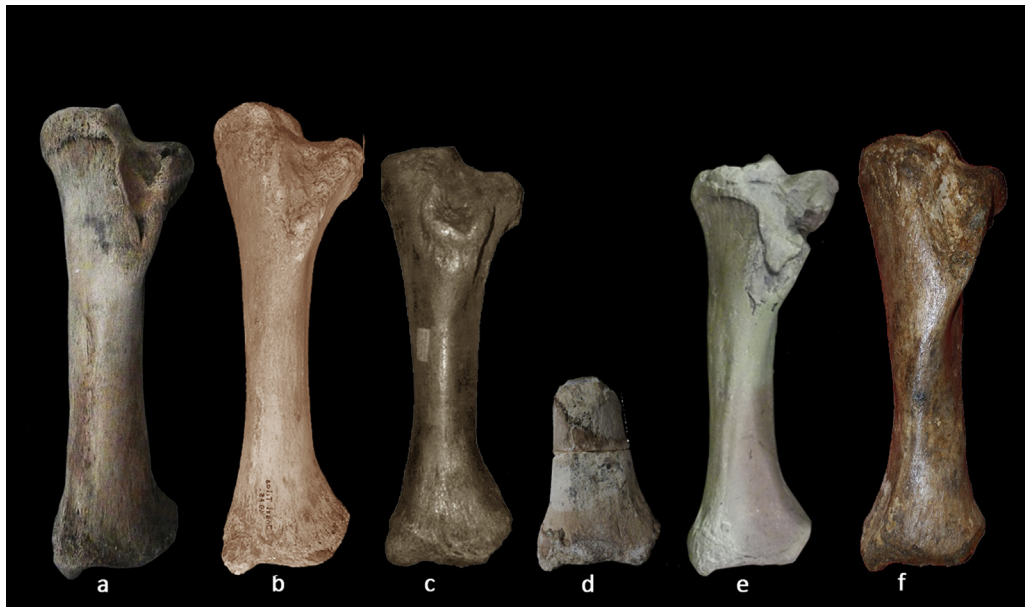
**Tableau 1**

Comparaisons entre les dimensions du tibia du spécimen d'Alghero, de *Mammuthus exilis* (Channel Islands, Californie) (données d'Agenbroad, 2009), *Paleoloxodon tiliensis* (Charkadio Cave, Tilos, Grèce) (données de Theodorou, 1983), *Paleoloxodon ex gr. P. mnaidriensis* (Puntali Cave, Sicile, Italie) (données de Ferretti, 2008).

Tibia – measurements in mm	Alghero	<i>Mammuthus exilis</i>			<i>Palaeoloxodon tiliensis</i>			<i>Palaeoloxodon ex gr. P. mnaidriensis</i> (Puntali cave, Sicily)		
		min	Mean	max	min	Mean	max	min	Mean	max
Greatest length	–	314	385.4	505	280	312.6	374	360	402.1	535
Width of proximal articular surface in the latero-medial plane	–	–	–	–	90	106.4	122	125	142.4	152
Depth of proximal articular surface in the antero-posterior plane	–	–	–	–	60	73.6	85	70	99.4	121
Least circumference of diaphysis	c. 174	–	–	–	–	–	–	–	–	–
Diaphysial diameter in the latero-medial plane	c. 57	–	–	–	40	48.9	62	58	64.7	72
Diaphysial diameter in the antero-posterior plane	c. 54	–	–	–	35	43.7	55	54	59.8	71
Width of distal epiphysis in the latero-medial plane	105	–	–	–	82	94.4	115	–	–	–
Depth of the distal epiphysis in the antero-posterior plane	–	–	–	–	57	69.8	83	–	–	–
Width of distal articular surface in the latero-medial plane	c. 83	–	–	–	51	63.3	72	100	116.1	125
Depth of distal articular surface in the latero-medial plane	–	–	–	–	42	54.2	65	75	88.1	98

in the analysed specimen) using Christiansen's equation (Christiansen, 2004), provides a value of about 1650 kg. The inferred body mass is roughly consistent with the maximum body mass of about 1550 kg estimated for *M. lamarmorai* from Funtana Morimenta from the ulna's least circumference, but slightly higher than the values obtained for the same individual by using the least circumference of the humerus (1400 kg) and femur (1300 kg) and significantly higher than the body mass estimated for the same individual from the humerus length, using Roth's (1990) and Christiansen's (2004) equations (about 420 kg and 765 kg respectively). Although the limb bone dimensions of large mammals appear to have a very good predictive consistency to estimate their body mass because they support the body weight in static and dynamics conditions, it is extremely difficult to infer the weight of any individual by the dimensions of a single bone. Each dimension for each bone of an individual skeleton as, for instance the Funtana Morimenta mammoth, provides different body mass estimates. Indeed, this is even true for the elements having the higher  $R^2$  and the best per cent prediction

error (regarded as superior to the correlation coefficient in evaluating the predictive power of a regression equation). The maximum lengths of humerus and femur have been indicated as the best variables for estimating body mass in elephants weighing less than 2000 kg (Roth, 1990), while length and least circumferences of long bones have been recommended as the best parameters for the prediction of body mass for extinct proboscideans (Christiansen, 2004). The difference in the body mass values obtained by using different methods depends on the one hand on the scaling relationships, heterogeneous taxonomic composition and size range of samples used to generate the mass estimation equations (Christiansen, 2004; Palombo and Giovinazzo, 2005; Roth, 1990). On the other hand, equations giving good results if tested on living elephants can hardly be applied to dwarf elephants, because there are important differences in body proportions of these animals compared to the extant young individual or calves with the same height at the shoulder as adult insular elephants (see Larramendi and Palombo, 2015 for a discussion).



**Fig. 4.** Comparison among tibias of continental and dwarf *Paleoloxodon* and *Mammuthus* species: a: *Paleoloxodon antiquus* (specimen E8 from Neumark Nord, credit MRP); b: *Paleoloxodon tiliensis* (syntype of right tibia, T. 339, reversed, from Theodorou et al., 2007, Fig. 15, p. 31); c: *Paleoloxodon* ex gr. *P. mnaidriensis* (Puntali Cave, credit MRP, courtesy Museo Gemellaro, Palermo, Italy); d: Alghero specimen; e: *Mammuthus exilis* (California Channel Islands, credit MRP, courtesy Mammoth Site Museum, Hot Springs, South Dakota, US); f: *Mammuthus primigenius* (Siberia, credit MRP, courtesy Ice Age Museum, Moscow, Russia). Not to scale, all distal epiphyses at the same size.

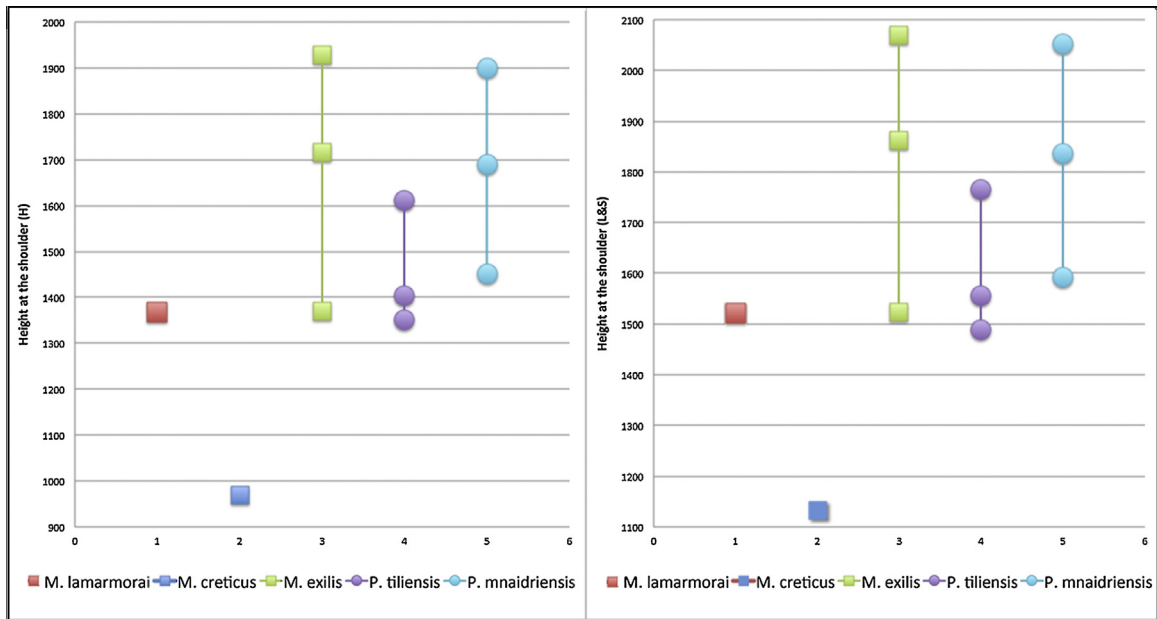
**Fig. 4.** Comparaison entre tibias d'espèces continentales et naines de *Paleoloxodon* et *Mammuthus* : a : *Paleoloxodon antiquus* (spécimen E8 de Neumark Nord, crédit MRP) ; b : *Paleoloxodon tiliensis* (syntype de tibia droit, T 339 retourné, d'après Theodorou et al., 2007, Fig. 15, p. 31) ; c : *Paleoloxodon* ex gr. *P. mnaidriensis* (Puntali Cave, crédit MRP, avec l'autorisation du musée Gemellaro, Palerme, Italie) ; d : spécimen d'Alghero ; e : *Mammuthus exilis* (Channel Islands, Californie, crédit MRP, avec l'autorisation du Mammoth Site Museum, Hot Springs, Dakota, États-Unis) ; f : *Mammuthus primigenius* (Sibérie, crédit MRP, avec l'autorisation du musée de l'Âge glaciaire, Moscou, Russie). À noter que les tibias ne sont pas à l'échelle, toutes les épiphyses distales sont à la même taille.

#### 4. Discussion

The fossil record of Sardinian mammoths known to date mainly consists of some isolated teeth reported from Tramariglio (Porto Conte, Alghero) (Malatesta, 1954), Campo Giavesu (Palombo et al., 2005) and San Giovanni di Sinis (Ambrosetti, 1972; Melis et al., 2001), and a largely incomplete skeleton, a few vertebrae, and a large fragment of tusk found at Guardia Pisano in the Funtana Morimenta area (Gonnesa basin, SW Sardinia) (Acconci, 1881; Major, 1883; Orrù and Ulzega, 1986; Palombo et al., 2012) (Fig. 1). The paucity of remains, the different sizes of molariform teeth from different localities, the lack of dental remains at Guardia Pisano and the uncertainties about the chronology of some remains hamper any attempt to infer the actual size range of the Sardinian elephant. Nor can it be affirmed without doubt that only one species, i.e. *Mammuthus lamarmorai*, inhabited the island. Palombo et al. (2005) tentatively suggested the possibility of the existence in Sardinia of a second mammoth species. The hypothesis is based on the large dimensions of two last upper molars belonging to two adult individuals of different ontogenetic ages, found in alluvial sediments deposited in the Campo Giavesu marshland environment after the end of Monte Annaru volcanic activity, which is dated at about 0.2 Ma (Beccaluva et al., 1981). The best preserved Campu Giavesu last upper molar shows dimensions definitely larger than the dimensions

consistent with the size of *M. lamarmorai* as inferred for the Guardia Pisano skeleton (Palombo et al., 2012). The height at the shoulder calculated for Guardia Pisano *M. lamarmorai* using equations proposed by Harington et al. (1974) (= 1367 mm) and Lister and Stuart (2010) (= 1520 mm) approaches those of the smallest *M. exilis* (1371 mm and 1523 mm respectively) and *P. tiliensis* (1350 mm and 1489 mm respectively), while it is less than the minimum height calculated for *P. ex gr. P. mnaidriensis* (1450 mm and 1592 mm, respectively) (Fig. 5). Conversely, available data for the last molars of *M. exilis* (lower last molar, length range = 171–223 mm) (Herridge and Lister, 2012), *P. tiliensis* (lower last molar, length range = 130–165 mm, upper last molar, length = 124 mm) (Theodorou, 1983), and *P. "mnaidriensis"* from Puntali cave (upper last molar, length range = 192–240 mm) (Ferretti, 2008), suggest for the mammoth from Campo Giavesu a size closer to that of the largest individuals from Puntali cave and *M. exilis* than to those of *P. tiliensis*. It is worth noting that, although teeth can be problematic for body size estimation in insular dwarfs due to the allometric negative size reduction of skull and teeth in large insular mammals (e.g., Azzaroli, 1982; Gould, 1975), and although the large difference in size related to sexual dimorphism known in living elephants seems to increase in insular dwarfs, male and female teeth are not so different in absolute size.

As a result, the dimensional scaling observed in the Sardinian specimens from Campo Giavesu and San



**Fig. 5.** Comparison among the height at the shoulder in *Mammuthus lamarmorai* from Guardia Pisano (Morimenta, Gonnese, SW Sardinia), *Mammuthus exilis* (Channel Islands, California), *Palaeoloxodon tiliensis* (Charkadio cave, Tilos, Greece), *Palaeoloxodon ex gr. P. mnaidriensis* (Puntali cave, Sicily, Italy), calculated following Harington et al. (1974) (height at the shoulder [H]) and Lister and Stuart (2010) (height at the shoulder [L&S]).

**Fig. 5.** Comparaison entre les hauteurs à l'épaule de *Mammuthus lamarmorai* provenant de (Guardia Pisano, Morimenta, Gonnese, Sud-Ouest de la Sardaigne), *Mammuthus exilis* (Channel Islands, Californie), *Palaeoloxodon tiliensis* (Charcadio Cave, Tilos, Grèce) ; *Palaeoloxodon ex gr. P. mnaidriensis* (Puntavi Cave, Sicile, Italie) ; calculées d'après Harington et al. (1974) (hauteur à l'épaule [H]) et Lister et Stuart (2010) (hauteur à l'épaule [L&S]).

Giovanni di Sinis (irrespective of whether the tooth from this locality is a penultimate or a last molar, see Melis et al., 2001) could be regarded as a progressive dwarfing anagenetic evolution within an endemic lineage or on repeated dispersal events that led, through time, to the presence on the island of small mammoth populations, not genetically related, which survived for a while and then became extinct. Alternatively, the appearance of large individuals might be related to an occasional genetic introgression. The hypothesis of an anagenetic process leading to a progressive size reduction would imply that the Campo Giavesu specimens were the oldest known to date. Some features of Campo Giavesu tooth (e.g., number of plates, lamellar frequency, and enamel thickness) are apparently more archaic than those of specimen from San Giovanni in Sinis, but the hypsodonty index is higher (Melis et al., 2001; Palombo et al., 2005), confirming the impossibility to formulate any convincing hypothesis on the basis of data available to date.

Furthermore, the paucity of the Sardinian fossil record and the vague chronology of Campo Giavesu specimens make it problematic to firmly establish the age of dispersal of the ancestor of Sardinian mammoths, although some data seem to indicate a presence of dwarf elephants in Sardinia at least during the latest middle Pleistocene. The San Giovanni in Sinis tooth, indeed, was retrieved from pedogenized beach sediments deposited during an interglacial phase tentatively correlated to MIS 7, if not older (Andreucci et al., 2009; Chesi et al., 2007; Lecca and Carboni, 2007; Melis et al., 2001). It has been suggested that also the deposition of sediments yielding the Guardia Pisano skeleton may predate MIS 5e, but researchers disagree as regards

to the age of Aeolian deposits of the Funtana Morimenta Formation (FMF), to which the Guardia Pisano fossiliferous layer has been correlated (see Palombo et al., 2012, pp. 161–162 for a discussion). Moreover, it is challenging to say whether the ancestor actually was *Mammuthus trogontherii*, as suggested by some authors (e.g., Palombo et al., 2012), or *Mammuthus meridionalis*, for at least two reasons: (i) on the one hand “a long-standing problem attached to the European transition from *M. meridionalis* to *M. trogontherii*, viz. the lack of good criteria for the referral of late Early to early middle Pleistocene molars with more or less mixed morphological characteristics to either of the said species” (Van Essen, 2011 p. 1); (ii) on the other, the insular elephants generally show more primitive dental features (i.e. enamel thickness and lamellar frequency) than their mainland ancestors. As regards the Campo Giavesu last upper molar, although the enamel thickness (2.8) falls in the range of *M. meridionalis* from Valdarno (2.6–3.9, mean 3.2), number of plates (15), lamellar frequency (7), and hypsodonty index (1.68) are higher. The hypsodonty index, lamellar frequency and enamel thickness fall within the variation range of *M. trogontherii* from the early middle Pleistocene site of Süssenborn (about 600 ka), while the plate number is less than the minimum (Guenther, 1969), supporting a phyletic relationship with the steppe-mammoth. Assuming that the Sardinian mammoth lineage originated from *M. trogontherii*, the ancestor may have swum to the island during any low-stand phase between about 750 ka (lowest stratigraphical occurrence of the steppe-mammoth in Italy in the PG1 sequence of Ponte Galeria Formation) and the end of the middle Pleistocene

(highest stratigraphical occurrence in central Italy at km 8 and 7.2 of via Flaminia, Rome) (Palombo and Ferretti, 2005; Palombo and Milli, 2011). Van der Geer et al. (2010, p. 130) hypothesised that an “ancestry from the woolly mammoth seems the most parsimonious. This fits also with the arrival of the megacerine deer on the island, because both woolly mammoth and giant deer are elements of the same fauna in the rest of Eurasia for the late Pleistocene”. This suggestion seems, however, poorly convincing because the ancestor of the endemic Sardinian megacerine entered the island during the early middle Pleistocene (if not earlier) (see Melis et al., 2016; Palombo, 2009; Palombo and Rozzi, 2014), while available data indicate that in the Italian peninsula *M. primigenius* is recorded mostly during MIS 4 and 3 (Braun and Palombo, 2012, and references therein).

## 5. Conclusion

The morphology and dimension of the elephant tibia found in the sandy Aeolian deposit in the vicinity of Alghero allow us to refer it, although with caution, to *Mammuthus cf. M. lamarmorai*.

The characterisation of the sediments embedding the tibia suggests they likely belong to the dunes deposited in the area during MIS 3/4, suggesting a possible presence of endemic elephants in Sardinia till about 57–29 ka BP. This new datum, however, provides very little or no clue to support the parsimonious hypothesis that only one *Mammuthus* phyletic lineage inhabited Sardinia during the late middle and late Pleistocene.

We are still far from having a convincing hypothesis about the evolutionary processes and the population dynamics of elephant populations in Sardinia. A richer fossil record and a firm chronology of the elephant remains known to date may enable us to answer intriguing questions such as the colonisation by the Sardinian mammoth ancestor and whether only one mammoth species inhabited Sardinia, as well as whether the dimensional scaling may result from a progressive dwarfing due to anagenetic evolution, or mainland mammoths entered the island more than once, giving rise to different species, or whether size may depend on some introgressive hybridisation.

## Acknowledgments

We thank the anonymous reviewers and the Associate Editor L. H. van den Ostendefor critically reading the manuscript.

This research was funded by Italian MURST (Sapienza University 2014 project C26A14BNRM led by M.R. Palombo).

## References

- Acconci, L., 1881. Sopra alcune ossa fossili di elefanti rinvenute nel Quaternario di Morimonta in Sardegna. *Atti della Soc. Toscana Sci. Nat. Processi Verballi* 2, 266–267.
- Agenbroad, L.D., 2002. In: Browne, D.R., Mitchell, K.L., Chaney, H.W. (Eds.), *New localities, chronology, and comparisons for the pygmy mammoth (Mammuthus exilis): 1994–1998*. Proc. 5<sup>th</sup> California Islands Symp. Santa Barbara Mus. Nat. Hist., Santa Barbara, CA, pp. 518–524.
- Agenbroad, L.D., 2003. *New absolute dates and comparisons for California's Mammuthus exilis*. *Deinse* 9, 1–16.
- Agenbroad, L.D., 2009. In: Damiani, C.C., Garcelon, D.K. (Eds.), *Mammuthus exilis* from the California Channel islands: height, mass, and geological age. Proc. 7<sup>th</sup> California Islands Symp. Institute for Wildlife Studies, Arcata, CA, USA, pp. 15–19.
- Ambrosetti, P., 1968. The Pleistocene dwarf elephants of Spinagallo (Siracusa, south-eastern Sicily). *Geologica Romana* 7, 277–398.
- Ambrosetti, P., 1972. L'elefante fossile della Sardegna. *Boll. Servizio Geologico d'Italia* 91, 117–131.
- Andreucci, S., Pascucci, V., Murray, A.S., Clemmensen, L.B., 2009. Late Pleistocene coastal evolution of San Giovanni di Sinis (Western Mediterranean). *Sediment. Geol.* 216 (3–4), 104–116.
- Andreucci, S., Clemmensen, L.B., Murray, A.S., Pascucci, V., 2010. Middle to late Pleistocene coastal deposits of Alghero, Northwest Sardinia (Italy): chronology and evolution. *Quatern. Int.* 222, 3–16.
- Athanassiou, A., Herridge, V., Reese, D.S., Iliopoulos, G., Roussiakis, S., Mitsopoulou, V., Tsiolakis, E., Theodorou, G., 2015. Cranial evidence for the presence of a second endemic elephant species on Cyprus. *Quatern. Int.* 379, 47–57.
- Azzaroli, A., 1982. Insularity and its effects on terrestrial vertebrates: evolutionary and biogeographic aspects. In: Montanaro Galitelli, E. (Ed.), *Palaeontology Essential of Historical Geology*. Modena, Italy, pp. 18–23.
- Beccaluva, L., Deriu, M., Macciotta, G.P., Savelli, C., 1981. Carta geopetrografica del vulcanismo plio-pleistocenico della Sardegna nord occidentale—Scala 1:50.000. L.A.C. Firenze, Italy.
- Braun, I.M., Palombo, M.R., 2012. *Mammuthus primigenius* in the cave and portable art: an overview with a short account on the elephant fossil record in southern Europe during the last glacial. *Quatern. Int.* 276, 61–76.
- Chesi, F., Delfino, M., Abbazzi, L., Carboni, S., Lecca, L., Rook, L., 2007. New fossil vertebrates from San Giovanni di Sinis (late Pleistocene, Sardinia): the last *Mauremys* (Reptilia, Testudines) in the central Mediterranean. *Rivista It. Paleont. Stratigr.* 113 (2), 287–297.
- Christiansen, P., 2004. Body size in proboscideans, with notes on elephant metabolism. *Zool. J. Linn. Soc.* 140 (4), 523–549.
- Ferretti, M.P., 2008. The dwarf elephant *Palaeoloxodon mnaidriensis* from Puntali Cave, Carini (Sicily; late middle Pleistocene): anatomy, systematics and phylogenetic relationships. *Quatern. Int.* 182 (1), 90–108.
- Gould, S.J., 1975. On the scaling of tooth size in mammals. *Am. Zool.* 15, 351–362.
- Guenther, E.W., 1969. Die Elefantenzähne aus den Kiesen von Süßenborn bei Weimar. *Paläozoolog.* A 3 (3–4), 711–734.
- Harrington, C., Tipper, H., Mott, R., 1974. Mammoth from Babine Lake, British Columbia. *Canad. J. Earth Sci.* 11, 285–303.
- Herridge, V.L., (Ph.D. thesis) 2010. (Dwarf middle Pleistocene on Mediterranean islands: a natural experiment in parallel evolution). University College, London.
- Herridge, V.L., Lister, A.M., 2012. Extreme insular dwarfism evolved in a mammoth. *Proc. Royal Soc. London B: Bio. Sci.* 279 (1741), 3193–3200.
- Johnson, D.L., 1980. Problems in the land vertebrate zoogeography of certain islands and the swimming powers of elephants. *J. Biogeogr.* 7, 383–398.
- Larramendi, A., Palombo, M.R., 2015. Body size, biology and encephalization quotient of *palaeoloxodon ex gr. P. falconeri* from Spinagallo cave (Hyblean plateau, Sicily). *Hystrix* 26 (2), 1–8.
- Lecca, L., Carboni, S., 2007. The Tyrrhenian section of San Giovanni di Sinis (Sardinia): stratigraphic record of an irregular single high stand. *Rivista It. Paleont. Stratigr.* 113, 509–523.
- Lister, A.M., Stuart, A.J., 2010. The West Runton mammoth (*Mammuthus trogontherii*) and its evolutionary significance. *Quatern. Int.* 228, 180–190.
- Major, F.C.J., 1883. Die Tyrrhenis: Studien über geographische Verbreitung von Tieren und Pflanzen im westlichen Mittelmeergebiet. *Kosmos* 13, 81–106.
- Malatesta, A., 1954. Primo dente di elefante fossile rinvenuto in Sardegna. *Quaternaria* 1, 97–105.
- Mangano, G., Bonfiglio, L., 2012. First finding of a partially articulated elephant skeleton from a late Pleistocene hyena den in Sicily (San Teodoro Cave, North Eastern Sicily, Italy). *Quatern. Int.* 276, 53–60.
- Masseti, M., 2006. Deer and dwarf elephants of the Dodecanese. In: Karageorghis, V., Giannikouri, A. (Eds.), *The Holocene redefinition of the faunal ecosystems of Rhodes and other nearby islands. Conservation and Preservation of the Cultural and Natural Heritage of the Large Islands of the Mediterranean*. Ministry of Culture, Archaeological Institute of Aegean Studies, Foundation Anastasios G. Leventis, Athens, pp. 113–122.



- Melis, R., Palombo, M.R., Mussi, M., 2001. *Mammuthus lamarmorae* (Major, 1883) remains in the pre-Tyrrhenian deposits of San Giovanni in Sinis (Western Sardinia; Italy). In: Cavaretta, G., Gioia, P., Mussi, M., Palombo, M.R. (Eds.), *The world of elephants*. CNR, Roma, pp. 481–485.
- Melis, R.T., Palombo, M.R., Ghaleb, B., Meloni, S., 2016. The Su Fossu de Canas cave (Sadali, Italy): a key site for inferring the timing of dispersal of giant deer in Sardinia. *Quat. Res.* 86, 335–347.
- Orrù, P., Ulzega, A., 1986. Geomorfologia costiera e sottomarina della Baia di Funtanamare (Sardegna sud-occidentale). *Geogr. Fis. Dinam. Quaternaria* 9, 56–67.
- Palombo, M.R., 2004. Dwarfing in insular mammals: the endemic elephants of mediterranean islands. In: Baquedano, E., Rubio Jara, S. (Eds.), *Miscelanea en homenaje a Emiliano Aguirre, Zona Arqueologica 4 (II: Paleontología)*. Museo Arqueológico Regional, Alcalá de Henares, pp. 354–371.
- Palombo, M.R., 2009. Biochronology, paleobiogeography and faunal turnover in western Mediterranean Cenozoic mammals. *Integr. Zool.* 4 (4), 367–386.
- Palombo, M.R., 2010. Elephants in miniature. In: Meller, H. (Ed.), *Elefantenreiche Eine Fossilwelt in Europa. Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt. Landesmuseum für Vorgeschichte, Halle, Germany*, pp. 275–292.
- Palombo, M.R., Ferretti, M.P., 2005. Elephant fossil record from Italy: knowledge, problems and perspectives. *Quatern. Int.* 126 (1), 107–136.
- Palombo, M.R., Ginesu, S., Melis, R.T., Sias, S., 2005. The endemic elephants from Sardinia: an unsolved problem, 12. *Monografies de la Societat d'Història Natural de les Balears*, pp. 245–254.
- Palombo, M.R., Giovinazzo, C., 2005. *Elephas falconeri* from Spinagallo Cave (South-Eastern Sicily, Hyblean Plateau, Siracusa): a preliminary report on brain to body weight comparison. In: Alcover, J.A., Bover, P. (Eds.), *Proc. Int. Symp. insular vertebrate evolution: the palaeontological approach*, 12. *Monografies de la Societat d'Historia Natural de les Balears*, pp. 255–264.
- Palombo, M.R., Milli, S., 2011. Mammalian fossil record, depositional setting, and sequence stratigraphy in the middle–Upper Pleistocene of Roman Basin, II *Quaternario, It. J. Quatern. Sci.* 23 (2), 243–248.
- Palombo, M.R., Rozzi, R., 2014. How correct is any chronological ordering of the Quaternary Sardinian mammalian assemblages? *Quatern. Int.* 328, 136–155.
- Palombo, M.R., Ferretti, M.P., Pillola, G.L., Chiappini, L., 2012. A reappraisal of the dwarfed mammoth *Mammuthus lamarmorai* (Major, 1883) from Gonnese (south-western Sardinia, Italy). *Quatern. Int.* 255, 158–170.
- Poulakakis, N., Mylonas, M., Lymberakis, P., Fassoulas, C., 2002. Origin and taxonomy of the fossil elephants of the island of Crete (Greece), problems and perspectives. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 186, 163–183.
- Roth, V.L., 1990. Insular dwarf elephants: a case study in body mass estimation and ecological inference. *Body size in mammalian paleobiology: estimation and biological implications*. Cambridge University Press, New York, pp. 151–179.
- Rozzi, R., Palombo, M.R., 2013. Do methods for predicting paleohabitats apply for mountain and insular fossil bovids? *Integr. Zool.* 8 (3), 244–259.
- Scarborough, M.E., Palombo, M.R., Chinsamy, A., 2016. Insular adaptations in the astragalus-calcaneus of Sicilian and Maltese dwarf elephants. *Quatern. Int.* 406, 111–122.
- Sechi, D., 2013. Reconstruction of the Sardinia the north-west coast evolution: a chronologic and sedimentologic approach. Doctoral dissertation. University of Sassari, Italy.
- Sen, S., Barrier, E., Crété, X., 2014. Late Pleistocene dwarf elephants from the Aegean islands of Kassos and Dilos, Greece. *Ann. Zool. Fennici* 51 (1–2), 27–42.
- Theodorou, G.E., 1983. The dwarf elephants of the Charkadio cave on the island of Tilos (Dodecanese, Greece). Doctoral dissertation. University of Athens (in Greek).
- Theodorou, G., Symeonidis, N., Stathopoulou, E., 2007. *Elephas tiliensis* n. sp. from Tilos island (Dodecanese, Greece). *Hell. J. Geosci.* 42, 19–32.
- Van der Geer, A.A., 2014. Parallel patterns and trends in functional structures in extinct island mammals. *Integr. Zool.* 9 (2), 167–182.
- Van der Geer, A., Lyras, G., de Vos, J., Dermitzakis, M., 2010. *Evolution of island mammals: adaptation and extinction of placental mammals on islands*. Wiley-Blackwell, Oxford.
- Van der Geer, A., Lyras, G.A., Van den Hoek Ostende, L.W., Fe Vos, J., Drinia, H., 2014. A dwarf elephant and a rock mouse on Naxos (Cyclades, Greece) with a revision of the palaeozoogeography of the Cycladic Islands (Greece) during the Pleistocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 404, 133–144.
- Van Essen, J.A.V., 2011. Tracing transitions. An overview of the evolution and migrations of the genus *Mammuthus* Brookes, 1828 (Mammalia, Proboscidea). Doctoral dissertation. Faculty of Archaeology, Leiden University, Leiden, The Netherlands.