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THE ENDEMIC ELEPHANTS FROM SARDINIA:
AN UNSOLVED PROBLEM

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Resum

Mammuthus lamarmorae (Major, 1883) (= *M. lamarmorai,* d'acord amb el ICZN 2000) fou identificat en base a restes molt escasses: alguns ossos tarsians, carpians i llargs obtinguts als dipòsits de la darrera edat glacial que afloren a Fontana Morimenta (Gonnesa, sud-oest de Sardenya); alguns molars aïllats descoberts a les bretxes post-tirrenianes (posteriors al MIS 5e) de Tramariglio (l'Alguer), a una bretxa pre-tirreniana (pre-MIS 5e, MIS 6?) que aflora a San Giovanni in Sinis (Oristano, Sardenya occidental) i a uns dipòsits al·luvials del Pleistocè Mitjà tardà que omplen la conca de Campu Giavesu (nord-oest de Sardenya, Sassari). En base a l'evidència morfològica i biomètrica, sembla possible que a Sardenya visquessin dos elefants endèmics de diferent mida. Degut a la incertesa amb les edats dels espècimens més grans, no es pot descartar la suposició que els elefants assolissin Sardenya en més d'una onada migratòria, talment com ja s'ha confirmat per a Sicília i Creta.
Paraules clau. Elefants endèmics, Pleistocè, Sardenya.

Abstract

Mammuthus lamarmorae (Major, 1883) (= *M. lamarmorai* according to ICZN 2000) was identified on the basis of very scanty remains: some tarsal, carpal and long bones, recovered from the last glacial deposits cropping out at Fontana Morimenta (Gonnesa, southwestern Sardinia); some isolated molars discovered in post-Tyrrhenian (post-MIS 5e) breccias at Tramariglio (Alghero), in a pre-Tyrrhenian (pre-MI substage 5e, ?MIS 6) beach deposit cropping out at S. Giovanni in Sinis (Oristano, western Sardinia) and in late Middle Pleistocene alluvial deposits filling the Campu Giavesu Basin (north-western Sardinia, Sassari). On the basis of morphological and biometric evidence, it seems possible that two endemic elephants of different size existed in Sardinia. Due to incertitude regarding the age of larger specimens, the supposition that mainland elephants reached Sardinia in more than one migration wave, as already affirmed for Sicily and Crete, cannot be completely ruled out.
Key Words. **Endemic elephants, Pleistocene, Sardinia.**

INTRODUCTION

During the Pleistocene, endemic elephants, descending from the Middle and Late Pleistocene continental *Elephas (Palaeoloxodon) antiquus* Falconer & Cautley, 1847, were quite common in unbalanced faunas on several eastern and western Mediterranean islands (Tilos, Crete, Cyprus, Sicily and Malta), whereas dwarfed taxa belonging to *Mammuthus* have been recorded only in Crete [*Mammuthus creticus* (Bate, 1907)] and Sardinia. Elephant remains were first discovered in Sardinia at the end of the XIXth century, when some tarsal, carpal and long bones were recovered from Late Pleistocene deposits near the village of Gonnesa (south-western Sardinia). On the basis of these bones, first reported by Acconci (1881) as similar in size to *"Elephas melitensis"*, Major (1883) described the new species *"Elephas lamarmorae"*, without providing any illustration.

Later, during the second half of the 20th century, two molars were discovered respectively in post-Tyrrhenian (post-MIS 5e) breccias at Tramariglio (Alghero; Malatesta,

1954a) and in pre-Tyrrhenian (pre-MIS 5, ?MIS 6) beach deposits at S. Giovanni in Sinis (Ambrosetti, 1972; Melis *et al.*, 2001). More recently, we have had the opportunity to examine two specimens (one fragment and one complete last upper molar) collected at the beginning of the last century in alluvial deposits cropping out at Campu Giavesu (Sassari; Palombo *et al.*, 2003; Fig. 1).

The aim of this paper is to illustrate the elephant remains thus far recorded in Sardinia, to provide synthetic information on their stratigraphic context and to highlight the complexity of understanding the colonisation and evolutionary processes of Sardinian elephant populations.

FONTANA MORIMENTA

At the end of the 19th century, several bones of a small-size adult elephant were found in the area surrounding the village of Gonnesa. As reported by Acconci (1881), the bones, partially connected anatomi-

Fig. 1. A map of Sardinia showing localities where elephant remains have been discovered: 1 = Fontana Morimenta; 2 = Tramariglio; 3 = San Giovanni in Sinis; 4 = Campo Giavesu.

Fig. 1. Mapa de Sardenya amb les localitats on s'han trobat restes d'elefants. 1 = Fontana Morimenta; 2 = Tramariglio; 3 = San Giovanni in Sinis; 4 = Campo Giavesu.

Fig.2. Gonnesa section.1: eolian sediments (Olocene); 2: eolianites (MIS 2); 3: alluvial deposits (parallel bedding MIS 3); 4: alluvial deposits (cross bedding MIS 3); 5: paleosol (MI substage5e); 6: eolianites (MIS 6); S: erosional surface (MIS 4).

Fig. 2. Tall de Gonnesa. 1: sediments eòlics (Holocè); 2: eolianites (MIS 2); 3: dipòsits al·luvials (sedimentació paral·lela MIS 3); 4: dipòsits al·luvials (sedimentació creuada MIS 3); 5: paleosol (MI substage5e); 6: eolianites (MIS 6); S: superfície erosiva (MIS 4).

cally, belonged to a skeleton found during railway construction. See Major (1883): "Dagegen nähert sich der sardische Zwerg am meisten – natürlich nicht in den Dimensionen, sondern die Cohnformation der Gelenkflachen, der Fußknochen – dem die Riesen der Gattung, dem *E. meridionalis* unserer Pliocäns...". Consequently, the English palaeontologist ascribed them to a new species, *"E. lamarmorae"*. Later, several authors either regarded *"E. lamarmorae"* as a valid species, belonging to the "*Palaeoloxodon*" genus (Osborn, 1942) or, more frequently, attributed the specimens to *Elephas mnaidriensis* or to *Elephas melitensis*, considering the Sardinian elephant very similar in size and morphology to specimens from Malta and Sicily (de Stefani, 1891; Novarese, 1913; Caterini, 1923; Joleaud, 1926; Vaufrey, 1929; Comaschi Caria, 1965). Unfortunately, at present, we have no certain information on the deposit containing the elephant remains, even if, in the course of time, the samples have always been recorded as belonging to "eolian" deposits. Indeed, strongly cemented, cross-bedded eolianites crop up at Fontana Morimenta. Consequently, it was generally believed that the elephant remains were found in these deposits. Nevertheless, in keeping with the taphonomic features of the acropo-
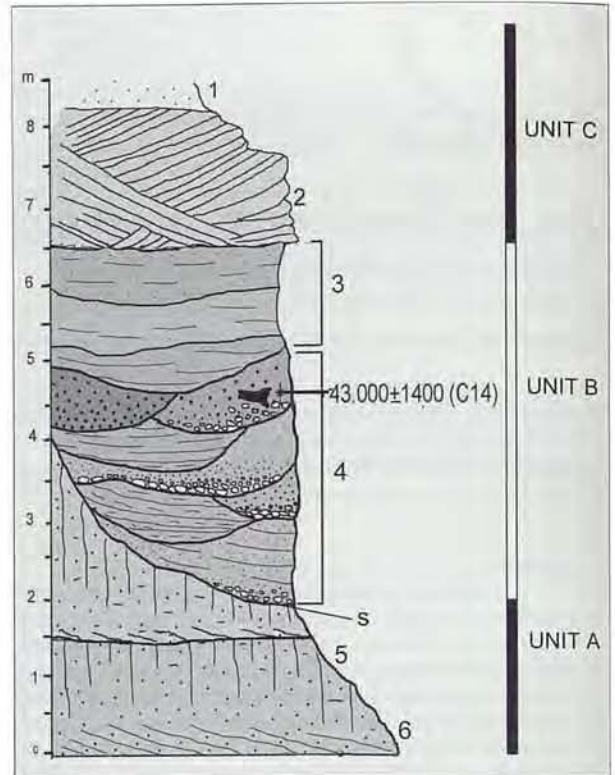
dium bones preserved at the Naturhischen Museum in Bale, it seems quite improbable that the skeleton was buried in the strongly-cemented sediments; accordingly, the hypothesis that the remains were uncovered in alluvial sediments cannot be completely ruled out.

Geological Setting

During the Quaternary, the Gonnesa Basin was affected by eolian processes, producing dunes extending several kilometres inland. Orrù & Ulzega (1982,1986) recognized several generations of dunes along the coast. The authors attributed the oldest eolian deposits, called the *"Funtana Morimenta Formation"*, to the Middle Pleistocene. Indeed, along the *Plage e Mesu* beach, a Tyrrhenian conglomerate (MI substage5e) lies on the erosional surface cutting the eolianites. A second eolian complex, well-cemented and with cross bedding, crops out in the valley of Riu Cabroila (Orrù & Ulzega, 1986). The complex has been attributed to the post-Tyrrhenian, and *Mammuthus lamarmorai* remains have thus far been thought to belong to these eolianites.

Nevertheless, about 200 metres south of the supposed discovery spot, a long stratigraphic sequence (about

Fig. 3. *Mammuthus lamarmorai* (Major, 1883); Fontana Morinentu (Gonnesa, Western Sardinia), Late Pleistocene. Anterior (a) and posterior (b) footh (Naturhistorische Museum, Bale), uncinatum in anterior-dorsal view (c), magnum in anterior-dorsal view (d), calcaneum in anterior view (e), navicular in dorsal view (f), cuboid in dorsal view (g) , ectocuneiform in dorsal view (h).
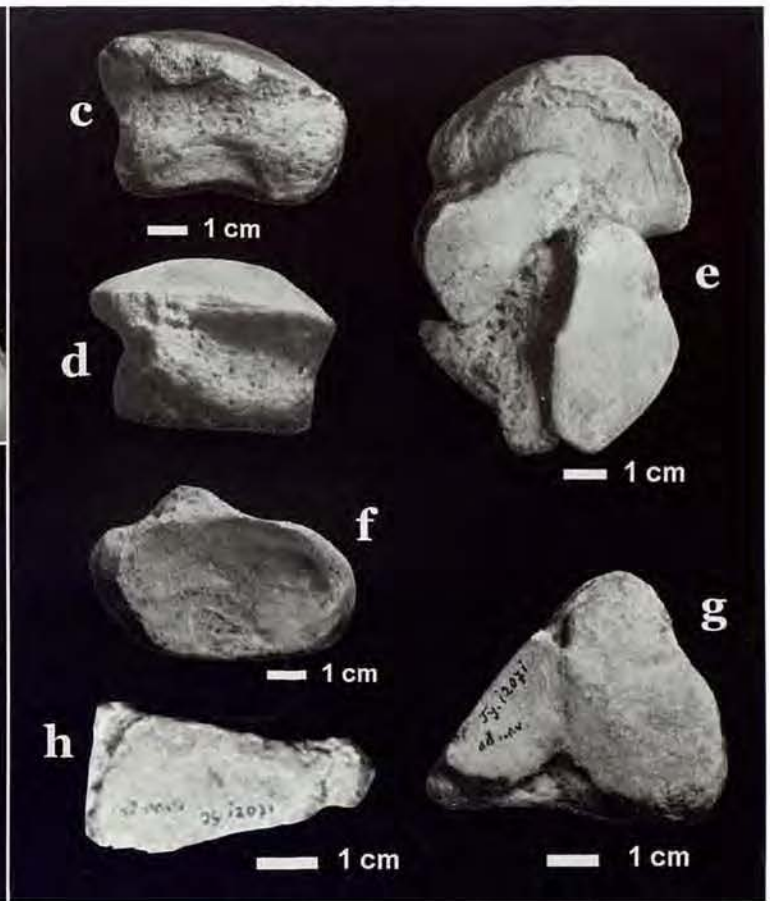
Fig. 3. Mammuthus lamarmorai *(Major, 1883); Fontana Morinentu (Gonnesa, Western Sardinia), Pleistocè superior. Peu anterior (a) i posterior (b) (Naturhistorische Museum, Bale), uncinatum en norma anterior-dorsal (c), magnum en norma anterior-dorsal (d), calcaneum en norma anterior (e), navicular en norma dorsal (f), cuboid en norma dorsal (g) , ectocuneiform en norma dorsal (h).*

20 m), including eolian and alluvial deposits, has been exposed in a sand quarry (Melis *et al.*, 2002). Three units have been distinguished from bottom to top (Fig. 2): 1) Unit A is made up of eolian cross-bedded deposits (at the bottom) overlaid by a palaeosol cut by an erosional surface, on top of which eolian sandy deposits and red soil lie. The microstucture of soils indicates climatic evolution towards more arid conditions. A deep incision separates Unit A from the superimposed Unit B. 2) Unit B corresponds to about 6 m of gravely, sandy and clayey alluvium, deposited by a braided stream system. 3) Unit C is made up of about 7-8 m of eolian cross-bedded deposits and by yellowish-red soil, documenting the occurrence of a more or less Mediterranean, seasonally contrasting climate (Duchaufour, 1983). At the top of the section, well-cemented eolianites crop out, and the old railway is still visible.

An absolute age of 43,000 ± 1400 BP obtained for charcoal remains found in the alluvial deposit (Melis *et al.*, 2002), as well as sedimentological and mineralogical data, enable us to hypothesise that: 1) Unit A sediments deposited during MIS 6 (eolianits), MI substage 5e (soil occurring at the top of this unit) and MI substage 5d (eolian sediments and rubified soil); 2) the deep incision,

separating Unit A from Unit B, probably testifies to erosional processes taking place during MIS 4; 3) the alluvial deposits of Unit B filled the small valley during MIS 3, under wet climatic conditions; 4) the eolian deposits, calcrete and paleosols on top of the alluvium could be respectively connected with the MIS 2 and the Early Holocene.

Elephant remains (Fig. 3)

The carpal of the second range of the Fontana Morimenta elephant, in particular the magnum and uncinatum (Fig.3 c,d), are higher than they are wide, more similar to those of *M. meridionalis* than to those of *E. antiquus*. In detail, on the magnum the articular facet for the trapezoid is divided, the articular surface for the lunatum and navicular is quite narrow and elongated and the articular surface for the second metacarpal is reduced. Moreover, on the uncinatum, the articular surface for the fourth metacarpal is concave. All these features resemble *M. meridionalis* carpal bones. As far as the tarsal bones are concerned, the navicular (Fig. 3 f) is considerably extended latero-medially and the articular surface for the astragalus is oval and notably concave; on the
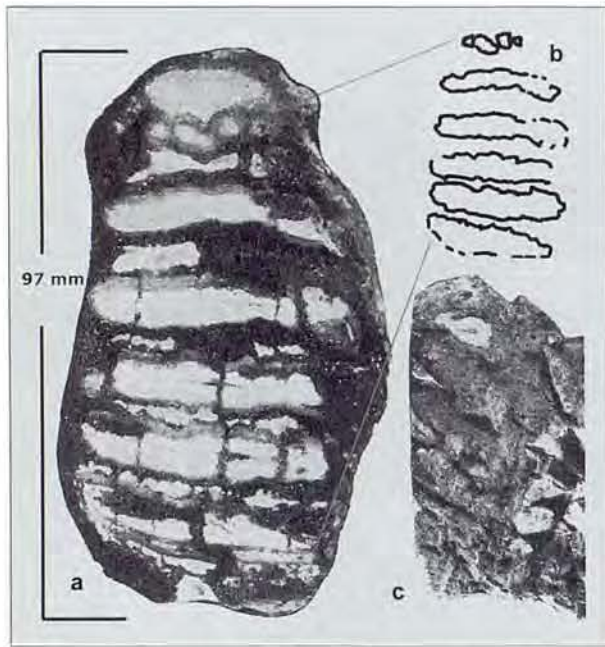
Fig. 4. *Mammuthus lamarmorai* (Major, 1883); Tramariglio, ? late Pleistocene. Right ?M¹ in occlusal (a, b) and labial (c) view.

Fig. 4. Mammuthus lamarmorai (Major, 1883); Tramariglio, Pleistocè superior?. ?M¹ dret, en normes oclusiva (a, b) i labial (c).

cudoid (Fig. 3 g), the extension and proportions of the articular surfaces for the calcaneum and navicular are more similar to *Mammuthus* than to *E. antiquus* tarsal bones; the ectocuneiform (Fig. 3 h) is narrower than in *E. antiquus*, extending much further towards the back than in *M. meridionalis* too, and it seems to articulate only with the third metatarsal, not with the fourth.

Moreover, the astragalus is very wide, almost completely impending over the fourth metatarsal. This corresponds to the considerable extension of the articular portion of the calcaneum (Fig. 3 c), in which the tuber is greatly extended transversely, providing a large attachment surface for the *gastrocnemius* and *soleus* muscles. The lower external profile of the calcaneum is greatly expanded.

In addition, carpals and tarsal bones seem to be arranged in a weakly-arcuated way. The structure provided better support for the body on the ground and better thrust in movements. All things considered, the limb posture of the Fontana Morimenta elephant might be quite different from that of continental taxa, adapted either to clear forest or more open environments. The Sardinian elephant possibly moved quite fast, even on rough terrain.

Furthermore, on the basis of the maximal length of the humerus (450 mm, according to Acconci, 1881), the Fontana Morimenta elephant was about 130-135 cm tall at the shoulder. This size exceeds the variability ranges of both *Mammuthus exilis* and *Elephas falconeri*, is notably less than the size hypothesised for *E. mnaidriensis* and parallels the size of elephants from Tilos (Palombo, 2004). It is worth noting that the smallest dwarfed elephants (Sicily, Crete, Tilos, the Santa Rosa islands) generally characterised strongly oligotypic faunas, where ele-

phants were the only large mammals (Palombo, 2004). Conversely, among impoverished and unbalanced Sardinian Middle and Late Pleistocene faunas, a middle-sized cervid, *"Paraemegaceros" cazioti*, also occurred.

TRAMARIGLIO

Geological Setting

The coastal area between Capo Caccia and Punta Giglio (north-western Sardinia) is characterised by high calcareous cliffs, broken by small bays. Recent studies (Antonioli *et al.*, 1998a,b; Fara *et al.*, 1998), have pointed out the presence of a continuous beach deposit, with inserted eolian deposits, attributed to isotopic stage 5e, previously identified by Malatesta (1954b) in the Punta Negra and Dragonara sections. The eolian deposits have consequently been attributed both to a previous cold stage and to one following the 5e isotopic stage (Antonioli *et al.*, 1998a; Fara *et al.*, 1998).

In the stretch of coast between Punta del Dental and Torre di Tramariglio, on the eastern side of the Capo Caccia headland, strips of Quaternary deposits, prevalently breccias (Malatesta, 1954a), are placed against the calcareous Mesozoic cliffs. Five metres above sea level, a shoreline furrow with date mussel holes is evident. According to Malatesta (1970), the breccias must thus originate, at least in part, from a period preceding the sea level attributed to isotopic stage 5e (Antonioli *et al.*, 1998a).

Near the beach in tiny Tramariglio Bay, calcareous breccias cover the Tyrrhenian conglomerate and are interspersed by a horizon of red soil with mammalian remains (Malatesta, 1954a). On top of the breccias, which in some places extend down to sea level, lie eolian sandstones (?MIS 2). The latter also outcrop under the Tramariglio Tower and are the source of the tooth reported by Malatesta (1954a).

Elephant remains (Fig. 4)

An elephant molar (?M¹) was recovered from post-Tyrrhenian breccia at Tramariglio (Alghero; Malatesta, 1954a). Malatesta (1954a) supposed the molar to be nearly complete, since the first root supports three plates; the dimensions do not contradict this hypothesis. Unfortunately, the molar is not available at present. According to Malatesta's pictures (1954a, fig.1,2), some tooth features, such as thick, quite simple enamel and low lamellar frequency, paralleled those of some quite advanced *M. meridionalis* specimens. Nonetheless, we have to take into account both: 1) the reduced size of the Tramariglio specimen (smaller molars have more closely-spaced plates, Lister & Joysey, 1992) and 2) the fact that endemic elephants, relative to the decrease in tooth size, reduced the number of laminae, whereas the enamel became thicker and less pleated. Consequently, enamel thickness and lamellar frequency, the variables most frequently used in tracing elephant evolution, have to be used with care when analysing dwarfed elephants, especially when studying isolated teeth, as in this case.
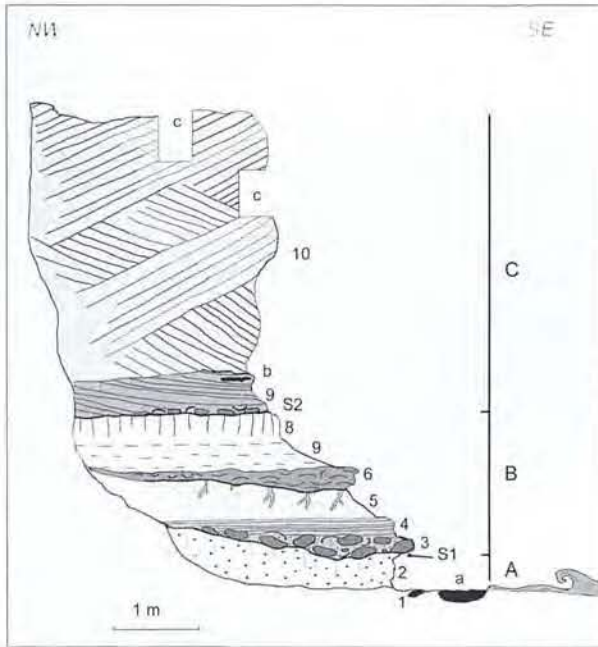
Fig.5. San Giovanni section. 1: calcrete; 2: palaeosol developed on beach sediments rich in *Helicoda* remains; 3 conglomerate containing pebbles from the erosion of the underlying level as well as basal pebbles; 4: beach sediments; 5: palaesols with rhyzoliths; 6: marine deposits rich in *Mytilus* and *Ostrea* shells (MI substage 5e); 7: lagoonal deposits with *Limnea*; 8: calcrete; 9: beach deposits, overlying a conglomerate with remains of *Ostrea* shells; 10: dunes; a: Elephant molar; b: cervid remains; S1 and S2 erosional surfaces.A, B, C: sequences.

Fig.5. Tall de San Giovanni. 1: calcreta; 2: palaeosol ric en restes d'Helicoda desenvolupat sobre sediments de platja; 3: conglomerat amb còdols procedents de l'erosió del nivell inferior al igual que còdols de basalt; 4: sediments de platja; 5: palaesols amb rizocrecions; 6: dipòsits marins rics en copinyes de Mytilus i Ostrea (MI subestadi 5e); 7: dipòsits de llacuna amb Limnea; 8: calcreta; 9: dipòsits de platja, cobrint un conglomerat amb restes de copinyes d'Ostrea; 10: dunes; a: molar d'elefant; b: restes de cèrvid; S1 i S2 superfícies erosives. A, B, C: seqüències.

SAN GIOVANNI IN SINIS

Geological Setting

In the southern Sinis Peninsula (western Sardinian coast), late Middle Pleistocene marine and continental deposits crop out near the village of San Giovanni (Fig. 1). Rather complex stratigraphic successions appear over approx. 1 km in a quickly-retreating cliff, and several papers have been devoted to clarifying them (Maxia & Pecorini, 1968; Ambrosetti, 1972; Caloi et al., 1980; Ulzega et al., 1980; Ulzega & Ozer, 1982; Ulzega & Hearty, 1986; Carboni & Lecca, 1985; Dudaud et al., 1991; Kindler et al., 1997). In 1968, Maxia and Pecorini reported an elephant tooth, found in the calcrete level at the bottom of the sequence. The molar was then extensively described by Ambrosetti (1972) as belonging to post-Tyrrhenian levels.

According to our recent studies, three different sequences can be detected, from bottom to top, (Fig. 5): 1) Sequence A, sloping towards the southeast and cha-

racterised by calcrete overlaid by a pedogenised sandy deposit, rich in Helicidae and bioclastic fragments (benthic foraminifers, echinoids and red algae). 2) Erosional surface (S1) that truncates sequence A. 3) sequence B, lying on the erosional surface, consisting of: polygenic conglomerate, containing fragments reworked from an underlying eroded level, and basalt pebbles; cross-bedding beach sands, on which a palaeosol with rhyzoliths has developed; calcarenite with tightly-packed *Mytilus* and *Ostrea* shells; lagoonal deposits with *Limnea*. 4) Erosional surface (S2). 5) sequence C, which includes: a thin conglomerate with fragments of the underlying *Mytilus* level; beach low-angle cross-bedding sandy deposits, including rare remains of "*P.*" *cazioti*; cross-bedded dune deposits. Ulzega & Hearty (1986), proposed an age of 90 ±15 ka (MIS substage 5c) for the *Mytilus* deposit (Sequence B). On the other hand, Duvaud *et al.* (1991) and Kindler *et al.* (1997) hypothesised that sequence A deposits could be earlier than MI substage 5e.

Studying the San Giovanni stratigraphic section confirms that, as already suggested by previous studies, the layer in which the elephant molar was found could be assigned to the pre-Tyrrhenian age (pre-MIS 5). The remains were buried within sandy beach sediments,

Fig.6. San Giovanni in Sinis (Western Sardinia), latest Middle Pleistocene. Right upper molar, in occlusal (above) and buccal (below) view. Approximately, x000 of natural size.

Fig.6. San Giovanni in Sinis (Sardenya occidental), Pleistocè Mitjà darrer. Molar dret superior en vista oclusiva (a dalt) i bucal (a sota). Aproximadament, x000 de la mida natural.

Fig. 7. Campo Giavesu landscape.

Fig. 7. Paisatge de Campo Giavesu.

affected by pedogenesis during a period of low sea level. Later, a calcrete developed under arid climatic conditions (?MIS 6). Furthermore, an increase in rainfall led to an erosive phase that truncated the soil overlying the calcrete. Marine transgression and deposition of "Tyrrhenian" (MI substage 5e) sediments followed, underlying the deposits containing the elephant molar.

Elephant Molar (Fig. 6)

The most important of the elephant remains discovered in the sixties by Prof. Giuseppe Pecorini is a well-preserved upper molar later described by Ambrosetti (1972). Ambrosetti considered it an M^3, although the gradually decreasing height typical of an M^3 elephant is not evident; moreover, the proportion of short and wide occlusal surfaces (greatest distal length =130 mm, functional (occlusal) length = 116 mm, greatest lingual breadth = 69 mm; functional (occlusal) breadth = 5.5 mm; height 90+ mm) is quite unusual for a penultimate *Mammuthus* tooth. On the other hand, there is no clear evidence of pressure from a posterior tooth; consequently, the hypothesis that the tooth is actually an M^2 of anomalous proportions cannot be definitively ruled out. The tooth is almost totally consumed by wear: of the 11 laminae, 9 are in use; the shape of the tooth suggests loss through wear of some other laminae at the front. The morphology of the molar, showing an oval- shaped occlusal surface, undulated enamel loops, and regularly folded enamel, suggests its attribution to the *Mammuthus* genus.

Enamel thickness (e = 1.8), average lamellar frequency (F = 8) and hypsodonty (HI = about 1,55) are consistent with this attribution. As far as the evolutionary degree of the San Giovanni tooth is concerned, we have to remember, as mentioned above, that in continental taxa, size reduction increases lamellar frequency (Lister & Joysey, 1992), whereas, in endemic elephant teeth, the number of laminae decreased and the enamel became
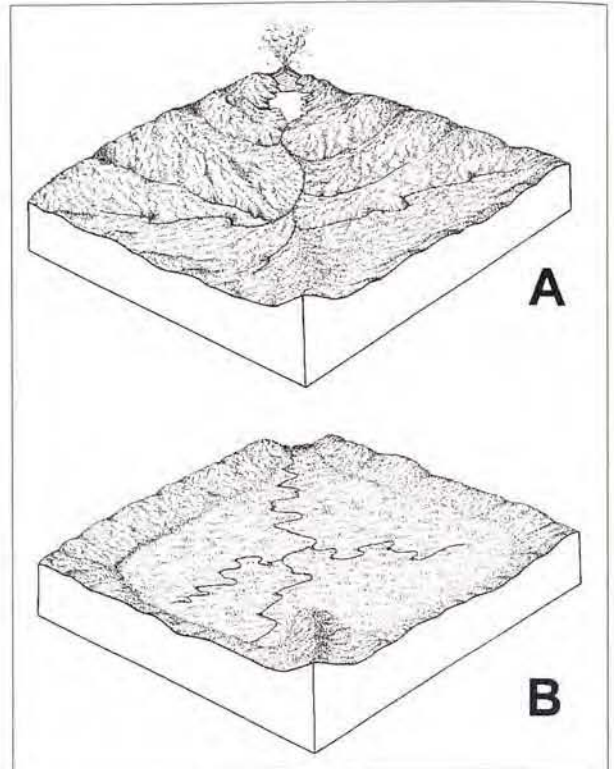

Fig 8. Blok diagrams showing geomorphological evolution of Campo Giavesu area

Fig 8. Diagrames de blocs que mostren l'evolució geomorfològica de l'àrea de Campo Giavesu.

thicker and less pleated with respect to their mainland ancestors. All things considered, on the basis of enamel thickness and lamellar frequency, the *M. lamarmorai* from San Giovanni in Sinis seems to be later than the Early Middle Pleistocene *Mammuthus trogontheri* (Pohlig, 1885). Nevertheless, due to the absence of any other remains, this hypothesis has not yet been fully substantiated.

Campo Giavesu

Geological Setting

The geomorphological evolution of the Campu Giavesu area (Fig. 7) was greatly influenced by the Pleistocenic volcanic activity starting around 0.8 My (K/Ar date by Beccaluva *et al.*, 1981) and ending around 0.1 My (Ar/Ar date, cfr. Sias, 2002). At the beginning of the Middle Pleistocene, basaltic lava flows invaded the inner parts of the south-western basin of the Coghinas River, producing an important alluvial episode due to the obstruction of fluvial patterns. This phase was followed, for a short period, by drainage reorganization. Then, the activity of the Austidu volcano produced complete fossilization of the main river (Rio Mannu di Mores; Sias, 2002). This condition gave rise to a progressive over-alluvial process along the drainage network. In the same way, M.Annaru-M.Poddighe volcanic activity (dated 0.2 My,
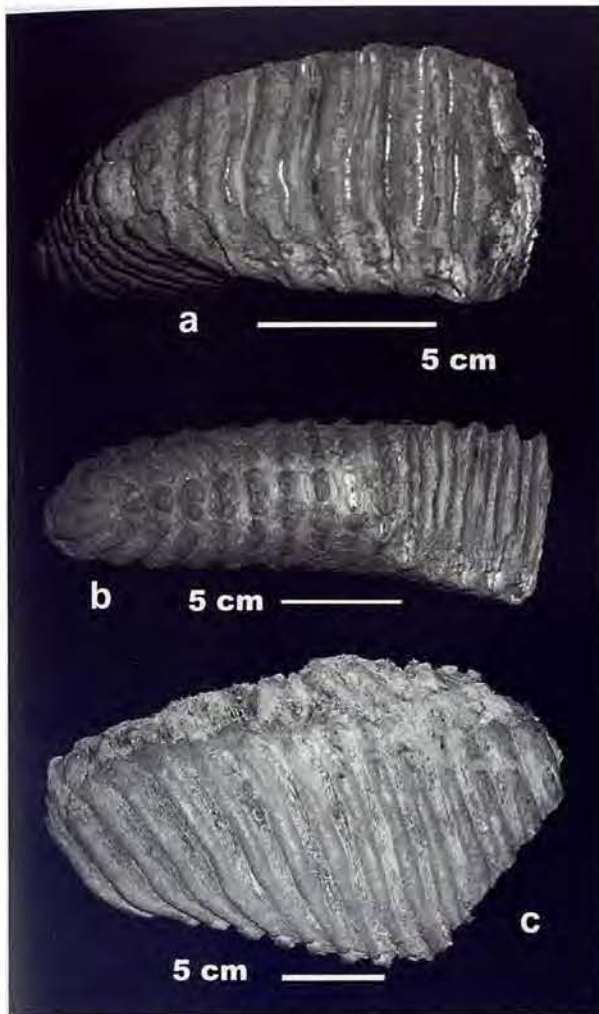
Fig. 9. Campu Giavesu (North-Western Sardinia), late Middle Pleistocene. Last right upper molar in occlusal (a), occlusal/posterior (b) and labial (c).

Fig. 9. Campu Giavesu (Sardenya nord-occidental), Pleistocè Mitjà darrer. Darrer molar superior dret en norma oclusiva (a), oclusiva/posterior (b) i labial (c).

▣ M3 Campo Giavesu	▥ M2 Suessenborn - min
▨ M2 Suessenborn - Mean	▦ M2 Suessenborn - max
▢ M3 Suessenborn - min	▥ M3 Suessenborn - Mean
▢ M3 Suessenborn - max	▢ M2 Voigsted
▢ M3 Voigsted - Mean	▢ M2 Pietrafitta - min
▢ M2 Pietrafitta - Mean	▢ M2 Pietrafitta- max
▢ M3 Pietrafitta - min	▣ M3 Pietrafitta- Mean
▣ M3 Pietrafitta - max	

Fig. 10. Scatter diagram comparing plate number (Pf) of Campu Giavesu molar with the range of variability of M^2 and M^3 belonging to some important European samples of the late Early Pleistocene *Mammuthus meridionalis* and the Middle Pleistocene *Mammuthus trogontherii*.

Fig. 10. Diagrama de dispersió on es compara el nombre de plaques (Pf) del molar de Campu Giavesu amb l'espectre de variació dels M^2 i M^3 d'algunes mostres europees de Mammuthus meridionalis del Pleistocè primerenc darrer i de Mammuthus trogontherii del Pleistocè Mitjà.

K/Ar method, Beccaluva *et al.*, 1981) constrained the geomorphological evolution of the Campu Giavesu Plain: first, lava flows blocked river drainage and later, colluvial sediments filled the valley (Fig. 8). During the Upper Pleistocene, clayey sediments produced by alteration of the piroclastic rocks cropping out around the basin border deposited over the whole valley. The filling-up of the Campu Giavesu Plain was completed in about 0.2 My, giving rise to a complex drainage network (Fig. 8). Elephant remains were buried in sediments deposited in the marshland environment formed after M. Annaru volcanic activity.

Elephant molars (Fig. 9)

The samples recorded from Giavesu consist of a nearly-complete upper molar and a fragment of a very worn one, belonging to two different individuals. The complete specimen is a last upper molar, as indicated by the lack of any evidence of pressure by a posterior tooth and by the typical reduced height of posterior plates. The
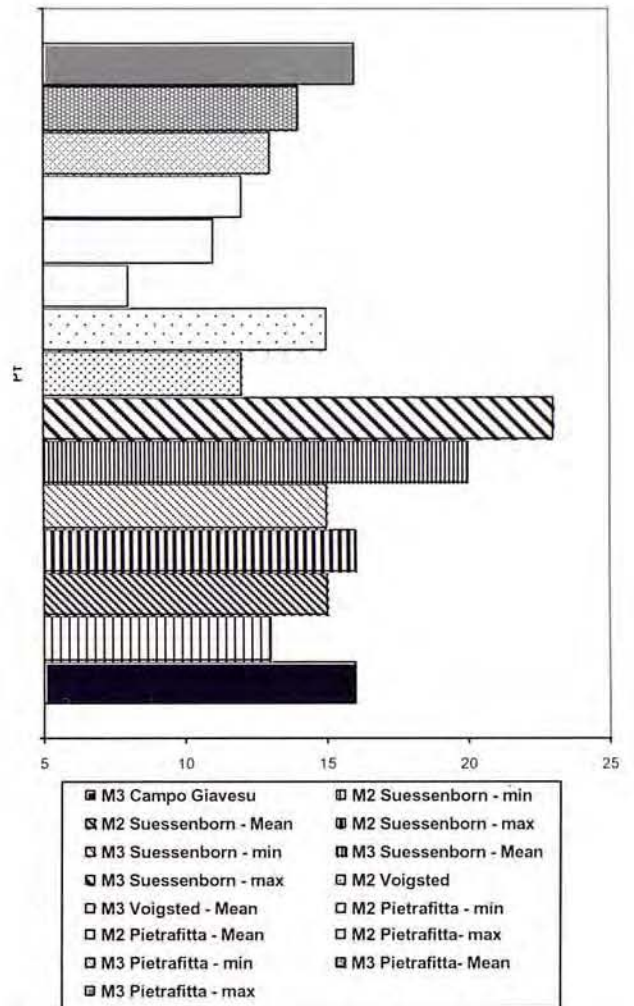
tooth has 15.5 plates (the anterior part of the molar is broken; consequently, only the posterior side of the first plate is present) including talon, the first seven in use. The three anterior plates apparently belong to the same root. The molar shows an elongated shape; its maximum length is 225 mm, the height of the first unworn plate 129 mm. The occlusal surface is ovoid, quite narrow, with a maximum width of 76.5 mm. The length and number of plates fall within the variability range for the "primitive" *Mammuthus trogontherii* M^2 (e.g. the teeth from Süssenborn, Guenther, 1969), whereas average enamel thickness is slightly greater and teeth are less hypsodont. Furthermore, according to Lister & Sher (2001), the laminae of the last upper molar range number from 16 to 22 in *M. trogontherii* and from 20 to 26 in *M. primigenius*.

On the other hand, the last upper molar of *Mammuthus trogontherii* representatives is usually larger, whereas the M^3 belonging to small specimens of
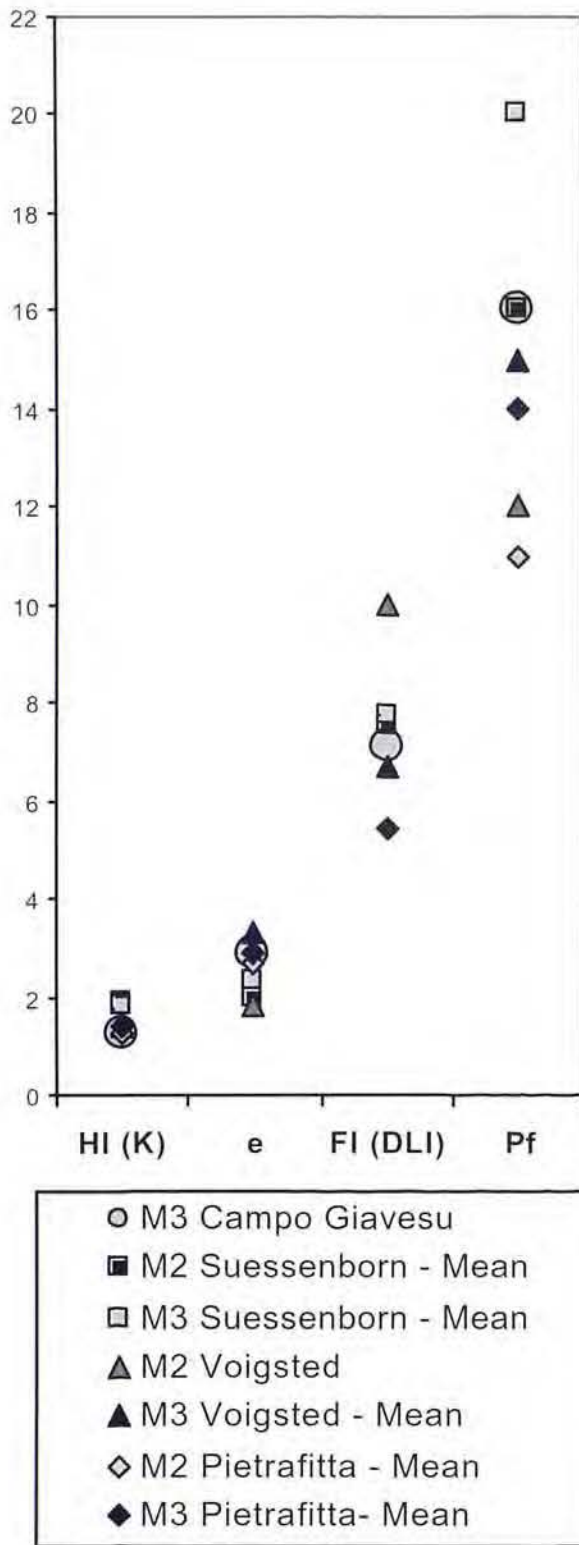
Fig. 11. Values of number of plates (Pf), hypsodonty index (HI), frequency index (DHI) and enamel thickness (e) of Campu Giavesu molar compared with the range of variability of M² and M³ belonging to some important European samples of the late Early Pleistocene *Mammuthus meridionalis* and the Middle Pleistocene *Mammuthus trogontherii*.

Fig. 11. *Valors dels nombres de plaques (Pf), index d'hipsodòncia (HI), index de freqüència (DHI) i gruixa de l'esmalt (e) del molar de Campu Giavesu en comparació amb l'espectre de variació dels M³ i M³ d'algunes mostres europees de* Mammuthus meridionalis *del Pleistocè primerenc darrer i de* Mammuthus trogontherii *del Pleistocè Mitjà.*

Mammuthus primigenius (e.g., some teeth from Predemostí, Musil, 1968) displays more advanced features and more plates. Compared with the above-described molar from San Giovanni in Sinis, the occlusal surface of the tooth from Giave shows almost oval, non-undulated enamel loops, regularly but less densely plicated, and a greater average enamel thickness and lower lamellar index. Nevertheless, it differs from the *Mammuthus meridionalis* of the Italian late Early Pleistocene basically in the larger number of plates and higher frequency index (Figs. 10, 11).

All things considered, according to enamel thickness, hypsodonty index, lamellar frequency and enamel loop morphology, the M³ from Giavesu appears more archaic than the specimen from San Giovanni in Sinis. Moreover, the molar from Giavesu belongs to a *Mammuthus* that is less reduced in size.

DISCUSSION

In the past few decades, several authors have emphasized the role played by different factors in explaining evolutionary patterns in isolated areas, especially changes in body size. For example, as in unbalanced insular faunas large terrestrial predators have not been recorded, the lack of their selection pressure was considered one of the most important factors in explaining insular dwarfing (see e.g. Thaler, 1973; Sondaar, 1977; Lomolino, 1985). Other authors have considered the host-island surface (e.g.Heaney, 1978; Burness et al., 2001), some behavioural features such as territoriality (Case, 1978), feeding specialization (Lawlor, 1982) or trophic requirements, and the metabolic rate (e.g. Damuth, 1993; Demetrius, 2000; Burness et al., 2001, and references therein) to be extremely important. Others have pointed to the impact of genetic segregation and endogamy (Malatesta, 1986) or reduction in the area, population density, overgrazing (Theodorou, 1988) or overcrowding (Roth, 1990). Accordingly, numerous hypotheses have been formulated to explain such body size modification; nevertheless, to date, no model seems to adequately explain the problems related to the origin and evolution of insular species (e.g., Foster, 1964; MacArthur & Wilson, 1967; Diamond & May, 1976; Alcover et al., 1981, and references therein; Azzaroli, 1982; Lomolino, 1985; Malatesta, 1986; Caloi & Palombo, 1989, and references therein; Wilson, 1992; Lister, 1994; Sondaar et al., 1996; Burness et al., 2001; Roth, 2001; Poulakakis et al., 2002). The process is the result of the interaction of several factors, whose dynamics vary from island to island or even on the same island at different times, as demonstrated by modification patterns in the Pleistocene elephant from Mediterranean islands (e.g., Crete, Sicily, Tilos; Palombo, 2004). Indeed, dwarfed elephant populations are especially appropriate subjects for such a study. On every island, each colonisation phase was generally followed by dwarfing processes: the same island and the same ancestor subsequently gave rise to endemic taxa of varying size. Moreover, it is worth noting that most dwarfed taxa (e.g. Sicilian *E. falconeri*) occurred in faunas where

no other large mammals emerged, whereas the largest-sized taxa occurred in more diversified faunas (e.g. Sicilian *E. mnaidriensis* or Crete *E. "creutzburgi"*). Based on these observations, it appears that in an insular environment and in the absence of competition factors, large herbivores reached the minimum body size depending on their baup plane, in accordance with the niche available on the island, changing metabolic rate an trophic requirements. In addition, body size could also have been affected by occasional dispersal from the mainland to a nearby island, possibly by crossing a narrow stretch of water; that event could have led to periodic genetic contact (genetic introgression) and could have stunted the dwarfing process (see Palombo, 2004 and reference therein).

Taking all this into consideration, we could hypothesise that Sardinian elephants had to be quite large, due to the occurrence on the Island of endemic middle–sized cervids. Nonetheless, explaining the apparently different sizes of elephant remains found thus far in Sardinia is not a simple task.

In keeping with the scantiness of elephant remains, are we authorized to suppose that in Sardinia elephant population density was very low and the process of size reduction quite slow?

Supposing a possible difference in age, could we hypothesize that the larger and more archaic molars from Campu Giavesu belong to a direct ancestor of the elephant from San Giovanni in Sinis?

In addition, body size could also be affected by occasional dispersal from the mainland to a nearby island, possibly by crossing a narrow expanse of water. That event could lead to periodic genetic contact (genetic introgression) and could stunt the dwarfing process, or lead to the presence of species as large as the mainland equivalents, even on relatively small islands. Consequently, taking only size into consideration, we cannot exclude that the Campu Giavesu elephant might have reached the island in successive migration waves. Nevertheless, such a hypothesis disagrees with the morphological features shown by the Campu Giavesu and, possibly, by the Late Pleistocene molar from Tramariglio.

CONCLUSION

On the basis of the available evidence, it is likely that at least two endemic elephants of different size occurred in Sardinia. If stratigraphic evidence demonstrates that the Sardinian medium-sized elephant is actually older than the smaller *M. lamarmorai* specimen from San Giovanni in Sinis, the hypothesis that the Campu Giavesu and San Giovanni in Sinis specimens might represent different stages in a progressive size reduction trend can be formulated.

Moreover, the occurrence of elephant remains in Middle Pleistocene deposits allows one to hypothesise that the ancestor of the endemic elephants from Sardinia (an advanced representative of *Mammuthus meridionalis* or an archaic *Mammuthus trogontherii*) reached the island during the Early - Middle Pleistocene transition,

when a noticeable drop in sea level reduced the distance between Sardinia-Corsica and continental coasts. Nevertheless, due to the scarcity of data, this hypothesis still has to be fully substantiated. Moreover, the supposition that mainland elephants reached Sardinia during several migration waves, as already stated for Sicily and Crete, cannot be ruled out.

A systematic review and a substantial increase in stratigraphic and biochronological data are needed to better understand the highly-complex colonisation of the island of Sardinia. Solving standing problems will further contribute to a more complete understanding of the process of elephant dwarfing, testing the hypothetical models proposed to date.

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