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Endemic elephants of the Mediterranean Islands: knowledge, problems and perspectives

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SUMMARY: Fossil remains of endemic elephants have been collected in Pleistocene deposits of several Mediterranean islands. Colonisation phases were generally followed on each island or group of islands by dwarfing processes that apparently allowed the parallel evolution of taxa exhibiting similar size reduction and similar morphological features. In some cases, as in Crete, the faunal biochronological setting allows us to recognise the taxa resulting from each migration phase. In other cases, as in Sicily and Malta, the time of colonisation, the phylogenetic relationships, and the taxonomic status of some specimens are doubtful. This paper summarises present knowledge and highlights the major unresolved problems.

1. Introduction

Elephants were the most characteristic and common taxa in Pleistocene unbalanced endemic island faunas. In the Mediterranean, their remains have been known since the 19th century in the islands of both the western (Sardinia, Sicily, Malta and the Egad Islands) and eastern (Crete, Cyclades, Dodecanese, Cyprus) basins (Caloi *et al.* 1996 and references within). Mediterranean insular elephants have generally been considered as paleoloxodontine, derived from the Middle and Late Pleistocene continental *Elephas (Palaeoloxodon) antiquus* Falconer & Cautley 1847. The only exception is the small Sardinian *Mammuthus lamarmorae* (Major 1883), descendent of an representative of the genus *Mammuthus* (*?M. trogontherii*), while the phylogenetic relationships of *"Elephas" cypriotes* Bate, 1907 and *"Elephas chaniensis"* Symeonidis, 2000 are uncertain.

Dwarfed elephant populations evolved independently on each island. Consequently, the endemic species of elephant, which inhabited the Mediterranean insular area during the Pleistocene, were taxonomically different in each island or group of very close islands (e.g. the Cyclades archipelagos).

Nevertheless, in comparison with their mainland ancestor, endemic elephants were characterised by similar evolutionary patterns that allowed parallel size reduction and, eventually, the appearance of homoplastic characters. Accordingly, the populations of different islands (even when represented by scanty remains) are characterised by common features such as size reduction, relative increase in brain size, scanty or absent cranial bone pneumanisation, decrease in the number of molar laminae and increase in enamel thickness relative to the size of the tooth, reduction of graviportal structure of limbs, and greater morphological variability. The latter may be associated, at least in part, with an increased morphological and dimensional gap between the two sexes.

2. Western Mediterranean

2.1 Sicily and Malta

In the Pleistocene mammal faunas of Malta, dwarf elephants have been known since the second half of the 19th century. In 1862,

Falconer first presented to the British Association at Cambridge the description of the small elephants found in Malta, concluding that there was probably a phylogenetic relationship between the dwarf species and *"Elephas africanus"* Blumenbach, 1797. On this occasion, Falconer also proposed the name *Elephas melitensis* Falconer, 1868 for the new species. Falconer's notes were published in 1868. In 1867 Busk had proposed the new species *Elephas falconeri* for many of the smallest molars selected from the material originally ascribed by Falconer to *Elephas melitensis.*

The endemic elephants of Malta and Sicily were considered for decades as representatives of a progressive size reduction trend, begun by the mainland species *Elephas (Palaeoloxodon) antiquus*. According to this historical hypothesis, the first step of this process was the Sicilian relatively large-sized *Elephas antiquus leonardii* Aguirre, 1969, recorded from Middle Pleistocene deposits at Via Libertà (Palermo) (Aguirre 1969). The second step was represented by the middle-sized Sicilian and Maltese specimens of the group *Elephas mnaidriensis* (Adams 1874); the third by the medium-small-sized *"Elephas melitensis"* (considered by some authors a younger synonym of *Elephas mnaidriensis*); and the last by the smallest species *Elephas falconeri.*

However, stratigraphic (Burgio 1997; Burgio & Cani 1988) and geochemical (Bada *et al.* 1991) data demonstrated that the Sicilian medium-sized elephants of the *Elephas mnaidriensis* group are actually more recent than the smaller *Elephas falconeri*.

Sicilian endemic elephants belong to three distinct faunal complexes: *E. falconeri* FC (?Early Middle Pleistocene) characterized by an unbalanced, low diversity and strongly endemic fauna; *E. mnaidriensis* FC (late Middle- early Late Pleistocene) with a mixed, impoverished fauna including both endemic and continental taxa, and Contrada Pianetti FC (?early last Glacial) (Bonfiglio *et al.* 1997), represented by a local fauna characterised by the only known co-occurrence of *E. mnaidriensis*, *Equus hydruntinus* and other continental taxa, typical of the latest Pleistocene balanced fauna of Sicily.

As already hypothesised by some authors (e.g. Bonfiglio *et al.* 1997; Burgio & Cani 1988; Caloi *et al.* 1996; Palombo 1986), more that one mainland elephant species might have reached Sicily during several migration waves. The first wave could have taken place at the Early Pleistocene/Middle Pleistocene boundary, when the low sea level, related to cold phases (OIS 24-22-?20), reduced the distance between island and mainland coastlines. A second set of migration waves supposedly took place during the low sea level stand correlated with the stadial oscillations of the late Middle Pleistocene (OIS 10, 8 and 6). These phases involved several mammalian taxa, including some with limited swimming ability. Nevertheless various questions are still open.

Some specimens of intermediate size between *Elephas mnaidriensis* and *Elephas falconeri* have been found in Sicily associated with the smallest elephant specimens (Bonfiglio & Insacco 1992 and unpublished data, from Spinagallo cave and south-west Sicily,), as well as in levels underlying those with *Elephas falconeri* (Lupparello: Imbesi 1956). Some others have been recorded from latest Pleistocene deposits at Favignana, a minor island then connected to Sicily (Capasso Barbato *et al.* 1989). On the basis of available data, the hypothesis of two different populations of "intermediate"-sized elephants cannot be ruled out. The earlier one, of Middle Pleistocene age, might have given rise in Sicily to *Elephas falconeri*; the later, endemic one of Favignana, might have originated with the immigration of *Elephas mnaidriensis* to the islet. The taxonomic status of these specimens is still indeterminate.

Large-sized specimens have also been found in conglomerates of the "Messina Formation" (Bonfiglio & Berdar 1979), as well as at Contrada Fusco (Siracusa) (Chilardi, this volume). Moreover, recent discoveries in eastern Sicily suggest the occurrence of three forms of different sizes (Bonfiglio & Burgio 1990). Nevertheless, according to Chilardi's data (Chilardi, this volume) the elephant population of Contrada Fusco might represent a long-term time-averaged assemblage, in which size dif-

ferences could be explained by intraspecific and sex-related patterns. "The presence of some larger elephants in the faunal assemblage possibly points to mixed herds involved in die-off events or even to animals that did not live together but visited the area at different times". This hypothesis has yet to be substantiated.

Consequently the main open questions are: how many elephant taxa inhabited Malta, Sicily and the neighbouring islands? What were the relationships among these island populations? To what extent did the Early Pleistocene fragmentation of Sicily influence elephant evolution? How much did the close proximity of the mainland allow for migrations and genetic flow? Can hypotheses suggesting adaptive radiation be put forward? These problems are also the consequence of a lack of detailed knowledge of stratigraphical/biochronological relationships among some Maltese deposits, and of scarcity of data concerning the morphological and dimensional range of each elephant population. Everything considered, it is impossible to accept *sic et simpliciter* the current specific designations of Sicilian and Maltese elephant taxa.

2.2 Sardinia

Mammuthus lamarmorae (Major 1883) is the only endemic elephant of the Mediterranean islands belonging to the mammoth line. It is represented by some tarsal, carpal and long bones, from last glacial eolian deposits outcropping at Fontana Morimento (Gonnesa) (Acconci 1881). More recently, two molars, whose morphology is more closely related to *Mammuthus* than to *Palaeloxodon*, have been discovered in post-Tyrrhenian breccias at Tramariglio (Alghero) and in Pre-Tyrrhenian levels at S. Giovanni in Sinis (Melis *et al.* 2001). Elephant remains are not recorded, so far, from earlier deposits. Even if other hypotheses cannot be ruled out, we suggest that that the ancestor of *M. lamarmorae* reached Sardinia during the late Middle Pleistocene.

3. Eastern Mediterranean

3.1 Crete

In Crete, endemic elephants were first mentioned by Bate (1905, 1907), who erected the new species *Elephas creticus* Bate, 1907, on the basis of the very small specimens of Maleka Cape. Moreover, Bate (1905) also recorded some remains from Kharoumbes, which were similar in size to the continental species *Elephas antiquus*. A third taxon, intermediate in size, was discovered at Grida Aviaki, and ascribed to *Elephas priscus* by Simonelli (1908). The occurrence of a middle-sized elephant has been confirmed by some remains from Kalo Chorafi, on which Kuss (1965) erected the new species "*Loxodonta" creutzburgi* (recte *Elephas creutzburgi*). Over time, several hypotheses have been put forward on the number and taxonomic status of the endemic elephants of Crete. On the basis of the previously available evidence, two elephantine species occurred on Crete, resulting from two distinct immigration phases and evolutionary processes. The earlier was *E. creticus*, found in association with *Kritimys kiridus* (Bate) and Early Pleistocene or early Middle Pleistocene in age. The later species, of Late Pleistocene age, was *E. creutzburgi*, discovered at Simonelli cave and in many other caves in association with *Mus minotaurus*.

A new species, "*Elephas" chaniensis,* was proposed recently for scanty remains, little reduced in size, found in submerged latest Pleistocene deposits in Kamos cave (Symeonides *et al.* 2001). According to these authors' opinion, continental "elephants were roaming the Chania area during the last climatic minimum, 18,000 yr BP". The phylogenetic relationship of this taxon is doubtful, in view of the lack of paleoloxodontine records in the Latest Pleistocene deposits of Greece.

3.2 Cyclades Islands

Remains of elephants probably belonging to the paleoloxodontine line, have been reported from the islands of Delos, Naxos, Kythnos,

Serifos and Milos. The remains from the three latter islands have not been described. The specimens of different islands exhibit very different sizes: e.g. the Naxos elephant is of similar size to *E. melitensis*, while the Delos molar (Vaufrey 1929) falls within the range of a small *E. antiquus*. This is consistent with the paleogeography of Delos and a neighbouring island, which remained connected to Eubea during most the Pleistocene.

3.3 Dodecanese Islands

Some long bones belonging to an endemic elephant similar in size to *Elephas mnaidriensis* were found in Late Pleistocene cave deposits on Rhodos island (Symeonidis *et al.* 1974), while many more remains, belonging to a more dwarfed species, were discovered in Charcadio cave on Tilos island. The endemic elephants from Tilos have been considered as two different taxa by Bachermayer *et al.* (1976) because of the occurrence of two distinct dimensional groups, falling respectively in the *E. mnaidriensis* and *E. falconeri* size ranges. Following Theodorou (1983, 1988) *"the two groups indicate sexual dimorphism and have no stratigraphic significance*". This author had previously named the taxon "*Palaeoloxodon antiquus falconeri* Busk".

Actually, the Tilos elephant clearly represents an independent endemic species, perhaps belonging to a palaeoloxodontine line, as also indicated by the width of the Schreger angle of enamel microfibres, which excludes any relationship with the genus *Mammuthus*. According to the available stratigraphic data, and taking into consideration the lack of elephants in earlier deposits with deer remains, the continental ancestor possibly reached the island during negative eustatic oscillations at the beginning of the last glacial, and was the latest paleoloxodontine to survive in Europe.

3.4 Cyprus

Some remains of a very small elephant, as small as *E. falconeri*, found at a few sites on Cyprus, have been described as *Elephas cypriotes* Bate, 1903. Moreover, two molars belonging to a larger elephant have been recorded from Achna (Boekschoten & Sondaar 1972). The relationships between the smaller elephant and the Achna specimens cannot be defined due to the lack of any chronological data. From theavailable information, any picture of hypothetical colonisation phases, phylogenetic relationships, and the evolutionary patterns of the endemic Cypriot elephants are still unclear. See Davies & Lister, this volume.

4. Concluding Remarks

With the possible exception of *M. lamarmorae* of Sardinia, all the endemic Mediterranean elephants probably originated from the same continental taxon, i.e. *Elephas (Palaeoloxodon) antiquus*. This species again and again colonised the Aegean and Western Mediterranean islands, giving rise, sometimes on the same island, to several species (or subspecies) of different body sizes.

Consequently, different taxa, all descendants of the same ancestor, inhabited different islands (or the same island at a different time). There is no direct relationship among taxa from widely separated islands. Instead, a parallel evolutionary process allowed similar, more or less advanced, size reduction patterns and morphofunctional adaptive changes. The taxonomic status and the phylogenetic relationships of some endemic elephants (most notably the Sicilian an Maltese ones) are not clear. A systematic revision and a substantial improvement of stratigraphical and biochronological knowledge are necessary to understand the complex picture of the colonisation of Mediterranean islands by elephants.

Solving standing taxonomic problems will allow us to test different models of speciation and size reduction, on the basis of the evaluation of different factors: island size and physiography, climate and microclimate, distance from the coast, length of isolation, number and type of immigrant taxa, pre-existing taxa, extinction rates, and so on.

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