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Elephas? Mammuthus? Loxodonta? The question of the true ancestor of the smallest dwarfed elephant of Sicily

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The smallest dwarfed elephants of Mediterranean islands occurred in Sicily during the Middle Pleistocene. First described by Busk (1867) on remains of Malta, *Elephas falconeri* was considered for more than fifty years as the last step of a progressive size reduction process, which started with *Elephas antiquus* and continued through ?*Elephas (Palaeoloxodon) antiquus leonardii*, *E. mnaidriensis* and ?*Elephas melitensis*. Actually, stratigraphic and geochemical data have demonstrated that the dwarfed forms were older than the medium-sized elephants of the *E. mnaidriensis* group, so the derivation of so-called '*E.*' *falconeri* from *E. antiquus* is not sure. There are no conclusive osteological evidences for this; on the one hand the skull exhibits paedomorphic features and it is strongly modified in comparison with the *Elephas antiquus* skull, on the other hand the very simplified molar morphology does not exclude a phylogenetic relationship with the *Palaeoloxodon* line. However, the tusk morphology seems closer to the *Loxodonta* or *Mammuthus* lines. With respect to the postcranial region, it is difficult to establish how the load and size reduction and how the locomotion has influenced morphological modifications of the limb, in comparison with those of the ancestor. In spite of this, our preliminary investigations of *E. falconeri* from Spinagallo cave (Southeastern Sicily) have shown that the peculiar morphological features of the skull are basically due to the extensive development of the brain and the brain case, that maintains the respiratory axis turned forward and downward. Conversely the typical features of the fan link *E. falconeri* more to *E. antiquus* than any other Pleistocene elephant species. The Schreger angle pattern of the tusk seems to confirm this hypothesis. The analysis of carpal and metacarpal bones is still in progress and, even if we need more data to definitively solve the problem of origin of the smallest elephants of Sicily, a derivation from *E. antiquus* seems the most appropriate.

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INTRODUCTION

Endemic elephants were the most common settlers on the western (Sardinia, Sicily, Malta and the Egad Islands) and eastern (Crete, Cyclades, Dodecanese, Cyprus) Mediterranean islands (Theodorou 1986, 1988; Burgio & Cani 1988; Caloi *et al*. 1988, 1996; Caloi & Palombo 1992; Capasso Barbato *et al*. 1989 with references included in those papers). The insular elephants are generally considered as *paleoloxodontine*, originated by the Middle and Late Pleistocene *Elephas* (*Palaeoloxodon*) *antiquus* FALCONER & CAUTLEY, 1847[1]. The only exception should be the small Sardinian mammoth *Mammuthus lamarmorae* (MAJOR 1883), descendent of an averagely evolved mammoth species of Late Villafranchian or Early Galerian age: *Mammuthus* (*Archidiskodon*) *meridionalis* (NESTI 1825) or *Mammuthus* (*Mammuthus*) *trogontherii* (POHLIG 1887).

Dwarfed elephant populations evolved independently on each island or group of islands. Consequently, the Pleistocene Mediterranean endemic island species of elephant are taxonomically different. Moreover, endemic elephants were characterised, in comparison with their mainland ancestor, by similar patterns of morphological and size modifications (Caloi & Palombo 1990, 1994; Palombo 1996).

The populations of the different islands (even when represented by a few remains only) are polymorphs, but the different forms all present more or less significant decreases in size, ranging from the minimal decrease in the case of *Elephas antiquus leonardi* AGUIRRE, 1969 of Sicily, to that of the smallest elephants of Malta and Sicily that measured not over 90 cm at the withers. The most common features of endemic elephants were a decrease in the number of molar laminae (with a parallel increase of enamel thickness) and decrease in graviportal morphofunctional characters of the bones of the limbs, which became more marked as size decreased. The greater morphological variability within the each insular population seems to be associated, at least in part, to an increase of sexual dimorphism.

Pleistocene dwarf elephants from Malta are known since the first half of the 19th century. In 1862 Falconer presented the description of the small elephants found in Malta for the first time to the British Association at Cambridge, concluding that there was probably a phylogenetic relationship between the dwarf species and '*Elephas africanus*' BLUMENBACH, 1797. Falconer proposed the name *Elephas melitensis* for the new species, his notes were published in 1868. In ?1867 Busk noticed a lot of smaller molars, considered of similar morphology as the Asian elephant in the material originally ascribed by Falconer to *Elephas melitensis*; for these specimens Busk proposed the new species *Elephas falconeri* BUSK, 1867(?).

The smallest elephants of Malta and Sicily have for decades been considered as the last step in a progressive size reduction trend, which started with the mainland species *Elephas* (*Palaeoloxodon*) *antiquus*. The first step of this process is represented by *Elephas antiquus leonardii*, little reduced in size, known only from Sicily; the second step by the Sicilian and Maltese specimens of the group of *Elephas mnaidriensis* ADAMS 1874,

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[1] According to Maglio (1973), several Authors consider *Elephas antiquus* as younger synonymous of *Elephas namadicus* FALCONER & CAUTLEY, 1846, the only straight-tusked elephant species present in the Pleistocene of Eurasia. Nevertheless, there are some reasons for treating the straight-tusked elephant of Europe as species distinct from its Asian relative: the source of type specimens, the different routes of diffusion followed by the ancestral population, the different distribution of the two groups of populations (which might make difficult the genetic flow between the two groups), finally some biometrics and morphological features of molars and skulls. Until additional evidence becomes available, it is preferable to retain both species as valid.

reaching a shoulder height of about 190 cm; the third step might be represented by '*Elephas melitensis*', reaching a shoulder height of about 140 cm, and considered by some authors as a younger synonym of *Elephas mnaidriensis* (cf. Ambrosetti 1968). Actually some specimens showing a size intermediate between *Elephas mnaidriensis*, and the so-called '*Elephas falconeri*', have been found also in Sicily, associated with the smallest elephant specimens (Spinagallo cave: Ambrosetti 1968 and unpublished data), or in a level underlying those with '*Elephas falconeri*' (Lupparello: Imbesi 1956). The taxonomic status of these specimens still remains indeterminate.

More recent stratigraphic (Esu *et al*. 1986; Burgio & Cani 1988; Burgio 1997) and geochemical data (Belluomini 1985; Bada *et al*. 1991) have allowed us to revise this point of view: the Sicilian medium sized elephants referred to *Elephas mnaidriensis* group are actually younger than the smallest elephants referred to '*Elephas*' *falconeri*. Consequently, the derivation of so-called '*E.*' *falconeri* from E. *antiquus* is not sure and apparently there is no conclusive osteology evidence for this. As already hypothesised by some authors (e.g., Palombo 1986a; Burgio & Cani 1988; Caloi *et al.* 1996, Bonfiglio *et al.* 1997) more than one mainland elephant species might have reached Sicily during more than one migration wave.

The first migration wave probably took place around the Early Pleistocene/Middle Pleistocene boundary, when the low sea level, connected to the 'Great Glacial' phases (24-22-?20 oxygen isotopic stage, Shackleton 1996), reduced the distance between island and mainland coastlines. A second set of migration waves took place during the low sea level correlated with the stadial oscillations of late Middle Pleistocene (10-8-6 o.i.s.). These phases involved several species, also those exhibiting a reduced swimming ability. Consequently, two faunal complexes of Middle and early Late Pleistocene, including dwarfed elephants, have been recognised in Sicily. The first is the '*Elephas falconeri* faunal complex' (? Early - Middle Pleistocene; Middle - Late Galerian, sensu Gliozzi *et al.* 1997). The faunal association of this complex is oligotypic and exhibits a strongly endemic character; it is characterised by the

Figure 1 *Elephas falconeri* Busk, 1867, Spinagallo cave. *E. falconeri* faunal complex, early Middle Pleistocene, Late Galerian Mammal Age: adult male (no. 7) in frontal (**A**) and ventral (**B**) views.

Figure 2 *Elephas falconeri* BUSK, 1867, Spinagallo cave. *E. falconeri* faunal complex, early Middle Pleistocene late Galerian Mammal Age: adult female (no. 4) in lateral (**A**), dorsal (**B**), ventral (**C**) and frontal (**D**) views.

dwarf endemic elephants, endemic reptiles, amphibians, birds and micromammals; the occurrence of an endemic fox is doubtful. The second faunal assemblage is the '*Elephas mnaidriensis* faunal complex' (late Middle Pleistocene, early Late Pleistocene; early, and early Late Aurelian). This faunal association is more balanced, the remains of some endemic species (generally less modified in comparison with those of the previous complex) were found alongside those of other species (including carnivores of middle and large size) which are almost identical to the normal sized mainland animals (Caloi *et al*. 1988, Bonfiglio *et al*. 1997). A frequent element in this faunal assemblage is the medium sized elephant *Elephas mnaidriensis*. According to some recent data, *Elephas mnaidriensis* also occurs in late Pleistocene mammal assemblages, together with *Equus hydruntinus*

(Bonfiglio *et al.* 2000)

It appears certain that the *E. antiquus* was the ancestor of the elephants of the group of *E. mnaidriensis*, as several morphological and biometrics characters prove. On the contrary, the phylogenetic relationships of the smallest Sicilian elephants still remain doubtful. The difficulty to recognise its ancestral mainland species is mainly due to the extreme modification of the skull, which exhibits a very peculiar morphology: the simple low-domed skull of adult *E. falconeri* specimens retains features that are typical of juveniles specimens of mainland elephants, yet the tusks are proportionally large as in adult continental species (Roth 1992; Caloi & Palombo 1994; Lister 1996; Sondaar 1997). It is also difficult to settle how the size, the load reduction or the different types of locomotion influenced the morphofunctional modifications of the limbs (Caloi & Palombo 1994; Palombo 1996). Several studies are still in progress; the aim of this paper is to point out characters that may link the smallest elephant of Sicily to one or another among the Pleistocene species of continental elephants.

MATERIAL AND METHODS

The most important specimens (skulls, mandibles, long bones of several individuals) of so-called '*E.*' *falconeri* are in Sicily: Lupparello (Vaufrey 1929; Imbesi 1956), Spinagallo (Ambrosetti 1968), and Alcamo (Burgio & Cani 1988) are among the richest and/or most interesting deposits. In Malta, the smallest elephant is mainly represent by isolate remains (teeth, vertebrae, limb bones) collected mostly from the Zebbug, Mnaidra and Benghisa sites (Vaufrey 1929). The richest Sicilian sample comes from the Spinagallo cave where an oligotypic and strongly endemic mammal fauna was recovered in the period between 1958 and 1960 (Accordi 1962). The remains from the Spinagallo deposits have been described in several papers and include amphibians (*Discoglossus* cf. *D. pictus* Otth, 1837; *Bufo* cf. *B. viridis* Laurenti, 1768; *Hyla* sp.), reptiles (*Testudo hermanni* Gmelin, 1789; *Lacerta viridis* (Laurenti, 1768); *Lacerta* sp., probably endemic, cf. *Lacerta siculomelitensis* Boehme & Zammit-Maempel, 1982; *Coluber* cf. *C. viridiflavus* Lacépède, 1789; *Natrix* sp.), several bird species (including giant endemic owls Strigiformes) and of bats,

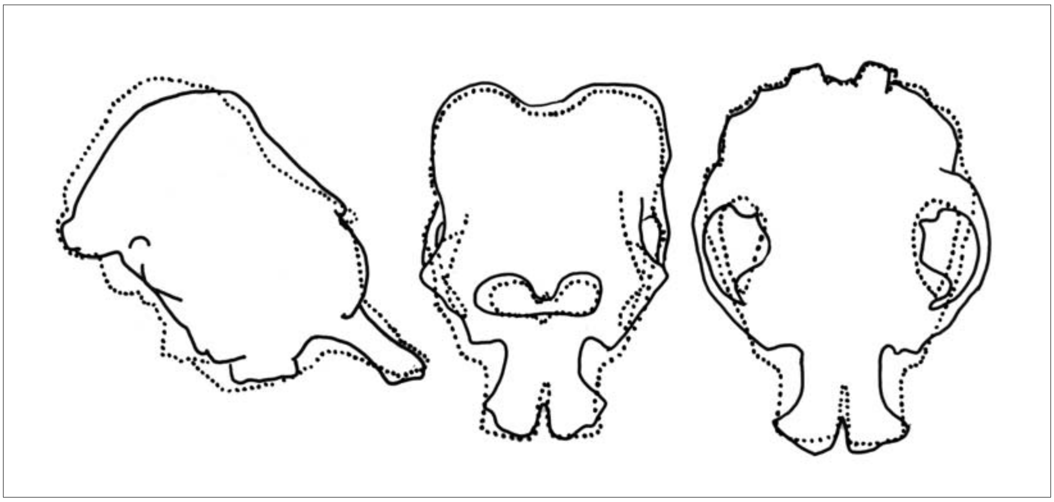

Figure 3 Profile of the adult female skull no. 4 of *Elephas falconeri* Busk, 1867 from Spinagallo cave (full line) compared with a juvenile specimen of *Elephas maximus* Linnaeus, 1758 (dotted line) in lateral (**A**), dorsal (**B**) and ventral (**C**) views. Not to scale.

terrestrial micromammals (the endemic dormice *Leithia melitensis* [ADAMS, 1874] and *Leithia cartei* [ADAMS, 1874], and a soricid *Crocidura esui* KOTSAKIS, 1984), ?*Vulpes* sp., and *Elephas falconeri* as the only large mammal.

Over 3000 elephant remains (21 skulls, 13 mandibles, 87 tusks, 335 molars, 724 vertebrae, several hundred of ribs, 804 bones of the forelimb, 831 bones of the hind limb) are found in the very rich sample of Spinagallo cave (Ambrosetti 1968); at least 104 individuals are represented. Six skeletons, both masculine and feminine, of adult, very young and young individuals have been reconstructed based on a statistical study made by Ambrosetti (1968). Four skeletons, a male, a female and two young individuals are kept at the Paleontological Museum of Department of Earth Sciences of University of Rome 'La Sapienza'. At present, our studies focus on finding distinctive characters that could link the elephants from Spinagallo cave to one or another elephantine taxon that inhabited the Mediterranean area during the Pleistocene. This preliminary report regards only the skull, tusks, and pelvis because of the slightly contradictory or doubtful indications given by the morphology of these elements.

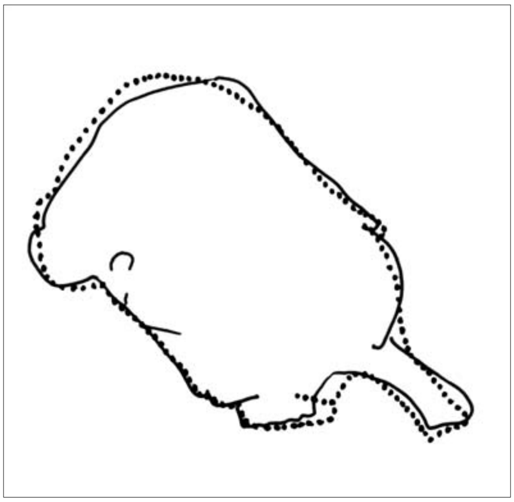

Figure 4 Profile of the adult female skull no. 4 of *Elephas falconeri* BUSK, 1867 from Spinagallo cave (full line) compared with a juvenile specimen of *Elephas maximus* LINNAEUS, 1758 from Sumatra (after Osborn 1942, modified) (dotted line) in lateral view. Not to scale.

One of the most showy character in the skull from Spinagallo (specimens no. 4 [the most complete], no. 7 [an adult female]; nos. 5, 6 and 7 [adult males]; and nos.1 and 9 [young males] is that of the different proportions between the splachnocranium (portion of the cranium derived from the primitive skeleton of the gill apparatus) and neurocranium (portion of cranium forming the braincase). The skull retains a globose shape - typical of juvenile individuals - also in adult specimens; this paedomorphic (*cf.* Gould 1977) feature is also supported by a reduction of the pneumatisation of the parieto-frontal bones. On this account, for the first time, the skull was compared with very young specimens of *Elephas maximus* LINNAEUS, 1758, of *Loxodonta africana* (BLUMENBACH, 1797), and of *Mammuthus* BURNET, 1830 (unfortunately a skull of very young *Elephas antiquus* are unknown), then with the skull of the adults. The angles of 'Schreger lines' (Espinoza & Mann 1993) in the tusks were also examined. As is known, an elephantine tusk exhibits a pattern of two sets of lines in transverse cross-section, one set curves clockwise and the other counterclockwise. The width of the angles, formed by the crossing of the two groups of lines, progressively increases from the centre to the peripheral area of the section. For this reason, the comparison of the Schreger lines of '*Elephas falconeri*', *Elephas antiquus*, *Loxodonta africana*, *Mammuthus meridionalis* and *Mammuthus primigenius* (BLUMENBACH, 1799) was made taking into account the width of all the inside angles (slightly concave and open to the medial area of the tusk) and outside angles (somewhat convex and open to the lateral area of the tusk) measured along a line drawn from the centre near the pulpal cavity, to the peripheral border of the tusk. The surface of the pulpal cavity of the tusk was also examined through a scanning electronic microscope in order to notice the density of dentinal tubules. The surface, recovered by a gold film, has been examined at a 1000x magnification.

Regarding to the post-cranial skeleton features, for the moment, only the morphology of pelvic bones was considered. In fact, under the same conditions of ontogenetic growth and gender, the morphology of iliac wing exhibits some distinctive features which on the one hand approach *Loxodonta* to *Mammuthus*, on the other hand distinguish both these forms from those of the genus *Elephas*. The shape of the iliac wing, especially the anterior border, seems to be not much affected by the locomotion. The morphology of long bones, on the contrary, is more strongly affected by the distribution of the body load and by the type of locomotion. A postcranial feature that has been given some importance in the taxonomy of elephants is the alignment of the carpal bones and the degree of overlap between the lunar and trapezoid (serial and aserial structure) (Trevisan 1949; Garutt 1954; Maccagno 1962, among others). In addition, some biometrics and morphological characters of each carpal bone have been indicated as being distinctive of genera. However, the structure of the carpus, the morphology and the propor-

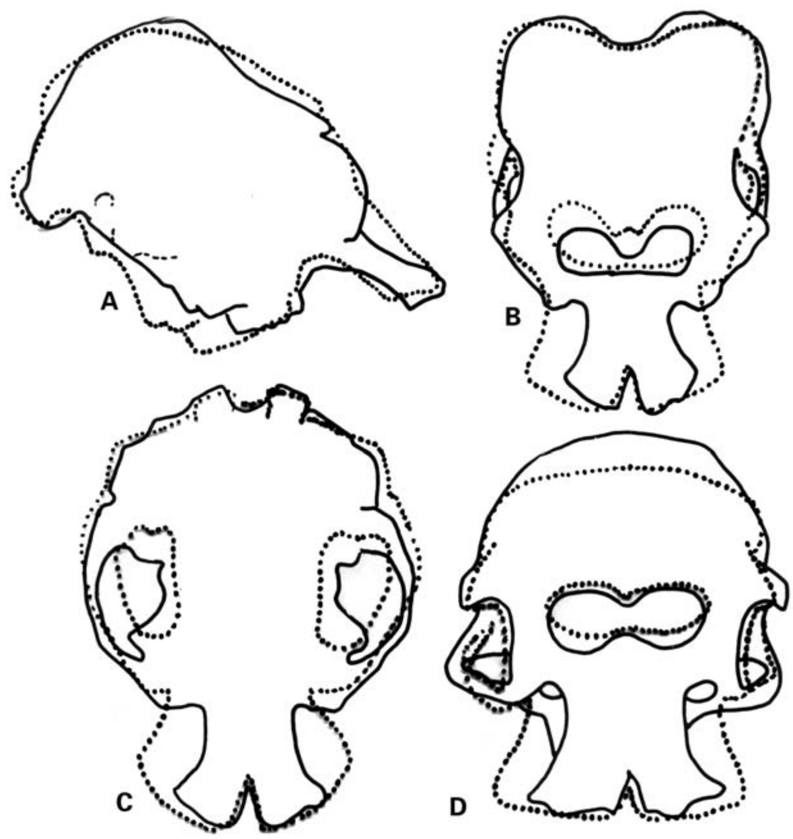

Figure 5 Profile of the adult female skull no. 4 of *Elephas falconeri* Busk, 1867 from Spinagallo cave (full line) compared with an adult-juvenile specimen of *Loxodonta africana* (Blumenbach, 1797) (dotted line) in lateral (**A**), dorsal (**B**), ventral (**C**) and frontal (**D**) view. Not to scale.

tions of each carpal bone are closely related to the distribution of the body load and to the type of locomotion. The examination of carpal bones of the Spinagallo elephants is still in progress; at present it seems to be very difficult to recognise diagnostic features that are not depending on morphofunctional, sexual or individual variations.

RESULTS AND DISCUSSION

The abundant elephantine material from Spinagallo cave was accurately studied by Ambrosetti (1968), basically in order to determine the most distinctive characters of the smallest elephant, taking into account modifications linked to ontogenetic development, sexual dimorphic characters, and in order clarify the evolution of dwarfism and to revise the taxonomic rank of the dwarf forms and their phylogenetic relationships. Ambrosetti (1968) considered *Elephas mnaidriensis* a director ancestor of ‘*Elephas*’ *falconeri* and, as a consequence, he postulated that both species derived from an archaic form of *Elephas antiquus* (or *Elephas namadicus* FALCONER & CAUTLEY, 1846). Hence, comparison was made prevalently with this latter species, more so in order to establish distinctive characters of the elephants from Spinagallo cave than to analyse their relationships with the continental elephants of the Mediterranean area. Only for skulls and the ulna some similarities with *Loxodonta africana* were pointed out.

Skull

One of the showiest characters of Spinagallo skull is that of the different proportions between the neurocranium and splachnocranium. The proportional increase in size of the cerebral mass observed in the elephants of Spinagallo (Accordi & Palombo 1971) may be due to neotenal factors which allow the adult to maintain a sufficiently globose cranium with very reduced pneumatisation. On the other hand, a reduction of the pneumatic bone tissue seems to be characteristic of dwarfed Proboscidea: for example, in ‘*Elephas*’ *celebensis* (Hooijer 1949) and *Mammuthus exilis* (Stock & Furlog 1928), the absence of parietal swelling could be due to this reduction (Roth 1993;Van den Berg *et al.* 1996). The skull from Spinagallo (Figs. 1, 2) is characterised by a relatively globose shape with flattened apex; the forehead is wide, convex both in vertical and in transverse profile in the juvenile individuals, almost plane in the adults; the frontal-parietal region is long and very slightly concave; external nasal choanae are in low position both in juvenile and in

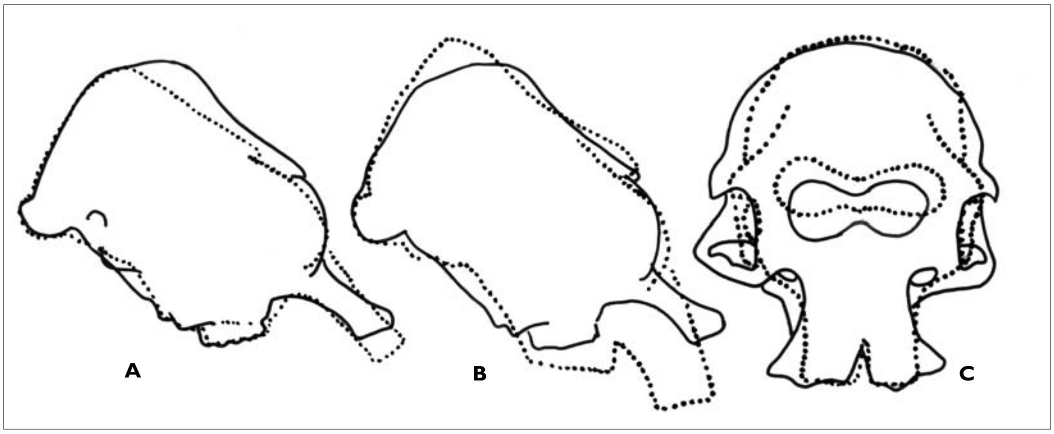

Figure 6 Profile of the adult female skull no. 4 of *Elephas falconeri* BUSK, 1867 from Spinagallo cave (full line) compared with a very juvenile (**A**) and a juvenile (**B**,**C**) specimen of *Mammuthus columbi* (FALCONER, 1868) (dotted line) in lateral (**A**,**B**) and frontal (**C**) view. Not to scale.

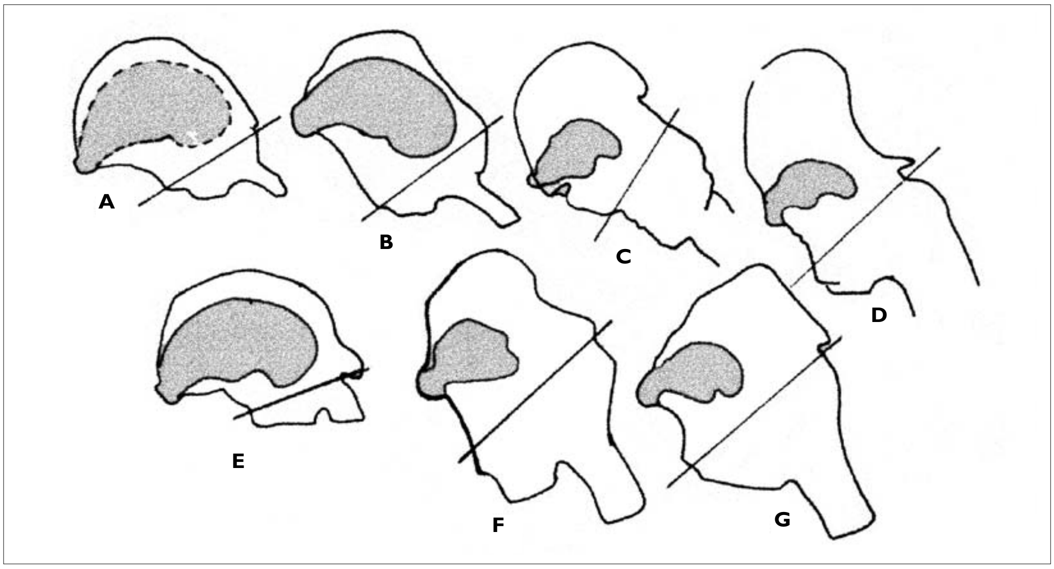

Figure 7 Cerebral cavity and respiratory axis in *Elephas falconeri* BUSK, 1867 from Spinagallo cave (**A** = juvenile no. 2, **B** = adult female no. 4), *Elephas antiquus* FALCONER & CAUTLEY, 1847 (**C**), *Mammuthus meridionalis* (NESTI, 1825) (**D**), *Loxodonta africana* (Blumenbach, 1797) (**E** = foetal individual, **F** = adult) and *Elephas maximus* LINNAEUS, 1758 (**G**). Not to scale.

adult individuals; orbital cavities take up a very advanced position, they are very large especially in the young specimens; the orbital plane is turned towards the outside and it forms an angle of about 80° with the sagittal plane; the occipital surface is convex, tilted forward and forming an obtuse angle with the frontal surface; intermaxillary bones are moderately enlarged in the male with convex distal edge, reduced in the female with shallow median fossa; the plane of the tusk alveoli is not much tilted upward towards, but far below, the fronto-parietal plane; besides the premaxillary bones, in the region which delimits the external choanae, form a noticeable angle with the part representing the tusk alveoli; the zygomatic arches are very arched; the maxillary process take up a high position. In spite of its globose shape, the vertical axis drawn from the skull vertex, in the juvenile specimens falls between the posterior border of the molar alveolus and the external auditive meatus, whereas in the adult specimens the vertical axis falls in the middle of the molar alveolus.

The vertex of skull dome (Figs. 3a, 5a, 6a,b) is in a more posterior position in the adult specimens of *Elephas*, *Loxodonta* and *Mammuthus*, whereas it is in a similar position in the sub-adult skull of *Loxodonta*. The Spinagallo skulls differ from those of *Loxodonta* in the shape of the parieto-frontal region, which is moderately convex in the young, but slightly concave in the adult. This morphology is more accentuated in juvenile *Mammuthus*, whereas in the young of *E. maximus* the upper region of the parietal bones is convex. The external choanae (Figs. 3b, 5b, 6c) are proportionally very large and in a very advanced position relative to the alveolar distal border also in comparison with very young specimens of *Elephas maximus* and *Mammuthus*. The Spinagallo elephant share the advanced position of the orbits with young individuals of *Mammuthus* and *Elephas*. However, the smallest Sicilian elephant clearly differs from the other species for the major angle that the orbital plane forms with the sagittal plane. The angle varies from 30-32 degrees in the adult male (skulls no. 7 and no. 9, respectively) to 39 degrees in adult female (skull no. 4), to 40 degrees in the

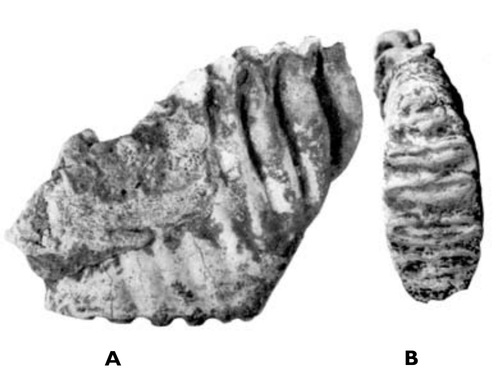

Figure 8 *Elephas falconeri* BUSK, 1867, Spinagallo cave. *E. falconeri* faunal complex, Early Middle Pleistocene, Late Galerian Mammal Age. Right M3 in buccal (**A**) and occlusal (**B**) views.

young (skull no. 1). In the extant elephants, the dihedral angle between orbital and sagittal planes is about 24 degrees on the average, whereas in *E. namadicus* the orbits are in a more lateral position and the value of angle generally does not reach 20 degrees. The Spinagallo skull also shows some morphological features similar to that of the young-adult specimens of *L. africana* (Fig. 5) for the very low positions of the orbits and of the external choanae that seems to maintain a proportionally constant position during the ontogenetic development; in addition the forehead is relatively large. This last character is present also in the young *E. maximus* (Fig. 3), whereas in the adult the width of the forehead in very reduced; in the young specimens of *Mammuthus* genus, the forehead is not so wide (Fig. 6c). In the elephant from Spinagallo cave as in *L. africana* the zygomatic arches are very arched and so the skulls exhibit a roundish shape in ventral view (Fig. 5c).

A characteristic feature of the Spinagallo skulls is the position of the plane of the tusk alveoli which, as in the young *E. maximus*, is under the forehead plane. It is slightly turned upward and forward, whereas in *E. maximus* the alveolar plane is almost parallel to the fronto-parietal plane, or turned a little downward. In *Loxodonta africana*, the alveolar plane falls almost in the same plane of the forehead. In the mammuthine lineage the position of the alveoli to the fronto-parietal plane varies; in the more evolved species as in *Mammuthus primigenius* and *Mammuthus columbi* (Falconer 1857-1868) the plane of the alveoli is turned downward and makes an obtuse angle with the forehead plane near the external choanae, whereas in *Mammuthus trogontherii* (POHLIG 1887) the two planes are almost coincident.

It is suitable to observe that in the partially reconstructed skull of adult *E. antiquus* specimens from Stoccarda (Osborn 1942), differently from how verifiable in others skull of the same species, the plane of the fan is under the plane of the forehead and the orbits are relatively low. The skull from Stoccarda is distinguished from other species in the *Elephas antiquus* - *Elephas namadicus* group (for example see the Italian specimens form La Polledrara di Cecanibbio, Palombo *et al.*, this volume) by the lack of frontal torus: the forehead is antero-posteriorly elongated and the apex of the skull is situated in a more posterior position.

On the other hand, the shape of the fan links *E. falconeri* more to *E. antiquus* than to any other species. The tusk alveoli of Spinagallo specimens, observed in frontal and ventral view (Figs. 1 and 2), are characterised by their scanty proximal-distal elongation in comparison with the to dimensions of the skull. Proportionally short alveoli are present in the juvenile skull of various elephantine species, in fact this character is related to small dimensions of the tusks. In the female specimens from Spinagallo (skull no. 4, Fig. 2) the lateral borders of the alveoli are almost parallel to the sagittal plane for about 2/3 of their length, whereas the alveoli become larger distally. The antero-lateral edge of the fan falls inward to the plane of the orbits. Moreover, the alveoli are closed in the female skull, signifying that during the life this skull was without tusks (in the extant female of *Elephas maximus* the tusks can also be lacking). In the male skulls (Fig. 1) the fan is larger and broader. Even if it was proportionally smaller and less transversally expanded, it was enlarged since from the proximal portion and the distal lateral edge extends almost as far as the lateral extremity of the maxillary bone, where it joints with the malar bone.

In *E. falconeri* as in *E. antiquus*, the tusk alveoli generally exhibit an oval distal section, they are separated by a wide subtriangular area, which has a reduced dorsal-ventral thickness. The very triangular laterally expanded shape of the fan is a distinctive morphological feature of the elephants of the *Elephas antiquus* - *Elephas namadicus* group. In the male skull from Spinagallo, the shape and the extension of the fan differs from those of other Pleistocene elephants; it does not amount to the typical width of *Elephas antiquus*. In the specimens of the subgenus *Elephas*, the lateral borders of the alveoli are not much divergent, even less so than in *Loxodonta* that exhibits a wider fan, almost quadrangular in shape. In *Mammuthus*, the alveoli have a subcircular section, they are scarcely separated and they have an arched or slightly divergent trend.

To explain the peculiar characters of the skulls of the Spinagallo elephants, the more important and determinant element is in the way of allometric growth of the neurocranium as to splanchnocranium; these ways are different from those of continental elephant species. In the latter, the hypsicephalic degree increases even if in different way according to phyletic lines and different species during ontogeny. The frontal and parietal bones greatly increase in thickness, the forehead changes its curvature, proportionally the brain case volume reduces considerably, allowing the rotation of the respiratory axis upward and backward; condyles and auditive meatus move to a higher position because of the greater posterior growing of maxillary bones; also the extension of premaxillary bones increases with development of the splanchnocranium. As to juvenile skull, even if in a different way in each species, the external choanae move to a more backward position in adult skulls, the post-orbital region of the forehead becomes proportionally less wide, the maxillary region extends, the angle between forehead and molar alveoli plane changes more or less notably.

The adult skull of the Spinagallo specimens maintains a very large cerebral mass and the noticeable proportional decrease of the brain volume with the growth is absent. On the other hand, the decrease is very important in other elephants. The encephalisation observed in the elephants of Spinagallo is due primarily to the functional impossibility of going below certain limits maintaining the basic encephalic structure when the size of the skull is strongly reduced; secondly to the loss of pneumatisation since the reduction of the bone thickness and of the load of the skull and the tusks. As a consequence the entire architecture of the adult skull is modified and exhibits paedomorphic features which allow the adult to maintain a sufficiently globose cranium like those of juvenile elephant specimens.

Consequently and in spite of some differen-

Figure 9 *Elephas falconeri* Busk, 1867, Spinagallo cave. *E. falconeri* faunal complex, early Middle Pleistocene, Late Galerian Mammal Age. Cross section of the tusks showing the Schreger Pattern lines. .

ces, the Spinagallo skulls are appear more closely related to the juvenile specimens of *Elephas*, *Loxodonta* and *Mammuthus* than to the adults. The main affinities are with *E. maximus*. Note the almost identical lateral profile of the skulls of *E. maximus* from Sumatra (Osborn 1942, see figure 4) and of the adult female from Spinagallo cave, that confirms the paedomorphic characters of the *E. falconeri* skull. Actually, the size increase of the skull of elephants from Spinagallo cave seems to be allometric and it concerns the posterior region of the maxillary bones (which increase in height as to the edge of tooth alveoli) more than the neurocranium. Consequently, the inclination of the respiratory axis does not vary much in the *E. falconeri* skull: the angle formed with the molar plane increase with the growth from 23 degrees in the very young specimens, to 40 degrees in the adult male. The forward extension of the brain case prevents the upward and backward rotation of the respiratory axis (Fig. 7). Thus the external nasal choanae and the orbits maintain a very low position, the forehead is very broad and extended longitudinally. The advanced position of the brain case prevents the depth of the temporal fossa and the reduction of transverse width of the forehead.

In addition, we can observe that the position of the encephalon of *E. falconeri* is more similar to that of *L. africana* than to the other species: the axis of the brain case is almost horizontal and it is directed forward, it is not turned upward. Consequently also in *Loxodonta* the external choanae maintain a sufficiently low position and the forehead is broad.

Molars and tusks

The existence of two morphotypes of molars has been recognised by various authors (Adams 1873; Osborn 1942; Vaufrey 1929; Ambrosetti 1968; Aguirre 1969) that hypothesised about the existence of two different taxa that were analogous in size, or, more correctly, they have attributed the two types (pachyganale or thick-plated and endoganale or thin-plated) to male and female individuals, respectively. Actually, in the Spinagallo sample, several molars exhibit morphological and biometrical features intermediate between those of typical male and female individuals.

Taking into account their very small dimensions, the Spinagallo molars are characterised by a very low number of laminae (average laminar frequency in 5 cm 5/6 in M3), thick enamel (average thickness ranging from 0.5/1 in Pd2 to 2/2,5 in m3 and 1,5/2 in M3). It is not much plicate, small and not much stressed (Fig. 8). Some upper molars are rather broad, closer in the proportions to those the *Mammuthus* line than to those of the *Elephas antiquus*-*Elephas namadicus* group; whereas the lower molars are prevalently narrow and long. Both in the upper and in the lower molars there is a precocious fusion of central pillars (secondary conelets), as it is usually

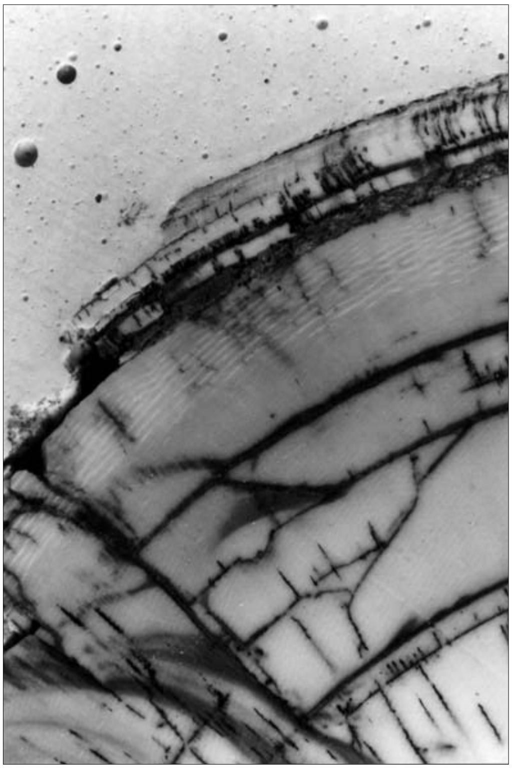

Figure 10 *Loxodonta africana* (BLUMENBACH, 1797). Cross section of the tusks showing the Schreger Pattern lines.

verified in the species of the subgenus *Palaeoloxodon* MATSUMOTO, 1924. The low laminar frequency, taking into account the small dimensions of the molars, the presence of broad and very spaced laminae with more or less oval shape may tend to exclude a relationship to the genus *Mammuthus*, at least to the averagely or more evolved species. On the other hand, the presence of a loxodontine type expansion in the worn plate of some pachyganale molars (that mostly due to the enlargement of the posterior pillar, maybe a homologous remnant of the central conule of gomphotheres) is not sufficient to hypothesise any relationship with *Loxodonta*. The morphometric variations of the molars are partially allometric and partially due to the fact that the molars had to maintain their chewing function even though they were smaller (on the other hand, when the size of the animal is reduced also the food requirement decreases). They were obliged to grind highly abrasive food, due to the more xerofilous vegetation of the Mediterranean island environment. Two different morphotypes of tusks are recorded in the Spinagallo sample: the first, very poorly represented, is thin and characterised by a slight curvature, and by small dimensions. The second type is larger, quite robust and more curved. Ambrosetti (1968) has referred these morphotypes to female and male individuals respectively. The lower number of the female type tusks may be explained with the lack of tusks in the major part of the adult females (as it is demonstrated by the very well preserved skull no. 4). In the respect to the alveolar plane, the tusks of Spinagallo elephants are turned upward and towards outside, as in *Mammuthus*, but their curvature leans on a plane and are not helicoidal. The dihedral angle formed between the sagittal plane of skull and the longitudinal plane of the tusk is of about 30 degrees. This position and curvature of the tusks are typical of Spinagallo elephants and do not have correspondence in any mainland species. Nevertheless, if the tusks are examined outside of the alveoli, their shape differs from that of straight-tusked elephants only in the major curvature; the diameter changes not much from the alveolar side to the apex.

Figure 11 *Elephas falconeri* BUSK, 1867, Spinagallo cave. *E. falconeri* faunal complex, early Middle Pleistocene, Late Galerian Mammal Age. Assembled adult male skeleton, height at the shoulder about 90 cm. [photo: Museo di Paleontologia, Dipartimento di Scienze della Terra, University of Rome, 'La Sapienza']

The tusks have been examined also in transverse cross-section. We know that in elephants the surface of the cross-section of the tusk seems to be divided into rhomboidal-shaped areas. This pattern, visible with naked eye, is unique within Proboscidea and it is due to an optical effect, formed when light is reflected from the cut surface of the dentinal tubules radiating from the pulpal surface. The rhomboidal areas have made by the crossing of two lines obtained by the ranging of the groups of dentinal tubules, this effect is generally named Schreger lines (Espinoza *et al*. 1990 Espinoza & Mann 1993). Various au-

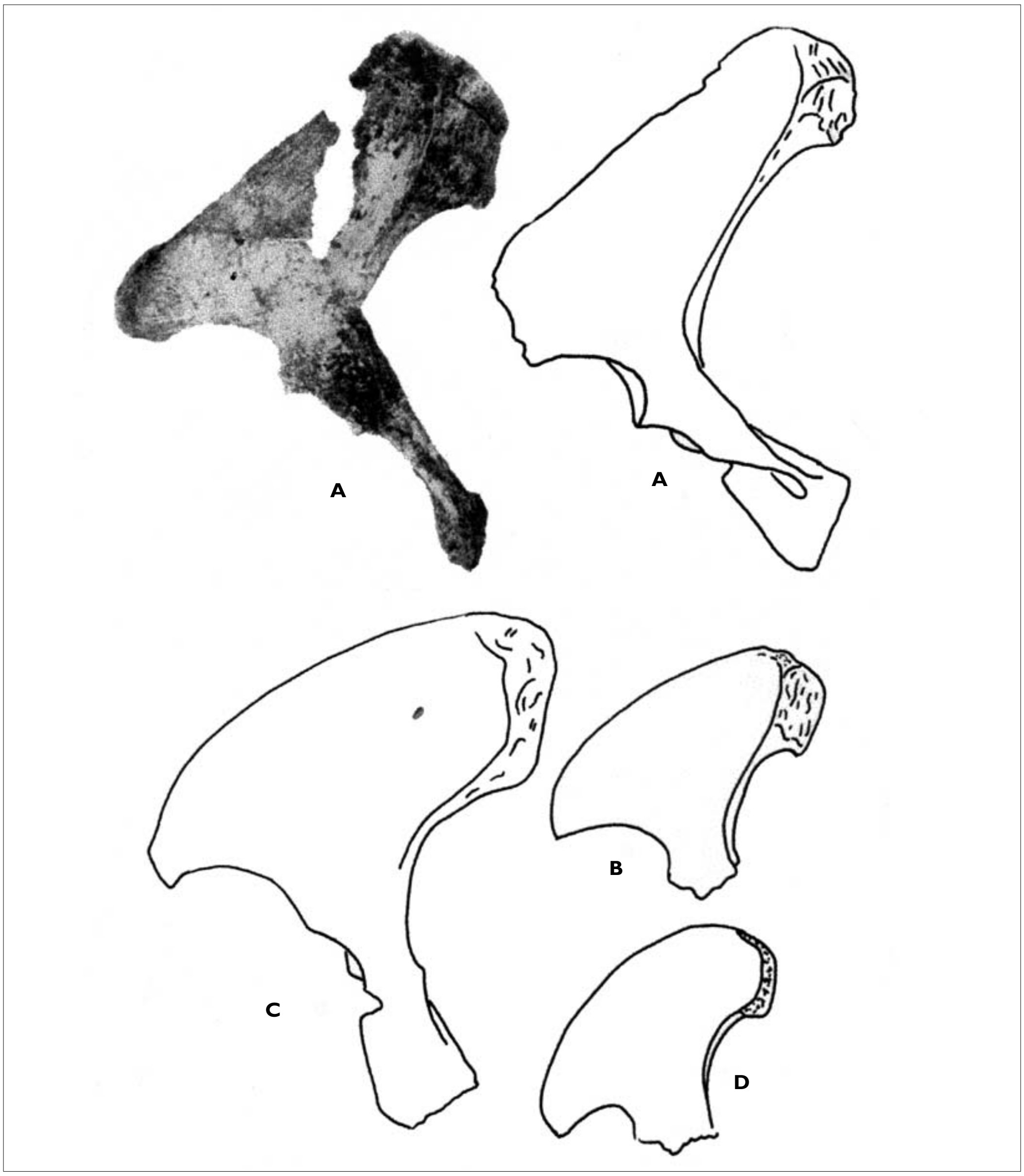

Figure 12 - Pelvic bone of *Elephas falconeri* BUSK, 1867 (**A** = adult, **B** = juvenile), *Loxodonta africana* (BLUMENBACH, 1797) (**C**) and a juvenile specimen of *Mammuthus primigenius* (after Coope & Lister 1987) (**D**). Not to scale.

thors (Espinoza *et al*. 1990; Penniman 1952; Sanford 1973; Espinoza & Mann 1993) have hypothesised that the angles formed by the Schreger lines should be used as taxonomical character to identify elephantine genera.

In transverse section, the Spinagallo tusks exhibit a pattern of crossing lines that appears as a thick band within the dentine. As in the other proboscideans two types of angles can be recognised: the inside angles (slightly concave and open to the medial area of the tusk) and outside angles (somewhat convex and open to the lateral area of the tusk). In *Elephas* and *Loxodonta*, the outside angles of the peripheral area are wider than in *Mammuthus* (Espinoza *et al*. 1990; Espinoza & Mann 1993), but the wide of the inside angles decreases notably in the medial and central areas of the section. Moreover, also in the peripheral area the width of angles notably changes in the same species and the single ranges of variability are superimposed. However, outside angles bigger than 120 degrees are unknown in *Mammuthus*. On the basin of our personal data, in the extant species *L. africana* the maximal values of the outside Schreger angles range from 83 degrees, near the pulpal cavity, to 111 degrees in the middle, to 141 in the peripheral area of the section, the maximal values of the inside Schreger angles range respectively from 90, to 113, to 139 degrees; in *Elephas maximus* the maximal values of the outside angles range from 79, to 113, to 140 degrees, the maximal values of the inside angles range from 87, to 118, to 145 degrees, in *Mammuthus primigenius* the maximal values of the outside angles range from 32, to 54, to 94 degrees, the maximal values of the inside angles range from 32, to 54, to 94 degrees.

According to Espinoza *et al*. (1990) modern elephant outside and inside Schreger angles, measured on the peripheral area, range respectively from 105/96 to 156/149 degrees, with a mean angle of 130/115 degrees. In *M. primigenius* the outside and inside Schreger angles range respectively from 39/40 to 100/95 with a mean of 76/73 degrees.

According to Espinoza & Mann (1993) the minimum value of the outside and inside Schreger angles in modern elephant reach 90 degrees, whereas in *M. primigenius* the maximal value of these angles is 115 degrees. In the Spinagallo specimens, the width of outside and inside Schreger angles range respectively from 94/89 near the pulpal cavity, to 105/108 in the middle, to 134/130 in the peripheral area. The presence of obtuse outside angles also in the inner part of the tusk seems to indicate a closer relationship with the *Elephas* than with *Loxodonta*, which exhibit almost rectangular inner angles and seems to exclude any relationship with *Mammuthus*.

One sample of pulpal cavity surface of *E. falconeri* tusk has also been examined through a scanning electronic microscope in order to notice the density of dentinal tubules. As a matter of fact, Saunders (1979) observed that more tubules are present in mammoth tusks than in those of American mastodon; this hypothesis has also supported by Shoshani (1996). In the Spinagallo specimens, the tubules are enough spaced out, they are not so numerous as in *Mammuthus*. Yet we need more additional data to consider this character as diagnostic.

Post-cranial skeleton

In the smallest elephants, the smaller size and the reduced weight favour a development of joints, which bring the limbs closer to the sagittal plane and facilitate anterior-posterior oscillation with respect to the ancestral forms. Furthermore, the foot becomes more digitigrade. However, it is possible that the fixing of apomorphical characters in the limbs is not due only to static elements connected with the lighter body weight, but also to the need for more secure movements on relatively uneven ground and in climbing rather steep slopes. Those modifications make it difficult to recognise synapomorphic and symplesiomorphic characters in the smallest elephants of the Sicily and Malta, that are strongly modified compared to the mainland ancestor. In the limb bones of the elephant from Spinagallo cave, some features seem more similar to savannah, grassland or steppe elephants than to forest elephants. For example, the acromion process in the scapula is more robust and in a lower position than the metacromion, the ulna exhibits a strong development of the olecranon, and in the tibia the diaphysis is thin but the epiphyses are robust. However, some other features of the long bones of the Spinagallo elephants are similar to those of juvenile specimens of *E. antiquus*. For example, the upper edge of the epicondylar crest is in a low position in the humerus (Ambrosetti 1968), the torsion of this bone and of the femur is reduced in the juvenile specimens of *E. antiquus* in comparison to the adult specimens. These resemblances are due to the fact that dwarfed adult elephant and younger individual of normal sized elephants share comparable size and mass of the body. Similar features occurred also in the dwarf *Mammuthus exilis* from the Californian islands (Roth 1992, 1993).

The morphology of the pelvis bone of adult specimens from Spinagallo cave is interesting, especially that of the iliac wing. The anterior border of the wing is almost straight as in *Mammuthus* and in *Loxodonta*, but the iliac wing of *E. falconeri* share only its noticeable mediolateral extension and its relative antero-posterior shortness with the former genus. Also, as in the juvenile specimens of *Mammuthus* (Coope & Lister 1987) the iliac wing is almost symmetrical in shape and its anterior edge in widely convex. On the contrary, in the specimens of the genus *Elephas* (also in the endemic *E. mnaidriensis*, Basile & Chilardi 1996), the anterior border of the iliac wing is convex also in adult specimens and the wing is almost symmetrical. The asymmetry exhibited by the ilium of adult specimens is due to the elongation of ischium-sacral part of the pelvis. This should be related to a shortening of the posterior part in comparison with the total dimension. This pattern seems to characterise the forms that have acquired an rather cursorial aptitude.

CONCLUSION

In the *Elephas falconeri* the peculiar features of the skull derive from the extensive development of the brain case, connected to the necessity to maintain the minimal functional volume of the brain also when the dimension of the skull is very reduced. Therefore, the respiratory axis shifted far forward and downward. This feature conditions the position of the external choanae and all the morphology of the neurocranium, especially the domed apex and the forehead. On the other hand, the juvenile elephant specimens, especially those of *Elephas* and *Loxodonta*, exhibit a skull morphology very similar to that of the adult skulls of *E. falconeri*. Consequently, the paedomorphic features of the skull of Spinagallo elephant are not useful for taxonomic identification. Therefore, the taxonomically diagnostic characters of the skull seem to be only those related to the morphology of the tusk alveoli of the male. They are divergent from the midline, directed forward as well as downward and jointed to each other across the midline by a relatively broad, triangular flap bone. A very enlarged fan is characteristic for *L. africana* and for elephants of the *E. antiquus* - *E. namadicus* group. Nevertheless, in the former species the fan in proportionally larger and square in shape: the proximal width of the fan is slightly above the width of the distal portion; the lateral borders of the alveoli are less divergent than in *E. antiquus*, *E. namadicus* and *E. falconeri*. Besides, also the morphology of wearing plates of molars and the values of Schreger angles of *E. falconeri* are more similar to those of *E. antiquus* than any other elephantine species. At the same time, the peculiar features exhibited by the limb bones seem to be related to the size and load reduction of body and to a new way of locomotion.

The most problematic character is represented by the position of the tusks, divergent and turned upward, but without helicoidal curvature. *E. falconeri* is different from both paleoloxodontine and mammuthine elephants. In spite of this, the hypothesis that *E. antiquus* was been the mainland ancestor of *E. falconeri* can not be ruled out.

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