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Paedomorphic features and allometric growth in the skull of *Elephas falconeri* from Spinagallo (Middle Pleistocene, Sicily)

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SUMMARY: In *Elephas falconeri* Busk, 1867, the peculiar features of the skull derive from the extensive development of the brain case. This is necessary to maintain a minimal functional volume of the brain when the size of the skull is very reduced. Therefore, the respiratory axis acquires a forward and downward inclination. This feature determines the low position of the external choanae and all the morphology of the braincase, especially the extension of the forehead. On the other hand, the negative allometric growth of the anterior part of the maxillary and premaxillary bones, determines a proportional reduction of the facial region. Juvenile elephant specimens, especially those of *Elephas* and *Loxodonta*, exhibit a skull morphology very similar to that of adult skulls of *E. falconeri*.

1. Introduction

The richest sample (skulls, mandibles and long bones of several individuals) of the smallest elephant of Sicily *Elephas falconeri* comes from the Middle Pleistocene deposits of Spinagallo cave (Iblean Plateau) (Ambrosetti 1968) where, during the period between 1958 and 1960 (Accordi 1962), a low-diversity, unbalanced and strongly endemic mammal fauna was recovered. The Spinagallo vertebrate fauna has been described in several papers and includes 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 species of birds (including giant endemic stringiformes), bats, micromammals (the endemic dormice, *Leithia melitensis* (Adams 1874) and *Leithia cartei* (Adams 1874), and the soricid *Crocidura esuae* Kotsakis 1984), *?Vulpes* sp. and *E. falconeri*, the only large mammal.

The smallest endemic elephants of Malta and Sicily have been considered for decades as the last step of a progressive size reduction trend, started by the mainland species *Elephas (Palaeoloxodon) antiquus* Falconer & Cautley, 1847. Nevertheless, stratigraphic and geochemical data have demonstrated that *Elephas falconeri* is the earliest known endemic elephant in Sicily. Consequently its phylogenetic relationships have been reconsidered. Despite the peculiar morphology of the skull, *E. falconeri* seems to be more closely related to *E. antiquus* than to *Mammuthus* (Palombo, in press).

2. Description and Discussion

One of the most evident features of the Spinagallo skull is the peculiar proportions between the cranial and facial region of the skull. The proportional increase in size of the cerebral mass observed in the elephants of Spinagallo (Accordi & Palombo 1971), as well as the reduced pneumatization, allow the adult to maintain a rather globose cranium. On the other hand,

a functional reduction of the pneumatic bone tissue seems to be a characteristic of dwarfed Proboscidea, especially the smallest ones. For example, in *"Elephas" celebensis* (Hooijer 1949), *Mammuthus exilis* (Stock & Furlong 1928) and *Elephas (Palaeloxodon)* sp from Tilos (Theodorou 1983), this reduction can be detected by the absence of parietal swelling (Roth 1992, 1993; van der Berg *et al.* 1996).

The skull of an adult Spinagallo elephant (Fig. 1c) is characterised by a relatively globose shape with a rather flattened apex; the forehead is wide, almost plane both in sagittal and in transverse profile; the frontal-parietal region is long and very slightly concave. External nasal choanae are in a low position both in juvenile and in adult individuals, being proportionally very large and in a very anterior position with respect to the anterior border of the molar alveolus; orbital cavities take up a very anterior position and are very large, especially in young specimens. The orbital plane is turned towards the outside and it forms a noticeable angle with the sagittal plane; the occipital surface is convex and tilted forward, forming an obtuse angle with the frontal surface. The vertical axis, drawn from the skull vertex, falls in the middle of the molar alveolus in adult specimens, whereas in the juvenile specimens it falls between the posterior border of the molar alveolus and the external

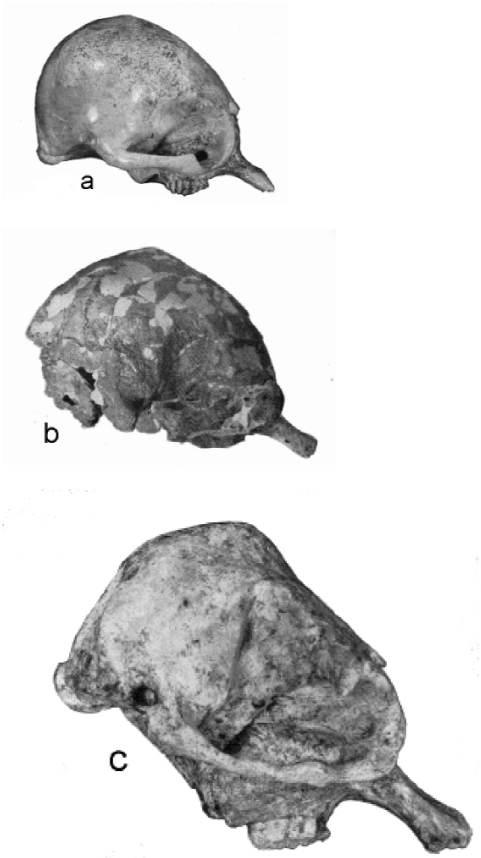

Fig.1 - *Elephas falconeri* Busk, 1867, Spinagallo cave. *E. falconeri* faunal complex, early Middle Pleistocene: skull in lateral view of: (a) very young specimen (n°1) with dp^3 tooth in function; (b) young specimen (n°9) with dp^4 in function (c) adult female (n° 4) with M^2 and M^3 in function. About 0.2x of natural size.

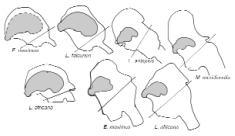

Fig.2 - Cerebral cavity and respiratory axis in: a-b =*Elephas falconeri* Busk, 1867 from Spinagallo cave, a = juvenile (n°2), b = adult female (n°4); c = *Elephas antiquus* Falconer & Cautley, 1847; d = *Mammuthus meridionalis* (Nesti, 1825); e-f *Loxodonta africana* (Blumenbach, 1797), e = foetal individual, f = adult; g = *Elephas maximus* Linnaeus, 1758. Not to scale.

auditory meatus.

A characteristic feature of the Spinagallo skulls is the position of the plane of the tusk alveoli under the forehead plane, slightly turned upward and forward. The tusk alveoli of the Spinagallo specimens are characterised by minimal proximal-distal elongation in comparison with the size of the skull; intermaxillary bones are moderately enlarged with a convex distal edge in the male, reduced with shallow median fossa in the female. The alveolar plane is below the fronto-parietal plane; and the premaxillary bones, in the regionwhich delimits the external choanae, form a noticeable angle with the proximal part of the tusk alveoli.

To explain the peculiar characters of the Spinagallo skulls, the most important and determining element is the allometric growth of the cranial and facial regions of the skull, which differs from that of continental elephant species.

At Spinagallo, during ontogenetic development (Fig. 1), the morphological and biometric variation of the maxillary region and, as a whole, of the skull base, are similar to those displayed by continental elephants, being characterised by a positive allometric development. In very young and young specimens, the palate is wide and transversely flattened, the molar alveoli are slightly protruding, and their lingual sides are almost parallel. During growth, the space between the molars becomes more and more deep and narrow, the alveoli converge forwards, and the height of the posterior maxillary bones notably increases. Consequently, a strong heightening of the occipital condyles can be detected, whereas the inclination of the zygomatic arches increases. This modification results from the need to make room for increasingly tall and wide teeth. The ontogenetic modification of the fan-shaped tusk sockets and triangular, flattened area between them is similar to that of the continental ancestor, but a strong negative allometry and a retardation of somatic development reduce its proportions. Short tusk alveoli are typical of juvenile skulls of elephantine species, in fact this character is related to the small tusk size. Nevertheless, in the male skulls of Spinagallo, the fan, even if rather short, is larger and broader: the distal lateral edge extends almost as far as the lateral extremity of maxillary bones.

In the continental taxa, during ontogenetic growth, the cranial region of the skull displays the greatest positive allometric change (cf. Maccagno 1962). The frontal and parietal

bones greatly increase in thickness; the forehead changes its curvature; the brain case volume notably decreases in proportion to the skull size, allowing the rotation of the respiratory axis upward and backward; and the condyles and auditory meatus move into a higher position because of the increased posterior growth of the maxillary bones. Moreover, in adult skulls the external choanae move to a more backward position, the post-orbital region of the forehead becomes less wide, the maxillary region extends, and the angle between forehead and molar alveolar plane changes to a greater or lesser degree. In contrast, the Spinagallo adult skull maintains a relatively very large cerebral mass, whereas its decrease is strongly marked in other elephants. The relative larger size of the brain of the Spinagallo specimens, with respect to the ancestor, is primarily due to the impossibility of proper brain function below a critical volume, as well as to the strong reduction in pneumatisation of the parietal and frontal bones. Consequently, the whole architecture of the adult skull is modified and exhibits some paedomorphic features, such as an overall globose shape, similar to young animals. According to Gould (1977) a large brain, "*by its own mechanical pressure, causes correlated features*" such as a short face, a vaulted cranium and a low foramen magnum. The absence of the latter character in the Spinagallo skull is consistent with the persistence of a positive allometric heightening of the posterior maxillary region.

Notwithstanding some different features, the skull of Spinagallo is, at least apparently, more similar to juvenile specimens of *Elephas, Loxodonta* and, in less degree, of *Mammuthus*, than to adult ones, even if some affinities with *Elephas antiquus* can de detected (Palombo, in press).

3. Conclusion

In *Elephas falconeri*, the peculiar features of the skull derive from the extensive development of the brain case, connected to the need for maintaining a minimal functional volume of the brain even when the overall dimensions of the skull are very reduced. The allometric positive size increase of the skull affects the posterior region of the maxillary bones (which increase in height to the edge of the molar alveoli) more than the cranial and facial region of the skull. Consequently in the skull of *E. falconeri*, the inclination of the respiratory axis does not change much: the angle formed with the molar plane increases during growth from 23° in very young specimens, to 40° in the adult male. The forward extension of the brain case prevents the rotation of the respiratory axis upward and backward. Accordingly, the external nasal choanae, as well as the orbits, keep a very low position, while the forehead is very broad and longitudinally extended. Furthermore, the anterior position of the braincase prevents the temporal fossa from deepening and the forehead from narrowing transversely. Conversely, juvenile elephant specimens, especially those of *Elephas* and *Loxodonta*, exhibit a skull morphology very similar to that of adult *E. falconeri.*

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