Functional morphology and ecology of Villafranchian Proboscideans from Central Italy

M.P. Ferretti[1], R.V. Croitor[2]

[1]*Dipartimento di Scienze della Terra and Museo di Storia Naturale, Sezione di Geologia e Paleontologia, Università degli studi di Firenze, Firenze, Italia* - mferrett@geo.unifi.it

[2]*Institute of Zoology, Academy of Sciences of Moldova, Kishinau, Moldova* 1360a@usm.md

SUMMARY: The morpho-functional and ecological interpretation of the skeleton morphology of *Anancus arvernensis, Mammuthus meridionalis meridionalis* and *M. m. vestinus* from the Villafranchian of Central Italy is given in the present study. Unlike in hoofed animals, the locomotion strategy seems to have a minor influence upon the postcranial anatomy in the studied proboscideans. The body weight, the tusk weight and the optimal height at which tusks are used for gathering food, are regarded here as the important factors that influence the morphology and proportions of the studied proboscideans skeleton. According to this interpretation and taking into account the associated fauna, i) *A. arvernensis* is suggested as a ground-level feeder; ii) *M. m. meridionalis* is supposed as a woodland inhabitant with feeding habits similar to modern *Loxodonta africana* iii) *M. m. vestinus* is a highly specialized parkland-savanna species and a high-level feeder.

1. Introduction

The skeletal morphology and ecology of elephants is greatly influenced by their large size. Extant elephants posses a postcranial skeleton characterized by predominant graviportal adaptations, and feed upon a great variety of vegetal matter, depending on the season and the characteristics of the biome, to sustain their large body (Guy 1976). Nevertheless, comparisons of body proportions in several fossil proboscideans and in the two extant species, evidenced a number of differences that hint to diverse locomotory and feeding adaptations (Garutt 1954; Gambaryan 1974; Haynes 1990). The aim of this paper is to describe the skeletal anatomy of three Villafranchian (Middle Pliocene to Early Pleistocene) proboscideans from Central Italy and to reconstruct their habits, focusing on their dietary and habitat preferences.

We studied skeletal material, including either complete or partial skeletons, belonging to the tetralophodon gomphotherid *Anancus arvernensis* from Lower and Upper Valdarno (Tuscany) and to the elephantids *Mammuthus meridionalis meridionalis* from Upper Valdarno and *M. m. vestinus* from Farneta (Tuscany), Scoppito (Abruzzo) and Pietrafitta (Umbria). Comparisons were made with osteological material of Recent and fossil proboscideans, and with data taken from the literature.

2. Morpho-Functional Analysis

2.1 Description and Comparisons

2.1.1 Anancus arvernensis

No complete skulls of *Anancus* are known from Central Italy. However, two skulls from Villafranca d'Asti (Piedmont), kept at the paleontological museum of the University of Bologna, show that *A. arvernensis* is characterized by a rather elevated neurocranium, with a convex lateral profile (Fig. 1c). The alveolar portion of the premaxillary bones are short and anteriorly diverging. The tusks are very long, almost straight, and slender. The body is relatively long and wide. The neural spines of the anterior thoracic vertebrae form a well pronounced hump. Even though in the specimens at our disposal some of the neural spines are reconstructed, one can observe that the tallest neural spine forms the peak of the hump, and is situated close to the head. The limb bones are massive, with very short autopodials. The humerus is longer than the ulna: the ratio of humeral to ulnar physiological length is between 1.31 and 1.40 in the studied specimens. The humerus is very robust and is characterized by a well developed deltoid tuberosity. The olecranon of the ulna is very strong and long, being extended some-what toward the posterior (Fig. 2b). As in most proboscideans, the radius is smaller than the ulna. Nevertheless in *Anancus* the radius is relatively robust and its distal end is well developed. The ratio of ulnar to radial distal diaphysal width in the studied skeletons falls between 1.12 and 1.17. In the carpus, the lunar is extremely expanded transversely and articulates with the trapezoid.

2.1.2 Mammuthus meridionalis meridionalis

The skull of *M. m. meridionalis* has bulging parietals projected backwards (Fig. 1a). The neurocranium is high and pointed. The forehead is concave. The alveolar part of the premaxillaries is more developed than in *Anancus*. The tusks are shorter with respect to the skull length than in *Anancus*, and markedly thicker. They are directed downward and laterally at their exit from the sheaths and then upwardly and medially in their distal end. The body is taller and shorter than in *Anancus*. The cervical vertebrae are situated almost on the same axis as the thoracic segment of the back bone. In *M. m. meridionalis* the thoracic hump has not a

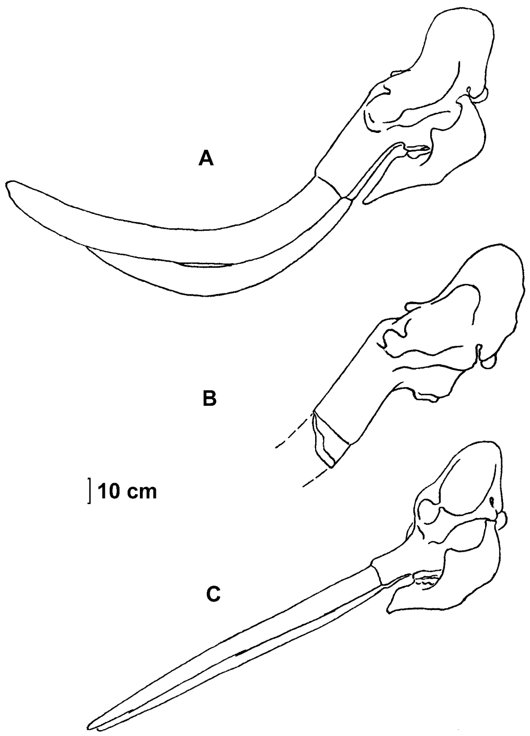

Fig.1 - Skull profiles of (A) *Mammuthus meridionalis meridionalis* (reconstruction), (B) *M. m. vestinus* (adapted from Azzaroli, 1977) and (C) *Anancus arvernensis* (reconstruction).

distinct peak, but it is somewhat more elevated caudally in comparison to *A. arvernensis*. No sexual dimorphism were evidenced with respect to this character. The proportion between forelimb segments is similar to that of *Anancus*, but *M. meridionalis* has relatively longer autopodials (Fig. 2a). The deltoid tuberosity of the humerus is less developed than in *Anancus*. The radius distal end is relatively smaller than in *Anancus*. The ulna to radius distal width ratio is 1.35. The lunar is consistently narrower and may either articulate with the trapezoid (aserial pattern) or not (serial pattern).

2.1.3 Mammuthus meridionalis vestinus

M. m. vestinus is characterized by a larger overall size (the shoulder height of the type specimen from Scoppito, is 3750 mm) if compared with *M. m. meridionalis* (the shoulder height of a male skeleton from Upper Valdarno is 3350 mm). The main differences with respect to *M. m. meridionalis* concern the morphology of the skull. *M. m. vestinus* is characterized by a shorter and deeper skull, with very long tusk sheaths (Fig. 1b). The neurocranium is higher and caudally displaced. The forehead is extremely concave. The tusks are larger, but similar in shape to that in *M. m.meridionalis*. The cervical section of the vertebral column is markedly dorsally flexed, even though this arrangement could be artificial. *M. m. vestinus* has slightly shorter limb distal segments, a condition possibly correlated with the larger body size. The observed differences in the limb proportions are, however, small if compared with the morphological divergence between modern *L. africana* and *E. maximus*.

2.2 Functional anatomy

The observed differences in skull morphology between *M. m. meridionalis* and *M. m. vestinus* can be related to the greater tusk weight of the latter subspecies. The lengthening and strengthening of the praemaxillary bones, and the concomitant shortening of the skull in *M. m. vestinus* give a strong support to the tusks and shifts the masse center of the “skull-tusks” system caudally (cf. Garutt 1954 and Maglio 1973). The tusk weight in *A. arvernensis* is significatively minor, so its biomechanical influence upon the morphology of the skull and the neck posture is limited. The very different tusk morphology between *M. meridionalis* and *Anancus* suggests a different use of this teeth in the two groups. In particular the three-dimentionally curved axis of *Mammuthus* tusks can be interpreted as an adaptation to lessen bending stresses (Khozatsky, 1990), which allows this teeth to reach a larger size, and possibly increases the variety of their use as tools. The upright position of the neck in *M. m. vestinus* may serve two functions: 1) shortening of the skull-neck lever system and 2) elevation of the head. This suggests a different posture and mobility of the head in the two *M. meridionalis* subspecies, possibly related to different feeding habits. In particular. *M. meridionalis vestinus* could be more specialized to a high-level feeding than *M. m. meridionalis*. The different shape of the lateral profile of the hump observed between *A. arvernensis* (the hump is peaked cranially) and both *M. meridionalis* subspecies (the posterior part of hump is elevated) may point out that the mastodon and the mammoths had basically different head posture and maneuverability, possibly in relation with tusk use. In particular they might have differed in the optimal height at which the tusks were used in gathering food.

The proportion between limb segments in terrestrial vertebrate was related to locomotion speed (Coombs 1978), to endurance (Hildebrand & Hurley 1985) or to feeding behavior (Garutt 1954). We observed in our sample that larger specimens posses a relatively longer humerus, which suggests also a possible allometric scaling effect. The lower humerus to ulna ratio of *Anancus*, with respect to *M. meridionalis*, could thus be explained by the smaller size of the former species. Anancus differentiates from the other two taxa by displaying a relatively larger radius distal end and a transversely more expanded lunar. According to Garutt (1954) the radius is relatively larger in such proboscideans (e.g.

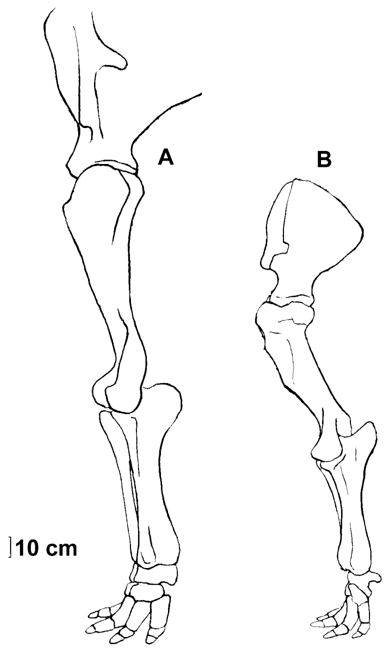

Fig.2 - Articulated forelimbs of (A) *M. m. meridionalis* and (B) *A. arvernensis*.

Moeritherium, Palaeomastodon), which are supposed to have fed on water vegetation and various underground parts of plants (rootstocks, root crops), and kept the forelimbs angled at the elbow joint while foraging. Such a position of the forelimbs supposes in fact an increased weight load upon the radius and, as a consequence, an increased dimension of this bone and of the carpals articulating with it (lunar). An additional functional load on the forelimbs occurred when the animal dig the soil in search of food using its tusks (Garutt 1954). The relatively enlarged radius and lunar, the strongly developed deltoid tuberosity, and the large and strong olecranon described in *A. arvernensis* suggest habitual flexion of the forelimbs in this species. This further supports the hypothesis that *A. arvernensis* was primarily a ground-level feeder. On the other hand, both serial and aserial carpal patterns were observed in the studied articulated skeletons of either *M. meridionalis* subspecies, so the functional importance of this character in these taxa is not supported by our observations.

3. Associated Faunas and Palaeoecology

Anancus occurs, in Central Italy, in Early (Triversa and Montopoli Faunal Units) to Middle (Costa S. Giacomo FU) Villafranchian localities. The interpretation of the Triversa mammal assemblage suggests a warm and humid climate and a forestal biotope (Gliozzi *et al.* 1997). In the younger Montopoli faunal assemblage, *Anancus arvernensis* is associated with *M.* cf. *gromovi* and *Equus liventzovensis.* The assemblage contains also small to large cervids and suggests a mixed habitat (forest and parkland), cooler than the Triversa episode. *A. arvernensis* appears to be a rather eurythermic species, but incapable to tolerate arid conditions. The interpretation of *Anancus* ecology, which is suggested here as a ground-level feeder, is problematic in the context of the faunal data reported above. One can suppose the species under consideration inhabited open landscapes or habitats near water bodies, however further study, that shall also consider dental adaptations, is needed to test this hypothesis.

M. meridionalis meridionalis is abundantly represented in Late Villafranchian (Olivola, Matassino-Poggio Rosso and Tasso local faumas) sediments from Tuscany, while *Anancus* is no more present or is extremely rare. The Late Villafranchian faunal assemblages are suggestive of a relative cool interval and a mixed, forest/parkland biotope (Gliozzi et al. 1997). In particular the functional analysis of the skeletal morphology of *Pseudodama nestii* and *Dama eurygonos* (see Croitor in this volume), which may be considered as the background elements of the Tasso fauna, suggests a landscape composed by forests, woodlands and, perhaps, more open savannahs. A palinological investigation of an Upper Valdarno sequence confirmed a cold and mainly dry episode in correspondence of the Matassino and Tasso faunas (Torre *et al.* 1996). *M. m. meridionalis* possibly occupied an ecological niche similar to that of modern *L. africana*, the food preferences of which depended on season (Guy 1976).

M. m. vestinus substitutes *M. m. meridionalis* in younger deposits from Central Italy, referred to the Farneta FU (Late Villafranchian). At Farneta, *M. m. vestinus* is associated with *D. eurygonos farnetensis*, *Equus stehlini, Leptobos* and *Castor plicidens* (Azzaroli 1977). Among these species, the advanced subspecies of Villafranchian fallow deer *D. eurygonos farnetensis* is represented by the highest number of remains. The morphological changes observed in the lineage *D. e. eurygonos – D. e. farnetensis* suggest a trend toward a more open, savannah-like habitat caused by cooling and aridisation of climate in Italy during the late Villafranchian (see Croitor in this volume). The occurrence in the Farneta assemblage of *M. m. vestinus*, that we interpreted as a specialized high-level feeder, suggests in particular, a savannah parkland (according to classifications of Cole 1963, and Reed 1998) with tall trees, shrubs and grasses. The rich fauna from Pietrafitta contains abundant remains of *M.m.vestinus* and records the first occurrence of *Praemegaceros obscurus* (Gliozzi *et al.* 1997). The occurrence of the giant deer at Pietrafitta indicate the presence of open areas and a relatively cold climate. The presence of permanent water bodies and of forested areas is on the other hand testified by the lignite deposits were the fauna was found, and by the occurrence of *Castor plicidens* in the assemblage. *M.m .vestinus* appears to have inhabited savannah parkland (according to classifications of Cole 1963, and Reed 1998) with tall trees, shrubs and grasses.

4. References

Azzaroli, A. 1977. The Villafranchian stage in Italy and the Plio-Pleistocene boundary. *Giorn. Geol.* 41:61-79.

Cole, M.M. 1963. Vegetation Nomenclature and Classification with Particular Reference to the Savannas. *S. Afr. Geogr. J.* 55: 3-14.

Coombs, W.P. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *Quart. Rev. Biol.* 53: 393-418.

Gambaryan, P.P. 1974. *How mammals run.* New York: Wiley.

Garutt, V.E. 1954. *Archidiskodon meridionalis* (Nesti) from Pliocene of the North Coast od Azov Sea (in Russian). *Trans. Comm. Quat. res*. 10 (2): 3-76. Moscow-Leningrad.

Gliozzi, E., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Capasso Barbato, L., Di Stefano, G., Esu, D., Ficcarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M.R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E., Torre, D. 1997. Biochronology of selected Mammals, Molluscs and Ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. *Riv. It. Paleont. Stratigr.* 10 (3): 369-388.

Guthrie, D. 1990. *Frozen Fauna of the Mammoth Steppe*. Chicago: Univ. Chicago Press.

Guy, P.R. 1976. The feeding behavior of elephants (*Loxodonta africana*) in the Sengwa Area, Rhodesia. *S. Afr. J. Wildlife res*. 6: 55-63.

Haynes, G. 1990. *Mammoths, mastodonts, and elephants*. Cambridge University Press.

Hildebrand, M., Hurley, J. 1985. Energy of the oscillating legs of a fast-moving cheetah, pronghorn, jackrabbit, and elephant. *J. Morph.* 184: 23-31.

Khozatsky, L.I. 1990. Biomechanic significance of some structural peculiarities of the tusks in proboscideans (in Russian). *Trans. Zool. Inst.* 212: 65-71.

Maglio, V.J. 1973. Origin and Evolution of the Elephantidae. *Trans. Amer. Philos. Soc.*, n. series, 63(3): 1-149.

Reed, K.E. 1998. Using large mammal communities to examine ecological and taxonomic structure and predict vegetation in extant and extinct assemblages. *Paleobiol.* 24 (3): 384-408.

Torre, D. Albianelli, A., Bertini, A., Ficcarelli, G., Masini, F. & Napoleone, G. 1996. Paleomagnetic calibration of Plio-Pleistocene mammal localities in Central Italy. *Acta Zool. Cracov*. 39(1): 559-570.