

A reconstruction of the facial morphology and feeding behaviour of the deinotheres

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SUMMARY: The skull morphology of the deinotheres suggests that they had no elephantine trunk. Instead, they had a large, broad and overhanging muscular structure resembling, to a certain extent, the trunk of the tapir and used for browsing. Deinotheres lost early in their evolution the “salad tongs” food-gathering apparatus of primitive proboscideans.

Deinotheres are a bizarre and ultra-conservative proboscidean group, unique in lacking upper tusks while preserving the lower ones. The absence of known direct ancestors contributes to the enigmatic aura of this family. The deinotheres seem to emerge from nowhere, persist for about 20 Ma and then disappear without splitting into numerous phyletic lines or significantly changing their appearance, except in respect of their size.

From an ecological viewpoint, this means that the deinotheres were so well adapted to their particular niche that there was no stimulus to cause them to evolve drastically. What, however, was this niche?

Deinotheres became known to science more than 150 years ago. Since then, the ideas about their appearance and mode of life have changed more than once. They were initially thought to be rhinos, giant tapirs, sirens (using their tusks as an anchor while sleeping), whales and even marsupials (see Shoshani *et al.* 1996 for a more detailed review). Only after the discovery of postcranial remains, deinotheres were included among the relatives of elephants. During the twentieth century, however, the “elephantization” of the deinotheres went too far. The best known, broadly established reconstruction of these animals, originally stemming from Abel (1922), shows them as little more than elephants with lower tusks.

We believe that this reconstruction, featuring a lower lip situated immediately under the elephantine trunk, with tusks protruding from the chin is rather improbable both from an anatomical and an evolutionary point of view. It seems logical to suppose that in the still unknown “proto-deinotheres” the small lower tusks were more or less horizontally positioned with the lip in its usual place below them. It is much easier to imagine the curving of the mandible downwards with the lip retaining its position, than a complicated process during which it “migrated” over the tusks. Thus, the anterior surface of the deinotheres tusks should correspond to the lingual surface of the basic mammal incisors, and the posterior surface to the labial one. The visible trough on the anterior surface of the symphysis, indicating a strong muscular tongue (as noted by Svistun 1974), also precludes a lower lip situated immediately in front of the cheek teeth.

As for the long elephantine proboscis of the deinotheres, its existence was doubted for anatomical reasons by several authors such as Svistun (1974), Tarabukin (1974), Harris (1975) and Tassy (1998).

We agree that the deinotheres probably didn't have a long, elephant-like trunk. Despite the large nasal opening, usually assumed to guarantee the presence of a trunk (see for example Vauflrey 1958), the general structure of the skull

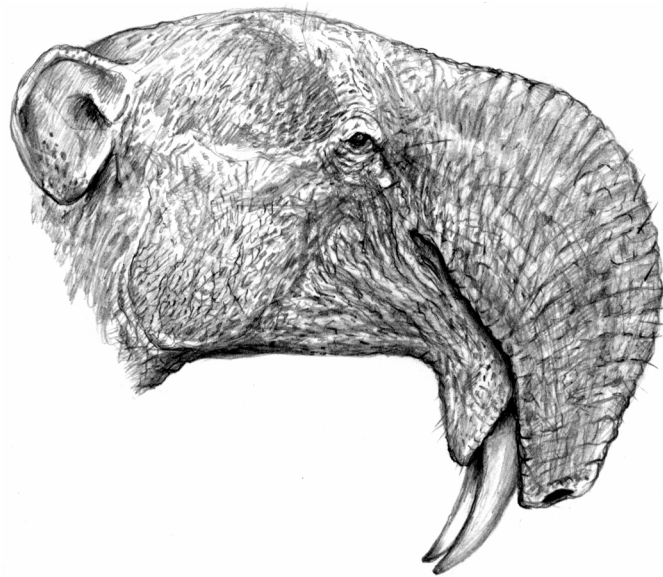


Fig.1 - Reconstruction of the head of *Deinotherium giganteum* (Drawing: Velizar Simeonovski).

speaks against it. As already pointed out by Tarabukin (1974), the deinother skull provides no sufficient insertion surface for a typical elephantine proboscis. The large, more or less horizontally positioned premaxillae would be a hindrance rather than help to an operating cylindrical trunk.

A complicated and still debatable problem is the use of tusks. Harris (1975) gave good enough reasons against their use as levers or for digging. As was pointed out by the same author, there is no data indicating apparent sexual dimorphism, and the most important role of the tusks should be related to feeding. Despite the lack of a consistent wear pattern, the presence of wear facets on the medial or caudal sides of some deinother tusks (K. Huttunen, pers. comm.) seems to support the idea that tusks were used when feeding in tree crowns.

The deinother's cheek teeth obviously indicate that it fed on succulent tree vegetation and lived in forest habitats, browsing on the higher branches of the trees. It was, in a sense, "the tapir of the upper floor". Later, with the aridification of the climate, the deinotheres probably inhabited hygrophilous forests and forest patches. It could be supposed that they had to cover vast territories which led to locomotory

adaptations in the distal segments of their limbs (see Tobien 1962).

As already said, the deinotheres fed in tree crowns. With its tusks the deinother could remove the larger obstructing branches (but not pull down branches to mouth level as supposed by earlier authors), reach out with its "proboscis" (see below) and put the foliage into its mouth, onto the long horizontal part of the symphysis. There, the food would have been manipulated by the long muscular tongue. Such a mode of feeding seems to be supported by the adaptations of the occipital region for increased mobility of the head noted by Harris (1975). We agree with this author that the downward-curving of the tusks was related to the need to keep them out of the way while gathering food - their position and the loss of upper tusks permitted direct contact with the food source. In this position however, they still had a function in the gathering of food and remained fully functional during the evolutionary history of the family.

Early proboscideans like Oligocene *Phiomia* and *Palaeomastodon* (as well as many other Palaeogene large forest browsers) had a food-gathering apparatus in which the two pairs of incisors played a role similar to that of "salad

tongs". During the evolution of elephantoids, with the development of a proboscis and the elevation of the skull, the tusks lost their initial feeding-related function, lower tusks were lost in many elephantoid lineages (also the mandible was shortened) and the upper ones became perigamic structures. The deinotheres were the only proboscideans that lost their superior tusks, but they also shortened their mandible by curving it downward. Here, the function of the "salad tongs" was taken by the upper lip, the muscular tongue and the long horizontal part of the symphysis.

Harris (1978) noted that juvenile deinotheres tusks had a different shape compared to the tusks of adult animals. It seems logical to suppose that juvenile deinotheres had also a somewhat different feeding behaviour due to their small size.

Additionally, the tusks of the deinotheres could also have a social function (as with all proboscidean tusks), related to intraspecific competition.

Our reconstruction (Fig. 1), based on the Eppelsheim skull of *Deinotherium giganteum*, shows an animal with a large muscular upper lip, laterally hanging over the lower one. This structure may be called a proboscis, because it is a result of the fusion of the tissues of the nose and the upper lip; but it is more a tapir-like proboscis than an elephantine trunk - cylindrical and fit for complicated operations, including with its tip.

As with the proboscis of the tapir, the deinotheres' nostrils must have been situated on the tip. Thus the olfactory contact with the substratum is preserved. If the nostrils were situated immediately below the premaxillae, and only the upper lip was elongated (as with the black rhinoceros), the distance between the nostrils and the tip of the lip would hinder their olfactory function. In other words, the deinotheres would not be able to use its sense of smell when in contact with its food. Another argument against such a position of the nostrils was given by Harris (1975.) The third possibility - that the nostrils were on the anterior surface of the lip, near its tip - seems to us highly improbable from the point of view of the anat-

omy of the cartilages of the nasal region.

We have to admit that, except for the position of the nostrils, our reconstruction strongly resembles Osborn's initial restoration (Osborn 1910), which he later abandoned for no apparent reason, preferring the reconstruction by Abel (Osborn 1936). Our analysis has convinced us that Osborn's original, practically forgotten concept was more realistic than later and better-known reconstructions.

CONCLUSIONS

Usually portrayed as curious elephants with misplaced tusks, deinotheres were in fact a group highly specialized in their feeding behaviour and narrowly adapted to a specific forest niche; a group that followed its own distinct and original evolutionary path for more than 20 Ma. After almost a century, evidence seems to revive H. F. Osborn's abandoned and nearly forgotten initial concept of the deinotheres' appearance.

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