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Évolution

L'origine et l'évolution des éléphants☆

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Résumé

D'importantes avancées paléontologiques récentes ont été faites sur l'évolution des proboscidiens, particulièrement sur les débuts de leur histoire. De nouvelles découvertes dans l'Eocène inférieur confirment en particulier l'hypothèse d'un morphotype lophodonte ancestral chez les Proboscidea et l'origine africaine de l'ordre, dont sont exclus les anthracobunidés asiatiques. Les proboscidiens primitifs de l'Eocène restent cependant mal connus. D'autres découvertes importantes concernent l'origine des moerithères, des déinothères, des éléphantimorphes et la différenciation des éléphantidés. La paléontologie documente chez les proboscidiens une histoire dont la richesse est sans commune mesure avec leur diversité relictuelle actuelle et l'un des plus extraordinaires cas d'évolution morphologique chez les Mammalia. ***Pour citer cet article : E. Gheerbrant, P. Tassy, C. R. Palevol 8 (2009).***

Abstract

Origin and evolution of proboscideans. Recent palaeontological research has significantly enhanced our knowledge of the evolution of proboscideans, especially the beginning of their evolutionary history. New discoveries in the Early Eocene support, in particular, a lophodont ancestral morphotype for the Proboscidea and the African origin of the order, from which the Asiatic Anthracobunidae are excluded. The primitive Eocene proboscideans remain, however, poorly known. Other important discoveries have been made on the question of the origin of the moeritheres, of the deinotheres and elephantimorphs, and on the differentiation of elephantids. Palaeontology demonstrates in the Proboscidea a remarkably rich history, unsuspected from the extant relictual diversity, and one of the most spectacular morphological evolutions in the Mammalia. ***To cite this article: E. Gheerbrant, P. Tassy, C. R. Palevol 8 (2009).***

Mots clés : Proboscidea ; Éléphants ; Darwin ; Évolution ; Origine ; Afrique

Keywords: Proboscidea; Elephants; Darwin; Evolution; Origin; Africa

"Since Darwin we know that we must explain the elephant not only in mechanistic terms (of mutation, selection and adaptation on the population level) but also in historical terms, as 'descent with modification', evolution in phylogeny." Georgy Koentges (2008: p.658) [44].

Abridged English version

With only two or three living species, the Proboscidea order displays a history nearly entirely made

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of fossil taxa (circa 180 species). From *Phosphatherium escuilliei*, 55 Ma, the earliest proboscidean known so far, up to extant elephants, the fossil record of the order has considerably increased since Darwin's days.

The evolutionary history of the proboscideans is characterized by three successive radiations [89], which follow their origination at Paleocene–Eocene transition: the Eocene radiation of primitive lophodont taxa, the Miocene radiation of gomphotheres and stegodonts, and the Mio-Pliocene radiation of the modern family Elephantidae.

The earliest proboscideans *Phosphatherium* and *Daouitherium* found in the early Eocene of Morocco do not show any of the most conspicuous proboscidean characters (no elephantine trunk, no tusks, no horizontal displacement of the molars, no graviportal gait), but minor, although fundamental, anatomical synapomorphic traits on the cranium and teeth (the postcranial skeleton being still unknown). Most recent cladistic analyses of *Phosphatherium* and other primitive Proboscidea strongly challenged the ancient hypothesis of the bunolophodont ancestral morphotype of the Proboscidea. The primitive proboscideans were lophodont follivorous animals; the bunolophodont and more crushing structure of the molars of the genus *Moeritherium* and elephantiforms are derived (Fig. 1). The primitive species of *Moeritherium*, *M. chehbeurameuri* from the Middle/Late Eocene of Algeria [22], represents an intermediate molar pattern between the primitive lophodonty and the derived bunolophodonty seen in more advanced species of the genus and in the Elephantiformes. In the same way, the species "*Numidotherium*" *savagei* from the Late Eocene and the Early Oligocene of Libya [15] is probably more derived than *Barytheriuum*, with intermediate features between primitive lophodont and advanced bunolophodont proboscideans [21,23]; for instance, the enamel microstructure is of the derived Elephantiformes pattern [93], and the postcranial skeleton is derived [21]. A reversal of the lophodonty is supported in the Deinotheriidae. Most recent finds in Late Oligocene strata of Ethiopia [81], Eritrea [91], and Pakistan [6] reduced a major and persisting stratigraphical gap between the famous site of the Fayûm in Egypt and the Early Miocene localities of the Old Word. The genus *Chilgatherium* from the Late Oligocene of Ethiopia is a possible forerunner of the deinotheriids, while *Eritreum* from the Late Oligocene of Erithrea anticipates Neogene elephantimorphs.

The highest taxonomic diversity of the proboscideans occurred during the Miocene. As soon as Late Miocene, seven genera of elephantids are described in Africa. A debated topic is the origin and differentiation of elephantids, where paleontological and molecular data concur and sometimes conflict. The earliest members of the extant genera *Loxodonta* and *Elephas* are Late Miocene (∼7 Ma, East Africa, Chad), while those of *Mammuthus* date from 5 Ma (South Africa). Molecular analyses of frozen carcasses of *Mammuthus primigenius* compared to living elephants bring contradictory results, although the most recent one supports the sister group relationships of *Mammuthus* and *Elephas*.

The fossil record and history of the proboscideans display probably the most spectacular morphological evolution in the Mammalia, from its earliest members, such as *Phosphatherium* which was a small generalized somewhat daman-like ungulate, to the huge and striking extant elephants. Most remarkable features of extant elephants – such as the trunk, the huge skull, the tusks, the graviportal stance, the shortening of the tooth row, the horizontal tooth displacement – evolved progressively since the Eocene. However, the large size evolved very early, since the beginning of the history of the order, as it is presently known. The proboscideans, which were indeed the first large mammals of Africa, are especially emblematic of the African mammal history.

Yet, the initial radiation and phylogeny of the Eocene lophodont proboscideans remains poorly known. Recent progress has been made, however, on their postcranial skeleton, for taxa such as *Barytherium* [21]. A significant increase of our knowledge of the proboscidean history is expected on the origin of the Deinotheridae, Elephantiformes, Elephantimorpha, and of the modern family Elephantidae.

1. Introduction

Dans « *On the Origin of Species* », Darwin prend l'exemple des éléphants – considérés par lui comme les moins prolifiques des mammifères – pour expliquer la croissance exponentielle des populations (un faible nombre de parents peut engendrer un très grand nombre de descendants), lesquelles dépasseraient rapidement et largement les ressources naturelles disponibles s'il n'y avait les contraintes environnementales. Selon Darwin [17,64], le calcul mathématique montre qu'un seul couple d'éléphants donnerait 15 millions d'individus en cinq siècles. Une manière aussi de laisser entendre, par analogie, que si le couple est tenu pour représentatif d'une spéciation, il y a peu de chances que des archives fossiles puissent indiquer les cheminements des 15 millions d'individus dans toutes les directions, du Nord au Sud de l'Afrique, pendant un laps de temps si court. Darwin fut gêné par le faible nombre d'arguments