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Original article

Dispersal of African mammals in Eurasia during the Cenozoic: Ways and whys☆

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ABSTRACT

Several groups of mammals originated in Africa and then immigrated to Eurasia during some intervals of the Cenozoic, thus greatly contributing to the mammalian biodiversity in Eurasia. Nevertheless, the African components of Eurasian mammalian faunas have had variable success in their diversification and survival. The Afro-Arabian plate remained separated from Eurasia by the Tethyan seaway, which was definitely closed in the Burdigalian, some 20 myr ago. Before its closure, the marine barrier between the Afro-Arabian and Eurasian plates did not totally prevent mammalian exchanges between these landmasses, as documented by the arrival of rodents and primates in Africa in the late Paleocene-early Eocene, the dispersal of embrithopods on both sides of the Tethyan seaway during the Eocene, and the immigration of elephantoids from Africa to Asia in late Oligocene. These events seem to be restricted to some groups of mammals, which apparently had abilities to use sweepstake dispersal routes. The massive mammalian dispersal from Africa to Eurasia started sometimes in the early Miocene, involving several groups of African mammals, in particular proboscideans, hyracoids, tubulidentates, and anthropoids. This contribution discusses the timing of these events under the light of recent discoveries of Africa-originated mammals in Eurasia. The impact of the evolving paleogeography of the area situated between the Afro-Arabian and Eurasian plates on the mammalian dispersal is reconsidered. The dispersal of land mammals from Africa to Eurasia is controlled not only by the paleogeographic changes (sea level changes, dispersal routes, terrestrial bridges, etc.), but also by climatic factors that modified the environments of terrestrial mammals, favoring or not the occurrence of dispersal routes and/or the enlargement or restriction of climatic belts and biogeographic provinces to which these mammals were adapted. These questions are discussed taking into account the present knowledge of the record of the Africa-originated mammals in Eurasia during the Cenozoic times.

1. Introduction

The fossil record shows that several groups of mammals migrated from Africa to Eurasia at some time intervals during the Cenozoic (e.g., Mein, 1999; van der Made, 1999; Gheerbrant and Rage, 2006). The dispersal area of these immigrant taxa covers parts of the northern continents of the Old World, and some of them, such as proboscideans, even conquered broad territories in North and South Americas. The best-known African immigrants are the proboscideans, which are barely absent in the fossil record of the northern continents before the early Miocene, except for a single tusk fragment record from the late Oligocene of Pakistan (Tassy, 1990; Antoine et al., 2003). Their early representatives inhabited Africa during almost all Paleogene times, at least since the late Paleocene (Gheerbrant, 2009), and they remained restricted to that continent up to the early Miocene. This is also the case for the hyracoids, which are as diverse as the proboscideans in the Paleogene record of Africa, although they occur much later in the Neogene of Eurasia.

The general consensus reached during the last decades, based on paleontological and geological evidences, is that the Afro-Arabian plate became isolated after the break of the Gondwanan landmass during the Jurassic. It was separated from Eurasia by a large Tethys seaway up to the early Miocene, although this seaway progressively narrowed because of the northern motion of the Afro-Arabian plate that started in the late Cretaceous. For vertebrate paleontologists, the endemic nature of faunas indicates an "Island Africa" period that lasted from the early Cretaceous (Albian-Aptian, *ca.* 120 Ma) to the early Miocene (*ca.* 20 Ma) (Gheerbrant and Rage, 2006). In such a paleogeographic context, several questions arise to explain some intriguing aspects of its mammalian faunas:

- where did the placental mammals inhabiting Africa during this "Island" period originate?
- how did they reach this continent in such a peculiar paleogeographic context;

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- how many waves of exchanges existed between Africa and the surrounding continents, when, and favored by which events?

The Mesozoic fossil record of the African continent (Africa and Arabian Peninsula) is poor and thus far from providing any reliable knowledge on the stem placental mammals of Africa. The mammalian orders grouped in the clade Afrotheria are considered the main, and probably the first mammal inhabitants of the African continent. The clade Afrotheria was defined by Stanhope et al. (1998) based on molecular data, including six living placental orders (Proboscidea, Sirenia, Hyracoidea, Macroscelidea, Tubulidentata and Tenrecoidea) which are presumed to be the stem inhabitants of Africa. The oldest representatives of Afrotherian mammals in Africa are the proboscideans and hyracoids, which are recorded in the late Paleocene and early Eocene deposits of North Africa, *ca.* 55–60 Ma (Tabuce et al., 2008; Gheerbrant, 2009). Based on molecular analyses, Meredith et al. (2011) proposed an age ranging between 74.4 and 96.5 Ma for the emergence of Afrotheria, i.e., during the late Cretaceous. However, the present paleontological record is far from documenting their antiquity beyond the late Paleocene.

2. Paleogene African mammals in Eurasia

Phylogenetic hypotheses based on molecular data identify the monophyletic clade Afrotheria that contains elephants, hyraxes, manatees, elephant shrews and aardvark, a group of African origin. Kuntner et al. (2011) identify in this clade a basal subdivision, on the one hand the Afroinsectiphilia (aardvark, tenrecs, golden moles, and elephant shrews), and on the other hand the Paenungulata (hyraxes, dugongs, manatees, and elephants). Before the definition of the molecular clade Afrotheria, Simpson (1945) erected the superorder Paenungulata to group the orders Proboscidea, Sirenia, Hyracoidea and Embrithopoda (an extinct order of hoofed herbivores from the Paleogene period), in addition to some North and South American and western European fossil groups (Pantodonta, Dinocerata, and Pyrotheria). Later on, the systematic status of paenungulates was highly debated, with the addition of new subdivisions and/or new groupings, so that it is still far to reach consensus (see Gheerbrant et al., 2005). The main causes of the controversies apparently issued from the large gaps in the fossil record, and to some extent from the contradictory molecular models. However, studying the periotic morphology, Court (1990) demonstrated the proximity of the embrithopod *Arsinoitherium* to proboscideans and sirenians, confirming once more Simpson's (1945) hypothesis regarding the inclusion of the Embrithopoda in the superorder Paenungulata. Recent molecular analyses seem also to support the superorder Paenungulata as demonstrated by Kuntner et al. (2011). Concerning the purpose of the present paper, it is relevant that the proboscideans, hyracoids, tubulidentates and embrithopods are the main African orders; some representatives of these groups also occur in Eurasia as immigrants in some intervals of the Cenozoic. The present paper focuses on these immigrants, and the paleobiogeographic context that favored their dispersal into Eurasia.

The Eurasian Paleogene fossil record does not include any of these African mammals, except for some elements referred to the Embrithopoda from Turkey and Romania (Sen and Heintz, 1979; Radulesco and Sudre, 1985; Maas et al., 1998), and for a fragment of proboscidean incisor from Pakistan (Antoine et al., 2003). In early Neogene times, the typical African orders, such as proboscideans, hyracoids and tubulidentates, massively appear in Eurasia. Their migration is apparently not synchronous, but surely related to the plate convergence between Afro-Arabia and Eurasia, and the related paleogeographic and paleoenvironmental changes that deserve a particular attention. In the following pages, the Eurasian occurrence of these African groups is reviewed.

2.1. Embrithopoda

The embrithopods form an enigmatic mammalian order that lived during the Paleogene and became totally extinct at the end of the Oligocene. They were herbivorous and represented by paleontologists as rhinoceros-like animals living in bushy or swamp environments. The dispersal pattern of embrithopods in the area situated at present to the north and to the south of the Mediterranean Sea deserves particular attention. The embrithopods were first discovered at Fayum in Egypt at the very beginning of the 20th century. Our knowledge remained restricted for a long time to two Fayum species, *Arsinoitherium zitteli* and *A. andrewsi*, from the late Eocene-early Oligocene Jebel Qatrani Formation in Egypt (Andrews, 1906). Consequently, up to the discoveries of other representatives of this order in the 1970s, *Arsinoitherium* was considered an endemic and enigmatic mammal restricted to Fayum. From the 1970s, new discoveries both in Africa and Eurasia modified this simplistic view on the systematics and diversity of the Embrithopoda. The present record shows that embrithopods have a long evolutionary history, spanning in time from the late Paleocene to the latest Oligocene (*ca.* 60–25 Ma). Their dispersal area covered parts of Eurasia and almost all Africa, i.e., the continents on both sides of the Tethys seaway. Indeed, the diversity of this order was actually greater than it was supposed.

At present, the earliest uncontested record of this order is from the late Paleocene-early Eocene of Turkey with the genera *Palaeoamasia* and *Hypsamasia* (Sen and Heintz, 1979; Kaya, 1995; Maas et al., 1998). Up to date five localities in Turkey yielded the remains of *Palaeoamasia kansui* Ozansoy, 1966 (Fig. 1(B)); its type-locality is the lignite mine of Eski Çeltek in north central Turkey (Ozansoy, 1966; Sen and Heintz, 1979). The fossiliferous Eski Çeltek Formation is correlated to the Ypresian based on the planctonic foraminifera from a thin marine intercalation above the mammal bearing lignite seam, and the rich benthic and planctonic foraminiferal assemblages from the overlying early Lutetian Armutlu Fm. (Koç and Türkmen, 2002). Lastly, Métais et al. (2012) analyzed phylogenetic relationships of an ungulate (*Parabunodon anatolicus* Ducrocq and Sen, 1991) from the same locality, and they stated that this species is probably derived from the late Paleocene pleuraspidotheriids of western Europe, confirming its early Eocene age. In addition to the Eski Çeltek lignite mine, *P. kansui* or *P.* cf. *kansui* are recorded from four other localities in Turkey, all correlated to the early-middle Eocene: Çiçekdağ, Boyabat, Bultu-Zile, and Uzunçarsıdere Fm. (Sen and Heintz, 1979; Kaya, 1995; Gül, 2003).

Maas et al. (1998) erected *Hypsamasia seni* on a fragmentary dentition from the Uzunçarsidere Fm. (UÇF) exposed on the northeastern margin of the Haymana-Polatlı Basin near Ankara (Kappelman et al., 1996; Maas et al., 2001). They advocated an early-middle Eocene age for the UÇF based mostly on the apparent lack of unconformity between this formation and the overlying marine Orhaniye Fm., which yielded Lutetian planctonic foraminifera. The UÇF fauna includes marsupials, ungulates and embrithopods, the latter represented by two taxa: *Hypsamasia seni* Maas et al., 1998, and *Palaeoamasia* sp.; the second taxon has been described by Gül (2003) in her unpublished master thesis. The age of the UÇF is debated because of the contradictory interpretations of the regional stratigraphy. For Kappelman et al. (1996) and Maas et al. (1998, 2001), the UÇF is conformably overlain by the marine Lutetian Orhaniye Fm., while for Kazanci and Gökten (1986) there is an unconformity between these formations, and the age of the UÇF is better correlated to the late