Discussion

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Relationships of the Malagasy fauna during the Late Cretaceous: Northern or Southern routes?

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Conjectures about the Cretaceous and post-Cretaceous vertebrate faunas of Madagascar are generally based on the fact that these faunas display similarities to those of South America, and that Africa lacks taxa that are common to Madagascar and South America. In order to account for this distribution, two ways of dispersal bypassing Africa have been proposed.

Averianov et al. (2003) have recently suggested relationships between Malagasy and Laurasiatic faunas during the Late Cretaceous; they have even hinted at a more or less direct connection between the Iberian and Malagasy faunas. This challenges the southern route Krause et al. (1997) used to explain the composition of the Late Cretaceous fauna of Madagascar, but is consistent with the hypothesis of a northern route (Rage 1996).

Obviously, this debate implies that the role of Africa as an intervening landmass between Madagascar and either Laurasia or Gondwanan areas is ruled out. In my opinion, this means that the absence of numerous taxa in Africa (more specifically, taxa present in South America and Madagascar, but lacking in Africa) represents true absences (these taxa never entered Africa), not an artefact (these taxa are lacking in Africa because they have not been recovered yet). I presume that, similarly, those authors who support either the southern or northern hypothesis implicitly regard the absences in Africa as true absences.

Krause et al. (1997) showed that a southern landmass comprised of South America, Antarctica, India, and Madagascar was inhabited by a faunal community (more specifically Gondwanatherian mammals). They assumed that the connection between Antarctica and Indo-Madagascar was provided by the Kerguelen Plateau until ca 80 Ma; India was located between Madagascar and the Kerguelen Plateau, the Seychelles Plateau providing a link between India and Madagascar (Krause et al. 1997: fig. 1; Hay et al. 1999: fig. 14) (Fig. 1A). The same opinion was expressed by Sampson et al. (1998). Case (2002) proposed an alternative connection between Madagascar and Antarctica, i.e. the Gunnerus Ridge that is located west of

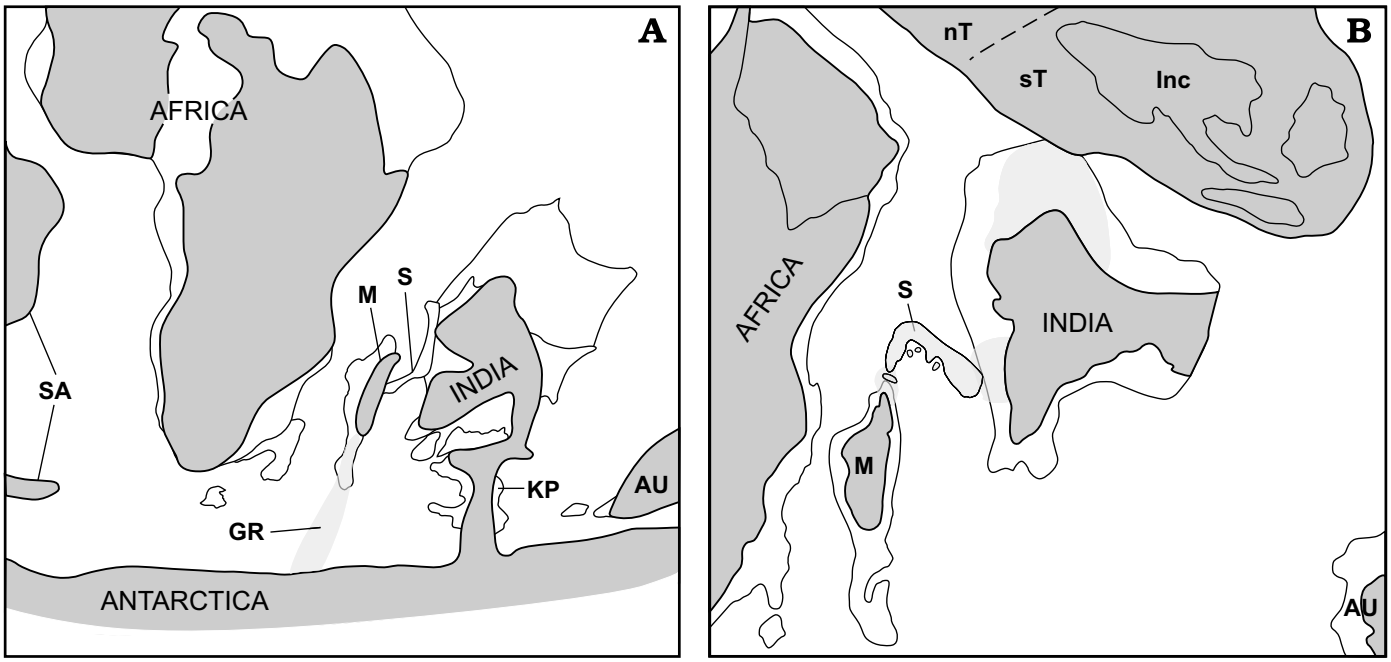

Fig. 1. Palaeogeographic relationships of Madagascar during the Late Cretaceous. **A**. Southern route (ante-Maastrichtian, ca. 80 Ma), modified after Krause et al. (1997) and largely based on Hay et al. (1999), showing the alternative connections suggested by Krause et al. (KP) and Case (GR). **B**. Hypothesized northern route (?Late Maastrichtian), redrawn after Rage (1996) and based on Jaeger et al. (1989) and Patriat and Segoufin (1988). Abbreviations: AU, Australia; GR, Gunnerus Ridge; Inc, Indochina; KP, Kerguelen Plateau; M, Madagascar; nT, northern Tibet; S, Seychelles Plateau; sT, southern Tibet; SA, South America. Dark grey: terrestrial areas; light grey: presumed terrestrial connections.

the Kerguelen Plateau (Fig. 1A). According to Case, and contrary to Krause et al. (1997), Madagascar was not the cul-de-sac of the route but was on the way to India. Whatever the precise terrestrial connection between Madagascar and Antarctica, the southern hypothesis is similar to that of Blanc (1982) who suggested a southern route to account for the presence of 'iguanid' lizards in Madagascar and South America and their absence in Africa; the only difference is that Blanc conjectured that 'iguanids' reached Madagascar from Antarctica owing to rafting instead of crossing over the Kerguelen Plateau or the Gunnerus Ridge.

Subsequently, Krause (2001) reported on a molar from the latest Cretaceous of Madagascar; he regarded it as a marsupial tooth, which in his opinion would provide confirmation of the southern hypothesis. But Averianov et al. (2003) have reinterpreted this fossil and have assigned it to zhelestids, a taxon of placental mammals that was restricted to Laurasia. More specifically, they have suggested affinities with *Lainodon*, a genus known only from the latest Cretaceous of the Iberian Peninsula (Gheerbrant and Astibia 1994, 1999). Therefore, Averianov et al. have 'reversed' the geographic affinities of the Malagasy fossil.

I would not venture to support particular relationships between Late Cretaceous mammals from Madagascar and the Iberian Peninsula, but I agree with the possible palaeogeographic relationships between Madagascar and Laurasia. On the basis of the past and present distribution of iguanid lizards and boine snakes I suggested a terrestrial route between Asia and Madagascar, through India and the Seychelles Plateau (Rage 1996). Sahni et al. (1982), Prasad and Rage (1991) and Rage and Jaeger (1995) showed that Laurasiatic taxa entered India following a terrestrial route by the end of the Cretaceous. Jaeger et al. (1989) proposed a possible connection resulting mainly from a rearrangement of south Asiatic blocks, and the recent discovery of the subduction of Indian continental lithosphere beneath Asia (Chemenda et al. 2000) lends credence to such a terrestrial link between Asia and India as early as the end of the Cretaceous. In addition, the Seychelles Plateau may have formed a link between India and Madagascar at that time (Patriat and Segoufin 1988). Therefore, a terrestrial route Asia-India-Seychelles Plateau-Madagascar (Fig. 1B) perhaps existed, and I suggested that Laurasiatic faunas, after having reached India, were perhaps able to enter Madagascar (Rage 1996). This hypothesized way, that is consistent with Averianov et al.'s opinion, accounts for the geographic distribution of iguanids and boines, and its role might perhaps be considered as far as the geographic origin of lemurs is concerned, more especially in the context of the recent discovery of a cheirogaleid lemur from the Paleogene of Pakistan (Marivaux et al. 2001).

This northern hypothesis is perhaps not incompatible with the southern one. The connection between Asia and the India-Seychelles Plateau-Madagascar assemblage was certainly established only at the very end of the Cretaceous, well after the latter assemblage separated from Antarctica. In other words, the northern route might have occurred after the southern one. Obviously, in view of the paucity of the Indian, Malagasy, and Antarctic fossil records, this remains only a working hypothesis.

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