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Paleobiogeography of Africa: How distinct from Gondwana and Laurasia?

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Abstract

Although Africa was south of the Tethys Sea and originally belonged to the Gondwana, its paleobiogeographical history appears to have been distinct from those of both Gondwana and Laurasia as early as the earliest Cretaceous, perhaps the Late Jurassic. This history has been more complex than the classical one reconstructed in the context of a dual world (Gondwana vs. Laurasia). Geological and paleobiogeographical data show that Africa was isolated from the Mid-Cretaceous (Albian–Aptian) to Early Miocene, i.e., for ca. 75 million years. The isolation of Africa was broken intermittently by discontinuous filter routes that linked it to some other Gondwanan continents (Madagascar, South America, and perhaps India), but mainly to Laurasia. Interchanges with Gondwana were rare and mainly "out-of-Africa" dispersals, whereas interchanges with Laurasia were numerous and bidirectional, although mainly from Laurasia to Africa. Despite these intermittent connections, isolation resulted in remarkable absences, poor diversity, and emergence of endemic taxa in Africa. Mammals suggest that an African faunal province might have appeared by Late Jurassic or earliest Cretaceous times, i.e., before the opening of the South Atlantic. During isolation, Africa was inhabited by vicariant West Gondwanan taxa (i.e., taxa inherited from the former South American–African block) that represent the African autochthonous forms, and by immigrants that entered Africa owing to filter routes. Nearly all, or all immigrants were of Laurasian origin. Trans-Tethyan dispersals between Africa and Laurasia were relatively frequent during the Cretaceous and Paleogene and are documented as early as the earliest Cretaceous or perhaps Late Jurassic, i.e., perhaps by the time of completion of the Tethys between Gondwana and Laurasia. They were permitted by the Mediterranean Tethyan Sill, a discontinuous route that connected Africa to Laurasia and was controlled by sea-level changes. Interchanges first took place between southwestern Europe and Africa, but by the Middle Eocene a second, eastern route — the Iranian route — involved southeastern Europe and southwestern Asia. The Iranian route was apparently the filtering precursor of the definitive connection between Africa and Eurasia. The relationships and successive immigrations of mammal (mostly placental) clades in Africa allow the recognition of five to seven phases of trans-Tethyan dispersals between Africa and Laurasia that range from the Late Cretaceous to the Eocene–Oligocene transition. These Dispersal Phases involve dispersals toward Laurasia and/or toward Africa (immigrations). The immigrations in Africa gave rise to faunal assemblages, the African Faunal Strata (AFSs). All successful and typical African radiations have arisen from these AFSs. We recognize four to six AFSs, each characterized by a faunal association. Even major, old African clades such as Paenungulata or the still controversial Afrotheria, which belong to the oldest known AFS involving placentals, ultimately originated from a Laurasian stem group. Africa was an important center of origin of various placental clades. Their success in Africa is probably related to peculiar African conditions (endemicity, weak competition). Although strongly marked by endemicity, the African placental fauna did not suffer extinctions of major clades when Africa contacted Eurasia. The present geographic configuration began to take shape as early as the Mid-Cretaceous. At that time, the last connections between

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Africa and other Gondwanan continents began to disappear, whereas Africa was already connected to Eurasia by a comparatively effective route of interchange.

Keywords: Africa; Gondwana; Laurasia; Paleobiogeography; Cretaceous; Paleogene

1. Introduction

During the Cretaceous distinct terrestrial faunas and floras inhabited Gondwana and Laurasia on either side of the Tethys seaway (Bonaparte and Kielan-Jaworowska, 1987; Rage, 1988; Hallam, 1994). The distinction between Gondwanan and Laurasian faunas is still perceptible during the Cenozoic. These paleobiogeographical provinces match geological and geophysical reconstructions (e.g., Hallam, 1994; Scotese, 1997; McLoughlin, 2001). The opening of the Tethys seaway, i.e., the full separation of Gondwana from Laurasia, took place in the Late Jurassic (Cecca et al., 1993). Within this framework, Africa always has been regarded as a part of Gondwana.

This dichotomous paleobiogeographical model of Gondwana vs. Laurasia has been recently supported for the Cretaceous by Luo et al. (2003), who hypothesized 'a dual origin of tribosphenic mammals'. According to their hypothesis, two groups evolved convergently as two ecological vicariant taxa: the Boreosphenida (i.e., tribosphenic therians: marsupials, placentals and early relatives) and the Australosphenida (monotremes and early relatives), which would have originated in Laurasia and Gondwana, respectively. The recent discovery of australosphenidans in the Late Jurassic of South America (*Asfaltomylos*) is in agreement with this view (Rauhut et al., 2002).

The consequences of the separation between Gondwana and Laurasia cannot be denied, but various paleobiogeographical data show that such a classical concept of a dual Cretaceous world is oversimplified and that Africa had a more complex and separate paleobiogeographical history. Even Luo et al. (2003), who support the classical view, provided data that emphasized the unusual paleobiogeographical history of Africa (see Section 3.1.). The points that raise questions about the paleobiogeographical history of Africa are the mixed Gondwanan and Laurasian nature of the fauna that inhabited Africa during the Cretaceous and Paleogene, the absence in Africa of numerous taxa that were widely distributed elsewhere in Gondwana (see Section 3.1.1., a discussion of the significance of African absences), and the endemic nature of numerous Cretaceous and Paleogene African taxa.

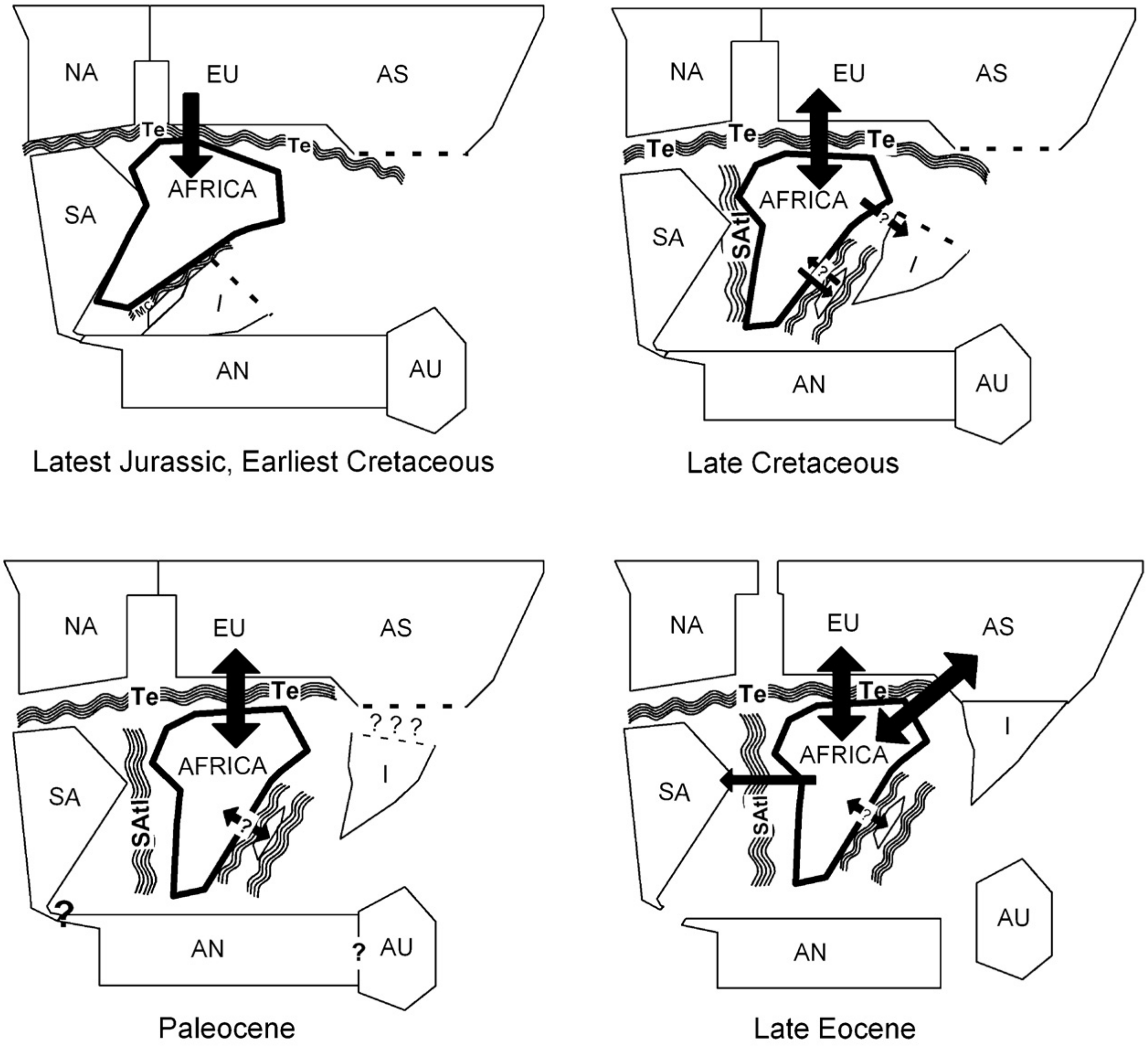
The problems that face us are as follows:

1) Africa and Gondwana: That Africa was part of Gondwana before isolation is unquestionable. But what was the nature and significance of the Gondwanan affinities of a large part of the Cretaceous and Tertiary fauna of Africa. Did these affinities result from vicariance (i.e., were the African taxa inherited from the West Gondwanan fauna that was present before isolation of Africa?) or from dispersals (i.e., did taxa from other Gondwanan continents enter Africa after the opening of the South Atlantic?). If dispersals occurred, did they involve the whole of Gondwana or only parts of it?
2) Africa and Laurasia: Biogeographical relationships between Africa and Laurasia are indisputable and they were evident as early as the earliest Cretaceous. What was the amount of trans-Tethyan interchanges and their impact on African faunas? What was the subsequent evolution of the Laurasian immigrants that entered Africa? Which Laurasian continent was linked to Africa?
3) Isolation of Africa: Occasional, filtered interchanges with other continents aside, the African fauna underwent marked endemicity. What has been the degree and biotic consequences of this endemicity?

2. Gondwanan affinities of the African Cretaceous and Paleogene faunas

2.1. The autochthonous African faunas and the final separation of Africa from Gondwana

Within Gondwana, from the Late Jurassic to the Mid-Cretaceous, Africa and South America formed a land mass called West Gondwana (e.g., McLoughlin, 2001) connected by a narrow link to other Gondwanan continents that made up East Gondwana (Antarctica, Madagascar, India, and Australia) (Fig. 1). Terrestrial vertebrates confirm the close geographical relations between Africa and South America until the middle part of the Cretaceous. It should be noted that in the present study, 'terrestrial vertebrates' include freshwater fishes. Not all freshwater fishes, however, can be regarded as reliable indicators of continental paleoenvironments



Latest Jurassic, Earliest Cretaceous

Late Cretaceous

Paleocene

Late Eocene

Fig. 1. Paleobiogeographical maps showing relationships of Africa and dispersals of terrestrial vertebrates on filter routes from the latest Jurassic/earliest Cretaceous to the Late Eocene. Latest Jurassic/earliest Cretaceous: Tethys seaway (Te) completed between Laurasia and Gondwana; Mozambique Channel (Mc) opened between Africa and Madagascar. All Gondwanan continents are in contact. Late Cretaceous: South Atlantic (SAtl) separates Africa from South America (West Gondwana broken), Africa isolated. Paleocene and Late Eocene: Africa isolated. AN: Antarctica; AS: Asia; AU: Australia; EU: Europe; I: India; NA: North America; SA: South America.

(Poyato-Ariza et al., 1998). They are used here only as paleobiogeographical data complementary to true land taxa.

Interchanges of terrestrial faunas between Africa and South America were possible up to the Aptian/Albian, perhaps the Cenomanian (Table 1). Marine faunas, however, argue for a pre-Cenomanian separation between Africa and South America. Maisey (2000) suggested that a seaway completely separated the two continents as early as the Aptian. According to Moullade and Guérin (1982), however, the seaway was completed slightly later, during the Middle Albian or even the Late Albian according to Förster and Scholz (1979). After the separation from South America, Africa was deprived of direct contacts with other continents until the Early Miocene, when a definitive connection through the Middle East was established with Eurasia.

As a consequence of the Africa–South America land continuity, the presence of most, perhaps all taxa of West Gondwanan origin in the Cretaceous of Africa likely resulted from vicariance from the ancestral stock common to South America and Africa. This is the case for taxa that are documented on the African–South

Table 1
Relationships between Mid-Cretaceous faunas of Africa and South America

Taxa	South America	Africa	References
T: *Araripemys*	Aptian/Albian	Aptian–Cenomanian	de Lapparent de Broin, 2000
T: *Cearachelys–Galianemys* group	Aptian/Albian	Albian/Cenomanian	Gaffney et al., 2002
T: *Hamadachelys– Brasilemys* group	Aptian/Albian	Albian/Cenomanian	de Lapparent de Broin, 2000
C: *Sarcosuchus*	Age indet. between Barremian and Aptian	Aptian	de Lapparent de Broin, 2000
C: *Hamadasuchus–Caririsuchus* group	Aptian/Albian	Barremian–Cenomanian	Prasad and de Lapparent de Broin, 2002
D: *Rebbachisaurus* group	Aptian–Cenomanian	Aptian or Cenomanian	Pereda Suberbiola et al., 2003
D: Spinosaurinae	Aptian/Albian	Aptian–Cenomanian	Sereno et al., 1998
D: Noasauridae	Campanian–Maastrichtian	Aptian–Cenomanian	Sereno et al., 2004
F: *Calamopleurus*	Hauterivien–Albian	Albian	Maisey, 2000
F: *Ellimmichthys*	Aptian	Barremian	Maisey, 2000
F: *Cladocyclus*	Aptian	Aptian	Maisey, 2000
F: *Mawsonia*	Hauterivian–Albian	Aptian–Albian	Maisey, 2000
F: *Neoceratodus africanus*	Cenomanian	Early Cretaceous–Campanian	Martin, 1984a
F: Lepidosirenidae	Maastrichtian–Recent	Ante Albian Cretaceous–Recent	Gayet et al., 1991; Martin, 1984b
F: *Dastilbe*	Aptian	? Aptian	Maisey, 2000; Poyato-Ariza, 1996
U: Noterpetontidae (or Sirenidae ?)	Maastrichtian–Paleocene	Albian ?–Cenomanian	Rage et al., 1993; Evans et al., 1996
A: Pipidae	Cenomanian–Recent	Cenomanian–Recent	Báez, 1996
D: Abelisauridae	Albian–Maastrichtian	Cenomanian	Sereno et al., 2004
D: *Carcharodontosaurus–Giganotosaurus* clade	Albian–Cenomanian	Albian/Cenomanian	Coria and Currie, 2002
S: Madtsoiidae	Cenomanian–Eocene	Cenomanian–Eocene	Rage and Werner, 1999
F: Polypteridae	Maastrichtian–Paleocene	Cenomanian–Recent	Gayet et al., 2002

A: anurans, C: crocodilians, D: dinosaurs, F: freshwater fishes, S: snakes, T: chelonians, U: salamanders.

American block before, or at the time of the disconnection. These taxa, which include turtles, crocodiles, dinosaurs, and freshwater fishes, are detailed in Table 1. In addition, beds that may be slightly younger than the final separation between Africa and South America (i.e., Albian and Cenomanian) have yielded representatives of various taxa such as salamanders, frogs, snakes, and freshwater fishes (see Table 1) that are present in both continents. The presence of these taxa on both sides of the primordial South Atlantic seaway likely involved vicariance. In Africa, all the above taxa probably represent an old West Gondwanan heritage and form part of the African autochthonous fauna (the 'natives'); these West Gondwanan vicariant taxa are autochthonous in Africa versus the later lineages recorded in the continent.

2.2. Interchanges with other Gondwanan continents during geographical isolation

Rage (1981, 1988) and Mourer-Chauviré (1982) suggested that various terrestrial vertebrates dispersed between Africa and South America after separation, owing to the emerged Walvis and Rio Grande Rises. But recent data and reinterpretations of taxa no longer support the role of these rises (Mourer-Chauviré, 1999). It should be kept in mind, however, that parts of these rises were emergent during the Late Cretaceous (Rage, 1988) and that they represented potential discontinuous routes between Africa and South America.

Another, younger filter route between these two continents was suggested by Tarling (1982): the Ceara and Sierra Leone Rises and related current system could have formed a trans-Atlantic dispersal route by Eocene–Oligocene times. This route may have been important for the dispersal toward South America of the African stem groups of the caviomorph rodents and the platyrhine anthropoids (i.e., African hystricognaths and anthropoids; Hoffstetter, 1972), but these rises cannot be regarded as complete land connections between these continents.

Other Gondwanan relationships of Africa involved only Madagascar and perhaps India during the Cretaceous and Paleogene. Interchanges with Madagascar are demonstrated by a few reptiles. The snake *Madtsoia* aff. *M. madagascariensis*, the earliest confirmed erymnochelyine turtle, and the crocodile *Trematochampsa taqueti* are present in the Coniacian or Santonian of Africa (Rage, 1981; Buffetaut, 1985; de Lapparent de Broin, 2000). *M. madagascariensis*, an erymnochelyine turtle (Gaffney and Forster, 2003), and a crocodile that might be related to *Trematochampsa* ('*Trematochampsa*' *oblita*; Buffetaut, 1985) occur in the Maastrichtian of Madagascar. Such ranges argue for dispersals between Africa and Madagascar. Taquet (1982) suggested that these interchanges took place on the Davie Ridge that extends across the Mozambique Channel. Subsequently, this Channel was crossed, mostly as "out-of-Africa" dispersals, by some reptiles (Raxworthy et al., 2002) and mammals, more specifically carnivores, tenrecids, and modern strepsirhine primates (McCall, 1997; Yoder et al., 2003) during the Paleogene. As far as the strepsirhines are concerned, the direction of the dispersal is debated. A westward dispersal of lorisiforms is consistent with the hypotheses of a center of origin of the strepsirhines in Asia (Godinot, 1998; Martin, 2000), or in Indo-Madagascar (Martin, 2003). This was recently supported by the description of a cheirogaleid from the Early Oligocene of Pakistan (Marivaux et al., 2001). Such a dispersal direction is challenged by i) current molecular studies that favor an alternative African origin of the strepsirhines (e.g., Yoder et al., 1996), and ii) the recent discovery of unquestionable lorisiforms in the Late Eocene of the Fayum (Seiffert et al., 2003). Here we endorse tentatively the African hypothesis of the origin of modern strepsirhines. According to McCall (1997), the Davie zone acted as a connection between Africa and Madagascar from the Middle Eocene to the Early Miocene, which may account for the above dispersals. Unfortunately, because of the lack of Cenozoic fossils from Madagascar, the dates of post-Maastrichtian interchanges are speculative or based on molecular evidence.

A poorly preserved lower jaw from the Late Cretaceous of Tanzania has been 'very tentatively' identified as a gondwanatherian sudamericid (primitive mammals of uncertain affinities) by Krause et al. (2003). If this identification proves accurate, then this fossil can be interpreted either as dispersal between Africa and East Gondwana (likely from Africa) or as a West Gondwanan vicariant taxon (the group is unknown from East Gondwana before the Latest Cretaceous). Briggs (2003) suggested that gondwanatherians and abelisaurid theropods dispersed from Africa to the India-Madagascar block during the Late Cretaceous. This would agree with the primitive features of the Tanzanian possible gondwanatherian and its possible pre-Campanian age (Krause et al., 2003). Brigg's hypothesis, however, is not consistent with the relationships within abelisaurids (Sereno et al., 2004) and the certain presence of gondwanatherians in Africa is not confirmed.

Terrestrial dispersals from Africa to India during the Latest Cretaceous and Paleogene are also suggested by angiosperm floras (Mehrotra, 2003). According to Chatterjee and Scotese (1999), Late Cretaceous and Paleogene interchanges between Africa and India took place on a hypothetical continuous land route named Greater Somalia. Chatterjee and Scotese (1999) primarily based their opinion on dinosaurs. But among the taxa on which this hypothesis rests, the significance of at least the abelisaurids is questionable (Sereno et al., 2004). Although Late Cretaceous and Paleogene interchanges between Africa and India appear to be plausible, the continuous land route conceived by Chatterjee and Scotese is not well supported.

2.3. Summary

The Gondwanan affinities of the African Cretaceous and Paleogene faunas primarily represent a West Gondwanan heritage and most, if not all, African groups of Gondwanan origin were present in Africa before its isolation (as a result of vicariance). Subsequently, during the period of isolation, dispersals between Africa and other Gondwanan continents were remarkably rare. Possible interchanges may have occurred between Africa and South America, Madagascar, and India, but only some of the African–Madagascan interchanges, and the dispersals of hystricognath rodents and anthropoid primates to South America can be confirmed on the basis of fossil evidence (Fig. 1). This means that according to the present fossil data, biogeographical links between Africa and the remainder of Gondwana have been rare since the Mid-Cretaceous; it is well known that the Cretaceous fossil record of Africa is poor, but we support the view that absences are significant in the case of Africa (see Section 3.1.1.). What evidence that does exist argues that interchanges between Africa and other Gondwanan continents were "out-of-Africa" dispersals.

3. Non-Gondwanan Africa

African faunas from the Late Jurassic through the Paleogene include a substantial component of Laurasian origin. Laurasian newcomers reached Africa owing to trans-Tethyan routes. By contrast, from the Mid-Cretaceous onward Africa has lacked several Gondwanan taxa that nevertheless occur on other Gondwanan landmasses.

3.1. Isolation of Africa

Despite filtered connections with other continents (Sections 2.2 and 3.2), Africa was largely isolated from at least the Mid-Cretaceous to the Early Miocene. The isolation of Africa is illustrated by the fact that the faunas from the Gondwanan landmasses that surrounded the continent were relatively cosmopolitan (Krause et al., 1997; Sampson et al., 1998) while this Gondwanan cosmopolitanism did not affect African faunas, i.e., various taxa could not reach Africa. The isolation also resulted in a high degree of endemicity.

3.1.1. Remarkable African negative evidences

As a preliminary important remark, we acknowledge that negative evidence, such as absences of taxa, are problematic. This is especially true in the case of Africa whose fossil record is unquestionably poor (e.g., as compared with South America). One may entertain whether this record really reflects low density and diversity of the African fauna (perhaps partly caused by paleoenvironmental conditions as suggested by Russell and Paesler, 2003), or it results from gaps in our knowledge. But Africa has been indeed investigated more than is generally realized. Some localities from the Cretaceous and Paleogene have produced terrestrial faunas that are rich in terms of number of specimens and taxa: Mid-Cretaceous of Wadi Abu Hashim (Sudan) and of the Kem Kem beds (Morocco), Santonian–Coniacian of In Beceten (Niger), Paleogene of the Fayum sites (Egypt). Such localities suggest that absences noted in Africa are not artefacts.

The oddity of Africa with regard to other Gondwanan areas is illustrated by several taxa that are more or less widely distributed in non-African Gondwanan continents, and even in Laurasian ones, but are lacking in Africa (Table 2). Several significant examples are reported below.

One of the best examples is the Australosphenida as defined by Luo et al. (2001). Australosphenidans represent a remarkable radiation of Gondwanan mammals known in South America (Middle–Late Jurassic, Early Paleocene), Madagascar (Middle Jurassic), and Australia (Early Cretaceous–Recent) (Table 2), but they remain unknown in Africa. Their absence from Africa is all the more significant because the group is known as early as the Middle Jurassic. The monophyletic *Ptychoceratodus madagascariensis* group (Dipnoi; Martin, 1982) displays a similar distribution: absence from Africa, but presence in South America, Madagascar, and Australia.

A non-African Gondwanan distribution is also clearly shown by the carnotaurine dinosaurs (Abelisauridae) that have been recovered from the Mid-Cretaceous of South America and the Late Cretaceous of South America, Madagascar, and India. According to Sampson et al. (1998), their distribution is explained by a southern dispersal route (South America, Antarctica, Kerguelen Plateau, and India–Madagascar) that bypassed Africa. The same route was suggested by Krause et al. (1997) for sudamericid gondwanatherian mammals.

The enigmatic Sudamericidae have been found in all Gondwanan continents that surround Africa: South America, Antarctica, Madagascar, and India (Krause et al., 1992; Krause and Bonaparte, 1993; Krause et al., 1997; Reguero et al., 2002), but their presence in Africa is doubtful (see above Section 2.2.). Obviously, if sudamericids are present in Africa (either as the result of a dispersal or vicariance), then this family would display one of the broadest known Gondwanan ranges. But if the African taxon does not belong to gondwanatherians, the absence of Sudamericidae in Africa ranks among the most significant.

The tree *Nothofagus* is another good example of a non-African Gondwanan range. Known since the Late

Table 2
Gondwanan taxa lacking in Africa

	South America	Africa	Madagascar	Antarctica	India	Australia
Australosphenida	m.–l. Jur.–Pal.		m. Jur.			e. Cret.–R.
Pt. madagascariensis group	l. Cret.		l. Cret.			e.–l. Cret.
Carnotaurinae	m.–l. Cret.		l. Cret.		l. Cret.	
Sudamericidae	l. Cret.–Pal.	?	l. Cret.	Eoc.	l. Cret	
Nothofagus	l. Cret.–R.			Pal., Mioc.		l. Cret.–R.
Hadrosauridae	l. Cret.			l. Cret.		
Uruguaysuchus–Simosuchus clade	l. Cret.		l. Cret.			
Mahajangasuchini	l. Cret.		l. Cret.			
Chelidae	m. Cret.–R.					Olig.–R.
Iguanidae	l. Cret.–R.		R.			
Boinae	Pal.–R.		R.			

Conspicuous Gondwanan taxa that are lacking in Africa, with their geographic and stratigraphic ranges. e.: early; l.: late; m.: middle; Cret.: Cretaceous; Eoc.: Eocene; Jur.: Jurassic; Mioc.: Miocene; Olig.: Oligocene; Pal.: Paleocene; R.: Recent.

Cretaceous, it spread as a South America–Antarctica–Australia assemblage (= Neogondwana or *Nothofagus* Province; Le Loeuff, 1998). It has been even found, as pollen, in Paleocene and Oligocene sediments of the Ninetyeast Ridge, in the Indian Ocean (Tanai, 1986), but it is unknown in Africa.

Less widely distributed in Gondwana, but still significant are several other taxa that are lacking in Africa. Hadrosaurid dinosaurs are known from the Cretaceous of South America and Antarctica (Case et al., 2000). They are also widespread on Laurasian continents. Despite this broad range, they did not reach Africa. Among crocodiles, the closely related notosuchids *Uruguaysuchus* and *Simosuchus* have been found in the Late Cretaceous of both South America and Madagascar (Buckley et al., 2000), and the mahajangasuchine peirosaurids show the same geographical range in the latest Cretaceous (Carvalho et al., 2004). Chelid turtles occur only in South America (Late Cretaceous–Recent) and Australia (Oligocene–Recent). Based on the number and diversity of chelids in the Oligocene of Australia, de Broin (1988) inferred that this family was present there long before that time.

Iguanid lizards and boine snakes provide additional arguments for the absence of contact between Africa and other Gondwanan continents. Extant iguanids and boines are present in the Americas, Madagascar and in islands of the Pacific region; both groups appear to be monophyletic (Kluge, 1991; Townsend et al., 2004). Iguanids are known since the Late Cretaceous in South and North America (Estes, 1983; Gao and Fox, 1996), in the Late Cretaceous of Europe (Rage, 1999) and Asia (Gao and Norell, 2000), and in the Paleogene of Europe. Boid snakes are known from the Late Cretaceous and Paleogene in Laurasia. Unfortunately, on the basis of fossil remains it is generally difficult to distinguish Boinae among them. The presence of boines in the Paleogene of Laurasia, however, is established (Rage, 1987; Szyndlar and Rage, 2003). Extinct iguanids and boines are still unknown from Madagascar and Pacific islands. From the range of extinct and extant iguanids and boines, Rage (1996, 2003) suggested that a northern route bypassed Africa through Eurasia and reached Madagascar. In addition, the referral of a tribosphenic molar from the Late Cretaceous of Madagascar (formerly identified as a marsupial by Krause, 2001) to zhelestid mammals (Averianov et al., 2003), affinities of part of the Malagasy flora (Schatz, 1996), and the relationships of the titanosaurid dinosaur *Rapetosaurus* from the Late Cretaceous of Madagascar (Curry Rogers and Forster, 2001) support this northern route. The latter connection may also account for the presence of a Cheirogaleidae in the Oligocene of the Indian Plate (Marivaux et al., 2001), and the range of the Crypteroniaceae flora (Conti et al., 2002; Rutschmann et al., 2004).

Thus, two dispersal routes bypassing Africa have been suggested: a southern route (South America, Antarctica, Kerguelen Plateau, Madagascar–India) and a northern one (Asia–India–Madagascar). Both routes may have occurred, the northern one postdating the severing of the southern way (Rage, 2003). Such routes explain the wide geographic ranges of various taxa that are absent from Africa.

3.1.2. African endemic taxa

The African endemicity is illustrated by the emergence of particular taxa (see below), some of them giving rise to remarkable radiations. It may be inferred that the evolution of the endemic taxa in Africa has been favored by the absences noted above and therefore by the presence of free niches and consequently weak competition on the continent. This endemicity was a direct consequence of the geographic isolation of Africa.

In fact, the African faunas included true endemic taxa, i.e., taxa that originated in, and have remained restricted to Africa, and autochthonous taxa that originated in the continent and subsequently dispersed out of Africa, i.e., taxa that were endemic to Africa before they spread out of the continent. As far as vertebrates are concerned, the first category includes at least elosuchid crocodiles (Cretaceous; de Lapparent de Broin, 2002) and a suite of mammals listed in Table 3. The second group of taxa comprises at least erymnochelyine podocnemidid, and pelomedusid turtles (both from the Cretaceous onward; de Lapparent de Broin, 2000), cordylid lizards (Mesozoic fossils unknown; Estes, 1982), hyracoideans, proboscideans, sirenians, phiomorph rodents (probable stem group of the caviomorphs from South America), zegdoumyids and related anomalurids (e.g., *Nementchamys*), tenrecids, probably hyaenodontid creodonts (Gheerbrant et al., 2006), possibly the anthropoids (African origin suggested by the Thanetian *Altiatlasius* and the Ypresian/Lutetian *Algeripithecus*; the alternative hypothesis being an origin from Asiatic eosimiid), and possibly also the strepsirhines. Taking into account the fact that this list deals only with vertebrates, and that the African faunas were not very diverse before the Neogene, we may surmise that an important part of the African faunas was endemic.

A peculiar point should be emphasized. While endemic reptiles apparently evolved from autochthonous Mesozoic forms (West Gondwana vicariants),

Table 3
Immigrant and endemic lineages of placental and marsupial mammals in Africa, and resulting African Faunal Strata (AFS)

African lineages	Known range	AFS	Laurasiatic stem group
Arsinoitheriidae* (Afrot.)	e.–l. Olig.	Pria.–Rup.? (or earlier)	Embrithopoda (Palaeoamasiidae)
Cricetidae	e. Olig.–R.	Pria.–Rup.?	Cricetidae
Manidae	e. Olig.–R.	Pria.–Rup.?	Pholidota (Manidae)
Phiomorphes: Phiomyidae–Thryonomyidae*	l. Eoc.– R.	Bart.–Pria. or Lut.–Bart.?	Histricognathi, “Baluchimyinae”?
“Baluchimyinae” (*Protophiomys**)	l. Eoc.	Bart.–Pria.?	“Baluchimyinae”
Anthracotheriidae (*Bothriogenys*)	l. Eoc.– Mioc.	Bart.–Pria.	Anthracotheriidae
Ptolemaiidae*	l. Eoc.?–e. Olig.	Bart.–Pria.?	Paroxyclaenidae (Merialinae)
Anchomomyini, *Aframonius**	e. Olig.	Lut.–Bart.?	Adapiformes (Anchomomyini, Caenopithecinae?)
Macroscelidea* (Afrot.)	Eoc.– R.	Than.–Ypr.? (or earlier)	Hyopsodontidae (Louisininae?, Apheliscinae?)
Zegdoumyidae*–Anomaluridae?	Eoc.–R.	Than.–Ypr.	Sciuravidae?
Cercamoniinae (*Djebelemur**)	e. Eoc.	Than.–Ypr.	Adapiformes (Cercamoniinae)
Marsupialia (*Qatranitherium**, *Kasserinotherium**?)	Eoc.–e. Olig.	Than.–Ypr.	Marsupialia (Didelphidae)
Azibiidae*	e.–m. Eoc.	Than.–Ypr.? (or earlier)	Plesiadapiformes (Carpolestidae)
Strepsirhini? Lorisiformes (Galagidae*)	l. Eoc?–R.	Than.–Ypr.? (or earlier)	Adapiformes? Plesiadapiformes?
Anthropoidea?, Parapithecoidea*, Oligopithecidae*, Propliopithecidae?, Cercopithecoidea, Hominoidea	l. Pal.?, Eoc.–R.	Than.–Ypr.? (or earlier)	Omomyiformes?, Tarsiiformes?, Eosimiidae?
Cimolestes, Palaeoryctes	l. Pal.	Than.	*Cimolestes*, *Palaeoryctes*
Adapisoriculidae (*Afrodon, Garatherium*)	l. Pal.–e. Eoc.	Than.	Adapisoriculidae (*Afrodon*, *Adapisoriculus*)
Condylarthra (*Abdounodus**)	Pal.?–e. Eoc	l. Cret.–e. Pal.	“Condylarthra” (Mioclaenidae?)
Paenungulata (Hyracoidea, Proboscidea, Sirenia, *Ocepeia**?) (Afrot.)	Pal.? Eoc.–R.	l. Cret.–e. Pal.	“Condylarthra” (Phenacodonta?)
Tubulidentata (Afrot.)	Mioc.–R.	l. Cret.–e. Pal.	“Condylarthra”
Tenrecidae (Afrot.)	Mioc.–R.	l. Cret.–e. Pal.	Cimolesta?
Chrysochloridae* (Afrot.)	Mioc.–R.	l. Cret.–e. Pal.	Cimolesta?
Hyaenodontidae	l. Pal.–m. Mioc.	l. Cret.–e. Pal.	Cimolestidae (*Cimolestes*?)
Todralestidae*	l. Pal.–e. Eoc.	l. Cret.–e. Pal.	Cimolesta (Pantolestidae?)
Cimolestidae	l.Pal.	l.Cret.–e.Pal.	Cimolesta (Cimolestidae)

*Asterisks denote strictly African endemic taxa.
Immigrations resulted in 4 to 6 African Faunal Strata (detailed study and references in Gheerbrant, 2001). AFS : African Faunal Stratum; Afrot.: member of Afrotheria; l.: late; e.: early; m: middle; Bart.: Bartonian; Cret.: Cretaceous; Eoc.: Eocene; Lut.: Lutetian; Mio.: Miocene; Olig.: Oligocene; Pal.: Paleocene; Priab.: Priabonian; R: Recent; Rup.: Rupelian; Than.: Thanetian; Ypr.: Ypresian. See Dispersal Phases in Table 4b. The Strepsirrhini, which includes the endemic African Galagidae (Late Eocene–Recent), are of uncertain origin, but might be of African origin. Their Laurasiatic stem group (Adapiformes?, Euprimates?, Plesiadapiformes?), and the age of its dispersal in Africa are uncertain. Strepsirrhini belongs to at least the Thanetian–Ypresian AFS or to an earlier AFS.

most of the mammals that were present in Africa before the closure of the Tethys were of Laurasian origin. The stem taxa entered Africa and evolved locally as new endemic lineages (‘African lineages’ in Table 3). Such a phenomenon was observed in South America by G.G. Simpson who named ‘faunal strata’ the successive colonization events (Simpson, 1950). In the present work, we use this notion for Africa and term these colonizing assemblages African Faunal Strata (AFS). Every AFS corresponds to the southward component of a Dispersal Phase (see Section 3.2) whose taxa entered and more or less successfully colonized Africa. It should be noted that some Dispersal Phases did not produce an AFS because they were unidirectional, only going from Africa to Laurasia (see Section 3.2.5. and Table 4b). Each African Faunal Strata is characterized by its suite of taxa, which are listed in Table 3. The AFSs include representatives of extinct and extant endemic African lineages that evolved from initial immigrant taxa, but also fossil taxa that apparently did not take root in Africa after having reached the continent (e.g., adapisoriculids, palaeoryctids, todralestids). It should be noted that the AFSs are based primarily on the First Appearance Datum (FAD) of the taxa known in Africa; however, we also include in the AFSs taxa known in Africa but with no adequate fossil record (e.g., no Paleogene fossils):

their membership in the AFSs is inferred from their phylogenetical relationships. This is especially true for the poorly known earliest AFS (see below), which includes African taxa unknown before the Late Paleocene or even before the Miocene (e.g., Tenrecidae, Chrysochloridae, and Tubulidentata; see Table 3). In Africa, the succession of arrivals of these lineages that subsequently became endemic there allows to identify four to six AFSs of placentals (Gheerbrant, 2001; Table 3), which are more or less well resolved taxonomically and dated:

- Late Cretaceous/Early Paleocene AFS. The earliest AFS of placental mammals involves several Laurasian immigrant stem taxa, among which are primitive 'insectivores' and primitive ungulates ('Condylarthra'). It has been the source of major endemic taxa such as paenungulates, African extant insectivores (potamogales and golden moles), hyaenodontids and primitive "insectivores" such as todralestids and cimolestids (Table 3). But, it cannot be definitely demonstrated that this AFS is homogeneous. It might be comprised of several faunal strata that cannot be discriminated on the basis of available data. The earliest fossil record for this AFS is Late Paleocene (Table 3); the Late Cretaceous/Early Paleocene age of this AFS is inferred (see above).
- Thanetian AFS. It includes mostly primitive 'insectivores': cimolestids, palaeoryctids, and adapisoriculids known in Late Paleocene of Morocco. Apparently, this AFS did not give rise to subsequent African radiations.
- Thanetian/Ypresian AFS. This AFS, close to the Thanetian/Ypresian boundary, contains typical African taxa such as macroscelideans, azibiid primates, and zegdoumyid rodents (and related anomalurids); it includes also African marsupials and cercamoniine primates. The African extant primates (strepsirhines and anthropoids) could belong to this AFS, according to the present fossil data, but we do not exclude an earlier AFS (as old as the Late Cretaceous/Early Paleocene AFS ?), especially for anthropoids (e.g., *Altiatlasius*), but also for strepsirhines (see above).
- Lutetian/Bartonian AFS? A doubtful or minor AFS might be coeval with the Lutetian/Bartonian boundary. It would include only anchomomyine primates and the cercamoniine primate *Aframonius*. But the age of the immigration of these taxa of European affinity, known from the Early Oligocene in Africa, is uncertain.
- Bartonian/Priabonian AFS. This AFS, that is coeval with the Bartonian/Priabonian transition, is characterized by anthracothere artiodactyls, the "baluchimyine" rodent *Protophiomys*, and the ptolemaiids (a striking endemic African family) if the Late Eocene occurrence of the latter is confirmed. Phiomorph rodents perhaps belong to this AFS, but we cannot rule out an earlier arrival in Africa.
- Priabonian/Rupelian AFS? This AFS, equivalent in age to the Priabonian/Rupelian transition, would be exemplified by the first appearance in Africa of embrithopods, pholidotans, and cricetids. This AFS, however, is somewhat doubtful because these taxa might have reached Africa earlier and might belong to the preceding AFS.

The Late Cretaceous/Early Paleocene, Thanetian/Ypresian, and Bartonian/Priabonian AFSs are the most important because they produced the most characteristic part of the African endemic placental fauna. The earliest of these includes striking African mammal taxa (see Table 3).

It is difficult to determine the number of taxa that entered Africa because it depends on phylogenetic hypotheses. This is especially true for the Late Cretaceous/Early Paleocene AFS. If the paenungulate hypothesis, which is a clade typical of Africa, proves correct, then a single immigration (instead of three) resulted in the subsequent origin in Africa of the three modern orders included in the Paenungulata (Hyracoidea, Proboscidea, and Sirenia). Similarly, molecular analyses such as Stanhope et al. (1998) place the chrysochlorids and tenrecids in a single clade, the Tenrecoidea (= Afrosoricida). A more inclusive African clade, the Afrotheria, was proposed on the basis of molecular analyses (Madsen et al., 2001; Murphy et al., 2001); Afrotheria, which includes the Paenungulata, Tubulidentata, Macroscelidea, and Tenrecoidea, is the most conspicuous representative of the Late Cretaceous/Early Paleocene AFS (although afrotherians FAD is only Late Paleocene or Early Eocene in Africa (paenungulates; Table 3); the inclusion of afrotherians in the Late Cretaceous/Early Paleocene AFS is inferred from their phylogenetical relationships; see above). This clade Afrotheria is, however, disputed (Robinson and Seiffert, 2004). The Late Cretaceous/Early Paleocene AFS includes the most important association of endemic taxa and represents the old African placental stock (including, chrysochlorids, tenrecids, tubulidentates, paenungulates, and hyaenodontids; see Table 3). It should be stressed that the systematic, phylogeny and origin of its mammal taxa remain very poorly understood, i.e., the origin of the placental fauna of Africa remains enigmatic. According to Murphy et al.

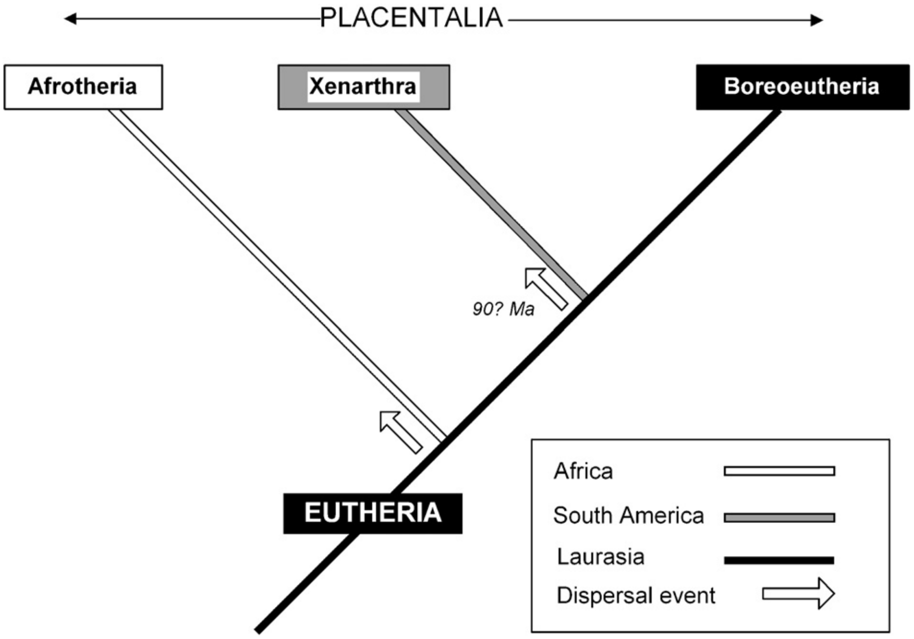


Fig. 2. Pattern of relationships and dispersals of the three basal lineages of modern placentals: Phylogenetic relationships according to molecular analyses (Madsen et al., 2001; Murphy et al., 2001) and hypothesis of Laurasian origin of eutherians and placentals after Archibald (2003). The earliest known fossil record of boreoeutherians is from Asiatic beds 90 Ma old.

(2001) and Springer et al. (2003), the most basal split among placentals was first between Afrotheria and Xenarthra plus Laurasian placentals (Boreoeutheria), and next between Xenarthra and Boreoeutheria (Fig. 2). On the basis of this phylogeny and the presumed time of separation of Africa and South America, they argue for a Gondwanan origin of placentals (Placentalia as the crown group Eutheria, but not the stem Eutheria such as *Prokennalestes*). The initial split between Afrotheria and Xenarthra–Boreoeutheria was thus a vicariant event related to the opening of the South Atlantic. Using dates estimated from their molecular study, their analysis argues for a very old placental origin in Africa, at least as old as the late Early Cretaceous (Springer et al., 2003 suggest a molecular age of 107 Ma for the Afrotheria). Archibald (2003) recently pointed out that the hypothesis of a Gondwanan origin of Placentalia is less well supported by the fossil record than is a Laurasian origin, and that it is biogeographically less parsimonious than the latter. The fossil record indeed favors a Laurasian origin of Eutheria (e.g., *Eomaia*, *Prokennalestes*) and Placentalia (e.g., Zalambdalestidae, "Zhelestidae"). Even a Laurasian origin of the Metatheria (e.g., *Sinodelphis*) and the Boreosphenida is the most likely (Luo et al., 2003; Kielan-Jaworowska et al., 2004). Zack et al. (2005) recently provided arguments that support the Laurasian origin of Afrotheria, or at least of the clade Paenungulata plus Macroscelidea and Tubulidentata (= Africana Springer et al., 1997). This Laurasian origin implies only two successive trans-Tethyan dispersal events from Laurasia toward Gondwana: (a) the stem group of Afrotheria (assuming that this clade is valid) entered Africa, and (b) the stem group of Xenarthra reached South America. As the sister group of the Xenarthra, the Boreoeutheria are 85–90 Ma old (as suggested for Zalambdalestidae and Zhelestidae, Archibald et al., 2001, but see Asher et al., 2005). In this context there are two possible interpretations of the age of the colonization of Africa by placentals.

(i) The strict African origin of the Afrotheria assumed in the molecular hypothesis implies an early age of the trans-Tethyan dispersal of the stem group in Africa. As a consequence, even hypothesizing a Laurasian origin of Placentalia, a molecularly calibrated phylogeny that takes into account the fossil record, implies a very old colonization of Africa, at least by Mid-Cretaceous times (before the earliest boreoeutherians). For the earliest AFS of placental mammals, this would imply an age markedly older than that documented by African fossils. We should remind here that we do not exclude that what we call here the Late Cretaceous/Early Paleocene AFS might in fact have comprised several faunal strata, of K/T age and older Cretaceous age.

Table 4a
Mesozoic mammals and non-mammalian taxa from Africa with trans-Tethyan affinities

Taxa	Africa		Laurasia	References
Earliest Cretaceous				
Albanerpetontidae:	*Anoualerpeton unicus* (?Berriasian)	?<<<?	*An. priscus* (Bathonian, Europe)	Gardner et al., 2003
Discoglossidae	Aff. *Enneabatrachus* (? Berriasian)	?<<<?	*Enneabatrachus* (Kimmeridgian–Tithonian, North America)	Jones et al., 2003
Hahnodontidae	*Hahnodon*, *Denisodon* (? Berriasian)	<<<	Paulchoffatioidea (Kimmeridgian–Barremian)	Hahn and Hahn, 2003
'Symmetrodontans':	*Thereuodon* (?Berriasian)	<<<	*Thereuodon* (Berriasian, Europe)	Sigogneau-Russell and Ensom, 1998
Boreosphenida:	*Tribotherium*, *Hypomylos* (?Berriasian)	<<<	Boreosphenida (?Berriasian)	Sigogneau-Russell, 1991a; Luo et al., 2001, 2002
Triconodontidae:	*Gobiconodon* (?Berriasian)	<<<	*Gobiconodon* (Early Cretaceous, Asia and North America)	Sigogneau-Russell, 2003
Post-Berriasian Early Cretaceous				
Dryosauridae:	*Valdosaurus* (Aptian)	?<<<?	*Valdosaurus* (ante-Aptian, Europe)	Galton and Taquet, 1982; Grigorescu, 2003
Spinosauridae:	*Suchomimus* (Aptian)	?<<<?	*Baryonyx* (Barremian, Europe)	Sereno et al., 1998
Iguanodontidae:	*Ouranosaurus*, *Gravisaurus* (Aptian)	<<<	Several taxa (Berriasian–Albian, Laurasia)	Taquet, 1976
Rebbachisauridae:	*Rebbachisaurus*, *Nigersaurus* (Aptian)	?>>>?	Unnamed (Barremian–Aptian, Europe)	Pereda Suberbiola et al., 2003
Abelisauroidea:	Several taxa (Aptian–Maastrichtian)	>>>	*Genusaurus* (Albian– ?Campanian, Europe)	Allain and Pereda Suberbiola, 2003; Sereno et al., 2004
Late Cretaceous				
Characidae:	Paleocene–Recent	>>>	Maastrichtian–Oligocene (Europe)	Grigorescu et al., 1985
Madtsoiidae:	*Gigantophis*, *Madtsoia* (Cenomanian–Eocene)	>>>	*Madtsoia*, *Herensugea* (Campanian, Europe)	Rage and Werner, 1999
Bothremydidae:	Several taxa (Albian?–Miocene)	>>>	Several taxa (Campanian–Maastrichtian, Europe)	de Lapparent de Broin and Murelaga, 1996
Crocodilians:	*Trematochampsa* (Coniacian–Santonian)	>>>	Close to *Trematochampsa?* (Campanian–Maastrichtian, Europe)	Buffetaut, 1980; Buscalioni et al., 1999
	Hamadasuchus (Aptian–Cenomanian)	>>>	Close to *Hamadasuchus* (Cenomanian, Europe)	Vullo et al., 2005
Paleogene				
Podocnemididae:	*Erymnochelys–Neochelys* group (Eocene)	>>>	*Erymnochelys–Neochelys* group (Eocene, Europe)	Broin, 1988
Crocodilians:	Ziphodonts?	>>>	Ziphodonts ?	Buffetaut, 1988

Genera and species from the areas of origin are only evidence of the presence of the taxa. They should not be regarded as stem groups.

(ii) Afrotheria has a Laurasian origin, as for instance suggested by Zack et al. (2005) at least for macroscelideans, tubulidentates and paenungulates, and their dispersal in Africa might have taken place much later than the oldest known boreoeutherians (Fig. 2), but earlier than the earliest known African placentals (Late Paleocene).

This emphasizes the importance of the African Cretaceous–Paleocene interval which is still a Terra incognita in mammalian evolution. Whatever the exact phylogenetic relationships within African placentals, it remains that Africa was the nursery if not the cradle of numerous major taxa of modern mammals. The origins of the major endemic African mammals (earliest AFS) remain enigmatic. What evidence is available, suggests that many, if not all of the stem clades of endemic African mammalian taxa were Laurasian.

3.2. Trans-Tethyan relationships of Africa

Paradoxically, whereas dispersals between Africa and the remainder of Gondwana were very rare during the Cretaceous and Paleogene, dispersals between

Africa and Laurasian areas were relatively frequent at that time. Such dispersals were perhaps initiated by the end of the Jurassic. In the Late Cretaceous and the Paleogene, a series of trans-Tethyan dispersals of mammals is recognized. Several dispersal events, or Dispersal Phases (hereafter referred to as DP), are identified. These Dispersal Phases involved the crossing of the Tethys in both directions, southward and northward. The southward components of the Dispersal Phases produced the African Faunal Strata (AFS) described above (Section 3.1.2.); therefore, below we detail only the lineages involved in the northward waves of the Dispersal Phases (Sections 3.2.4. and 3.2.5.).

3.2.1. Latest Jurassic

Rauhut et al. (2002) suggested trans-Tethyan dispersals of primitive mammals from Lausasia to Gondwana, implicitly Africa, during the latest Jurassic. Such dispersals would account for the presence of triconodonts, dryolestoids, and peramurids (the stem group of boreosphenidans), i.e., mammals of Laurasian origin, in the Kimmeridgian of Tendaguru (Tanzania; Heinrich, 1998). These three taxa also have been recorded from the earliest Cretaceous of Morocco (Anoual; Sigogneau-Russell, 1991a,c, 1999, 2003), while peramurids are also known from the Barremian–Aptian of Cameroon (Brunet et al., 1990). Triconodonts and dryolestoids are known to also occur in the Late Cretaceous of South America, which renders their significance questionable as dispersers from Laurasia; their Jurassic range was perhaps Pangaean, and thus their presence in Africa may have resulted from vicariance. The latest Jurassic range of the peramurids (which have not been found in South America) was regarded as a trans-Tethyan dispersal of unspecified direction by Rage (1988). Paramacellodid lizards, that display a range similar to that of peramurids (Broschinski, 1999), may also have crossed the Tethys from north to south. Such dispersals were also suggested by Galton (1977) to explain the presence of five very closely related genera of dinosaurs from the Late Jurassic in Africa, North America and Europe.

The geological age of these fossils is close to that of the final opening of the Tethys seaway between South and North America, i.e., between Gondwana and Laurasia. Therefore, their geographical ranges may be the result of vicariance. However, dispersal between Africa and northern areas cannot be discounted, especially for taxa such as peramurids and paramacellodids that are absent from South America.

3.2.2. Earliest Cretaceous

Earliest Cretaceous (?Berriasian) terrestrial vertebrates of Africa are known by the single locality of Anoual (Morocco), yielding taxa with Laurasian affinities. Anoual produced albanerpetontid and discoglossid amphibians (Gardner et al., 2003; Jones et al., 2003) and six significant mammals (*Thereuodon*, *Tribotherium*, *Hypomylos, Gobiconodon*, *Hahnodon*, and *Denisodon*) (Table 4a). These suggest very Early Cretaceous, perhaps latest Jurassic dispersals from Laurasia (Kielan-Jaworowska et al., 2004); therefore they deserve special mention.

Albanerpetontid and discoglossid amphibians are known on Laurasian continents as early as the Middle Jurassic. Other than Laurasia, albanerpetontids have been recovered only from Anoual, where they are represented by *Anoualerpeton unicus*. This species is regarded as the sister group of *A. priscus* from the Bathonian of England (Gardner et al., 2003). The diversity of albanerpetontids in Laurasia, their geological ages and their phylogenetic ingroup relationships strongly argues for a Laurasian origin. As albanerpetontids, discoglossids appear to be of Laurasian origin, but aside from Anoual they also reached India by the latest Cretaceous (Prasad and Rage, 1991). As far as these two amphibian families are concerned, vicariance is possible; but southward dispersals cannot be ruled out.

Tribotherium and *Hypomylos* were accepted as boreosphenidans by Luo et al. (2001) and Kielan-Jaworowska et al. (2004). Their occurrence in Africa is all the more striking given their placement among the earliest boreosphenidans along with taxa from the Purbeck Limestone Group (? Early Berriasian) of England (Sigogneau-Russell and Ensom, 1994). As for the albanerpetontids, the diversity of Early Cretaceous boreosphenidans in Laurasia and their phylogenetic relationships suggest a Laurasian origin (Luo et al., 2001, 2002). This is consistent with the classical view of an origin in ‘northern continents’ of metatherians and eutherians (Lillegraven, 1974). Nevertheless, as a consequence of the discovery of *Tribotherium* at Anoual, Sigogneau-Russell (1991c) did not excluded an African origin of boreosphenidans (called by her tribosphenidans). Subsequently, Kielan-Jaworowska (1992) and Sigogneau-Russell (1992, 1995) even suggested an African origin of eutherians, based on the putative affinities of *Tribotherium*. But, the recent discovery of the earliest eutherian (*Eomaia*; Ji et al., 2002) and metatherian (*Sinodelphys*; Luo et al., 2003) in the Barremian of China adds credence to the view that Laurasia, and more specifically Asia was likely the center of origin of both groups and of the whole boreosphenidan group.

In addition, the triconodont *Gobiconodon* was reported from the Early Cretaceous of Laurasia while the 'symmetrodontan' *Thereuodon* is known also from the Early Cretaceous of Europe. Apart from these records from Laurasia, the latter two genera have been found only at Anoual (Sigogneau-Russell and Ensom, 1998; Sigogneau-Russell, 2003; Kielan-Jaworowska et al., 2004).

According to Sigogneau-Russell (1991b) and Hahn and Hahn (2003), the Hahnodontidae *(Hahnodon*, *Denisodon*) is an endemic multituberculate family, but it is related to the Late Jurassic and Early Cretaceous paulchoffatioideans known in Europe, indicating a Late Jurassic trans-Tethyan dispersal.

3.2.3. Post-Berriasian Early Cretaceous

Some dinosaurs show that trans-Tethyan dispersals continued during the Early Cretaceous, after the Berriasian (Table 4a). The dryosaurid dinosaur *Valdosaurus* occurs in the Wealden of England, Barremian or Valanginian of Romania (Grigorescu, 2003), and the Aptian of Niger (Galton and Taquet, 1982). The close relationships between the European and African species argues for interchanges between the two continents, perhaps from Europe to Africa based on the geological ages. The Baryonychinae (Spinosauridae) represents another example of such a dispersal. They include two closely related genera: *Baryonyx* from the Barremian of England and *Suchomimus* from the Aptian of Niger. According to Sereno et al. (1998), baryonychines dispersed from Europe to Africa, an opinion that probably rests on the older age of *Baryonyx*. An opposite direction of dispersal cannot be definitively discarded, if the greater diversity of spinosaurids on West Gondwana is taken into account. The iguanodontid dinosaurs that are present in the Lower Cretaceous (Barremian–Albian) of the three Laurasian continents and in the Aptian of Africa, also provide evidence of trans-Tethyan dispersal, probably from Laurasia to Africa; but, the Jurassic center of evolution of iguanodontids is uncertain.

Rebbachisaurids are typical dinosaurs from the Cretaceous of West Gondwana. They entered Europe, probably during the Early Cretaceous, although an earlier, Pangaean history cannot be definitely ruled out (Pereda Suberbiola et al., 2003). *Genusaurus* from the Albian and perhaps Campanian (see below) of southern France is regarded as a possible abelisauroid (but not an abelisaurid) by Allain and Pereda Suberbiola (2003), and Sereno et al. (2004). If this referral proves correct, then this dinosaur is an evidence of a south to north trans-Tethyan dispersal.

3.2.4. Late Cretaceous

The terrestrial fossil record from the Cenomanian–Santonian interval is very poorly known in Europe. Vullo et al. (2005), however, noted the presence of at least one immigrant of African origin (a crocodilian close to *Hamadasuchus*) in the Early Cenomanian of southwestern Europe; it perhaps crossed the Tethys before the Late Cretaceous.

The Campanian and Maastrichtian provide stronger evidence of interchanges between Africa and Europe. These interchanges were mostly northward, as especially documented by the reptilian faunas. So marked are the African affinities of the Campanian–Maastrichtian of southern Europe that Le Loeuff (1991) named the latter area 'Eurogondwana'. Le Loeuff did not define the limits of this region, but it is true that taxa that came from Africa did not extend in Laurasia beyond southern insular Europe.

Madtsoiid snakes display a broad Gondwanan range (Rage and Werner, 1999). Out of Gondwana, madtsoiids were found only in the Campanian of Spain, and perhaps France (Sigé et al., 1997; Rage, 1999), and in the Maastrichtian of Romania (Folie and Codrea, 2005). The European madtsoiids were immigrants from Africa that reached Europe probably during the Late Cretaceous.

The bothremydid littoral or continental turtles were present in the latest Cretaceous of South America, Africa, and Europe (Campanian–Maastrichtian of southern France) (de Lapparent de Broin and Murelaga, 1996; de Lapparent de Broin, 2000). Their occurrence in Africa, and probably South America, during the Early Cretaceous strongly argues for a West Gondwanan origin of the family. The podocnemidid turtles from Southern France certainly result from a dispersal from Africa. de Broin (1988) noted that the European forms appear to be related to podocnemidids from the Early Cretaceous of Africa. Therefore, keeping in mind that the pre-Campanian Late Cretaceous of Europe is poorly known, this dispersal from Africa cannot be dated precisely; but, we presume that, as with the madtsoiids and bothremydids, they reached Europe during the Late Cretaceous.

Possible trematochampsid crocodiles were reported from Campanian–Maastrichtian beds of southern France and perhaps the Campanian of Spain (Buscalioni et al., 1999). Because *Trematochampsa* is present in the Late Cretaceous of Africa (see above), Buffetaut (1980) and Le Loeuff (1991) hinted at interchanges between southern Europe and Africa, implicitly from the south to the north. Although relationships of the European forms were questioned by Buscalioni et al. (1999), such interchanges cannot be definitively rejected.

According to Buffetaut et al. (1988), abelisaurid dinosaurs were present in the Campanian and Maastrichtian of southern France. But Allain and Pereda Suberbiola (2003) questioned this referral; however, they suggested that Abelisauroidea may be present. If that is the case, the Late Cretaceous abelisauroid(s) of Europe would be locally derived from older European taxa such as *Genusaurus* (see above). Apparently, abelisaurids did not take part in Late Cretaceous interchanges between Africa and Europe.

Characid fishes from the Late Cretaceous of Transylvania, Romania, have also been mentioned in support of Late Cretaceous trans-Tethyan dispersals (Grigorescu et al., 1985).

On the basis of the mammals known in the Paleogene of Africa, Gheerbrant (1987, 1990, 2001) inferred that a series of dispersal events (Dispersal Phases or DPs) occurred between Laurasia and Africa before the closure of the Tethys. The mammalian lineages involved in these Dispersal Phases are described below (Section 3.2.5) and listed in Table 4b (see also Section 3.1.2.). It should be noted that non-mammalian taxa are not included in these Dispersal Phases because they do not provide sufficiently precise biostratigraphic information (i.e., events that affected them are not as precisely dated as for mammals). These Dispersal Phases were either uni- or bidirectional (southward *and* northward). The earliest Dispersal Phase was unidirectional, from Euramerica or Europe to Africa, and took place during the Late Cretaceous or earliest Paleocene. It resulted in the establishment of the remarkable earliest African Faunal Stratum (Late Cretaceous/Early Paleocene AFS) described above (Section 3.1.2. and Table 3). In fact, it cannot be excluded that this earliest DP included several phases (and resulted in several AFS) that cannot be discriminated (see Section 3.2.6).

3.2.5. Paleogene

Milner et al. (2000) supposed that ranid frogs originated in Africa and crossed the Tethys area during the Eocene. But the identification of the center of origin of the family remains highly hypothetical (Bossuyt and Milinkovitch, 2001), and ranids cannot be regarded with confidence as trans-Tethyan immigrants during the Paleogene. More convincing information is provided by podocnemidid turtles. Representatives of the *Erymnochelys–Neochelys* group occur throughout the Eocene of western Europe and in the Late Eocene of Egypt (de

Table 4b
Successive dispersal phases of placental and marsupial mammals between Africa and Laurasia

	Africa		Laurasia	References
Priabonian/Rupelian Dispersal Phase	*Apterodon*	>>>	*Apterodon gaudryi*	Gheerbrant, 2001, this work
	Priab.–Rup. AFS?*	<<<	Laurasiatic stem groups*	
Bartonian/Priabonian Dispersal Phase	Bart.–Priab. AFS*	<<<	Laurasiatic stem groups*	Gheerbrant, 2001, this work
Lutetian/Bartonian Dispersal Phase?	Anthropoidea?	>>>	Amphipithecidae	Gheerbrant, 2001, this work
	Lut.–Bart. AFS?*	<<<	Laurasiatic stem groups*	
Ypresian/Lutetian Dispersal Phase?	*Garatherium*, Proboscidea, Anthropoidea?	>>>	*Garatherium*? (Turkey), Proboscidea (Turkey), Eosimiidae? (Asia)	Gheerbrant, 2001, this work
	Anomaluroidea	<<?>>	Anomaluroidea (S. Asia)	
	No confirmed southward dispersal known			
Thanetian/Ypresian Dispersal Phase	Hyaenodontidae	>>>	Hyaenodontidae	Gheerbrant, 1987, 1990, 2001, this work
	Than.–Ypr. AFS*	<<<	Laurasiatic stem groups*	
Thanetian Dispersal Phase	*Aboletylestes* ?	>>>	*Aboletylestes*	Gheerbrant, 1987, 1990, 2001, this work
	Than. AFS*	<<<	Laurasiatic stem groups*	
Late Cretaceous–early Paleocene Dispersal Phase	No northward dispersal known			Gheerbrant, 1987, 1990, 2001, this work
	l. Cret.–e. Pal. AFS*	<<<	Laurasiatic stem groups*	

Taxa involved in northern dispersals are listed on the first line(s) of each Dispersal Phase. Taxa involved in southward dispersals (African lineages and their Laurasiatic stem groups) are listed in second line and are marked by an asterisk. See Table 3 and Section 3.1.2. about African Faunal Strata (= AFS) and their stem groups, and Section 3.2.5 about Dispersal Phases. Note that the direction of the dispersal of the anomaluroid rodents remains uncertain. e.: early; l.: late; Bart.: Bartonian; Cret.: Cretaceous; Lut.: Lutetian; Pal.: Paleocene; Priab.: Priabonian; Rup.: Rupelian; Than.: Thanetian; Ypr.: Ypresian.

Broin, 1988). They are probably evidence of dispersals between Africa and Europe (Table 4a). Similarly, ziphodont crocodiles, whatever their exact taxonomic relationships, likely crossed the Tethys from Africa to Europe (Buffetaut, 1988).

As far as mammals are concerned, the history of trans-Tethyan Paleogene dispersals is more precisely known (Gheerbrant, 1987, 1990, 2001). Four to six Dispersal Phases of placentals and marsupials took place between Africa and Laurasia during Paleogene times: during the Early Thanetian, and by the Thanetian/Ypresian, Ypresian/Lutetian?, Lutetian/Bartonian?, Bartonian/Priabonian, and Priabonian/Rupelian transitions (Table 4b). An additional earlier Dispersal Phase occurred at Late Cretaceous or earliest Paleocene (earliest DP known for placentals).

- Late Cretaceous/Early Paleocene DP. This is a southward DP (see Section 3.2.4.). It is not illustrated by northward dispersals, but only by the immigrations that correspond to the earliest AFS described above. This DP includes the old African placental stock (paenungulates, tenrecoidean insectivores, primitive "insectivores" such as cimolestids and todralestids, and hyaenodontid creodonts; Table 3).
- Thanetian DP. This probably bidirectional, but mostly southward DP might account for an African origin of *Aboletylestes* that was reported from Walbeck (Europe, Paleocene) (Table 4b). It is also at the origin of the Thanetian AFS (Table 3) that did not evolve subsequently in Africa, i.e., the Thanetian immigrant taxa known in Africa apparently did not survive the Paleocene. The Thanetian DP implies trans-Tethyan relations of Africa with mainly Euramerica and Europe.
- Thanetian/Ypresian DP. It accounts especially for the African origin of Laurasian hyaenodontid creodonts (Gheerbrant et al., 2006), but also for the Laurasian origin of the important Thanetian/Ypresian AFS (see above Section 3.1.2 and Table 3). The Thanetian/Ypresian DP illustrates trans-Tethyan relations of Africa with Europe and perhaps Asia.
- Ypresian/Lutetian DP? A Dispersal Phase seems to have occurred by the Ypresian/Lutetian transition, but it is minor and of uncertain age. It is postulated for some remarkable trans-Tethyan lineages. The presence of both the lipotyphlan *Garatherium* (Kappelman et al., 1996) and of the unnamed proboscidean from Kartal, Turkey (Maas et al., 1998), and perhaps also that of the eosiimids in China (if anthropoids are of African origin; an alternative Asian origin is also possible in light of recent discoveries, e.g., Thanetian–Ypresian AFS), are related to this DP. The occurrence of anomaluroid rodents in the latest Middle Eocene of Myanmar also indicates interchange between Asia and Africa (Marivaux et al., 2005); if the age is correct, the dispersal is referable to this DP and it is possibly of African origin. No southward dispersals were involved in this DP; consequently, there is no associated AFS in Africa (i.e., there is no known immigration of mammals in Africa evidenced at the beginning of the Lutetian). The Ypresian/Lutetian DP? would involve relations with Southeastern Europe and Asia.
- Lutetian/Bartonian DP? Another doubtful, minor DP perhaps took place by the Lutetian/Bartonian transition. It might explain the dispersal of amphipithecids from Africa to Laurasia, if they are descendants of propliopithecids which is questionable (they might be alternatively direct descendants of eosimiids). In Africa, a minor, questionable AFS might have resulted from this possible DP. The Lutetian/Bartonian DP? would have taken place between Africa and both Europe and Asia.
- Bartonian/Priabonian DP. This Dispersal Phase is only southward; it accounts for the establishment of a significant AFS in Africa, which is illustrated especially by anthracotheres (Section 3.1.2 and Table 3). Both Europe and Asia were involved in this DP.
- Priabonian/Rupelian DP. The last DP took place by the Priabonian/Rupelian boundary; it is exemplified by the immigration into Europe of *Apterodon* and by a somewhat doubtful AFS in Africa. However it cannot be excluded that the newcomers recorded in the Early Oligocene of Africa (Table 3) might be issued from an earlier immigration (Section 3.1.2.). The Priabonian/Rupelian DP involved trans-Tethyan relations with Europe and possibly Asia.

In Africa, as shown by the above DPs, Laurasian affinities of mammalian faunas appear to have been first with Euroamerican and European faunas (the three older DPs, including those of possible Late Cretaceous age) and then with southeast European and Asiatic faunas (the two to four other DPs).

3.2.6. The trans-Tethyan route(s) (Fig. 3)

The above-listed interchanges demonstrate that a link was present between Africa and Laurasia. This is in agreement with paleogeographic reconstructions that show that a connection area, the Mediterranean Tethyan Sill, has stretched between Africa and western Eurasia

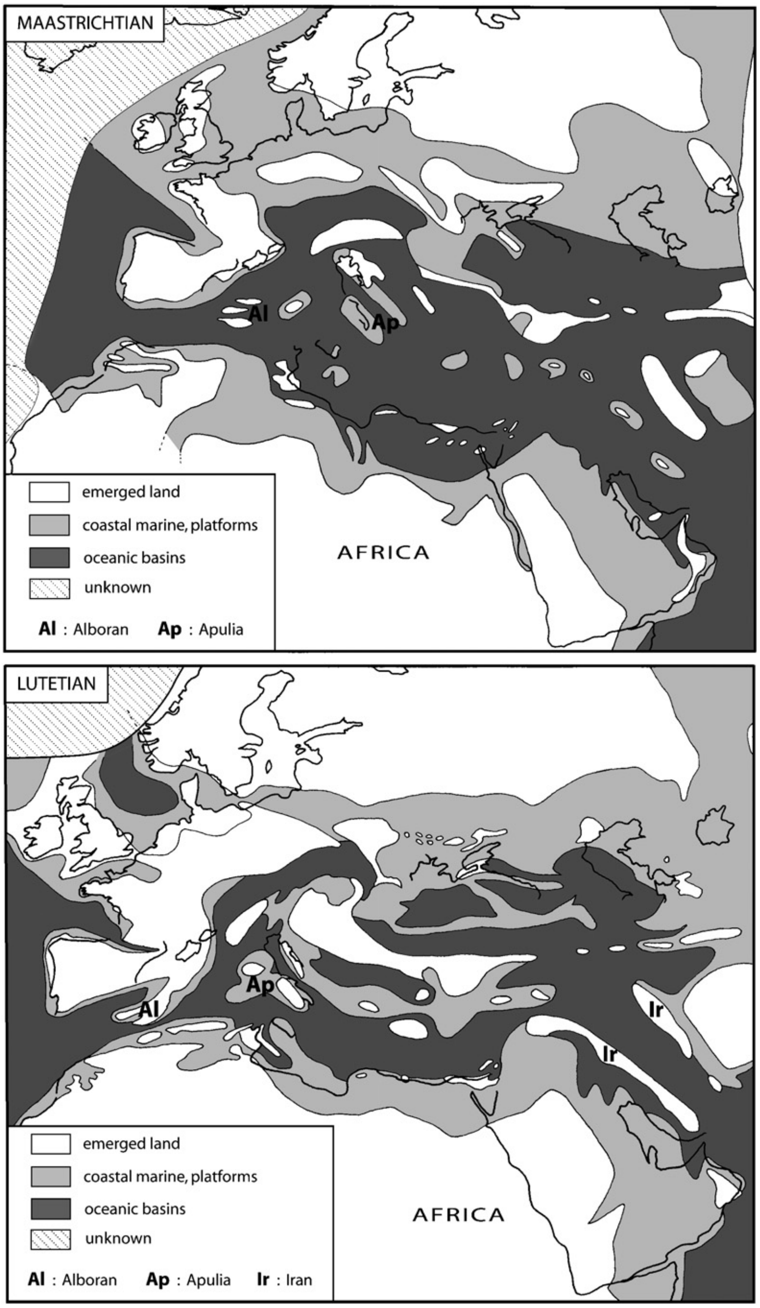


Fig. 3. Paleogeographical reconstruction of the Mediterranean Tethyan Sill at Maastrichtian and Lutetian times (from Dercourt et al., 2000; simplified).

from the Jurassic onward (Vrielynck et al., 1995) (Fig. 3). This Sill was not a true land bridge, but it included a series of emergent platforms that made up transitory, discontinuous land routes. These connections acted as selective filter routes controlled by sea-level changes during the Cretaceous and Paleogene (and Late Jurassic?). The recognized DPs are more or less well correlated with sea-level falls (Fig. 4). The poorly understood Late Cretaceous/Early Paleocene DP that could possibly correspond to several phases, might be correlated with several sea-level falls. Major sea-level falls (second order supercycles of Haq et al., 1987) are especially related to the Early Thanetian DP (base of supercycle TA2, by 59 Ma), the Bartonian/Priabonian

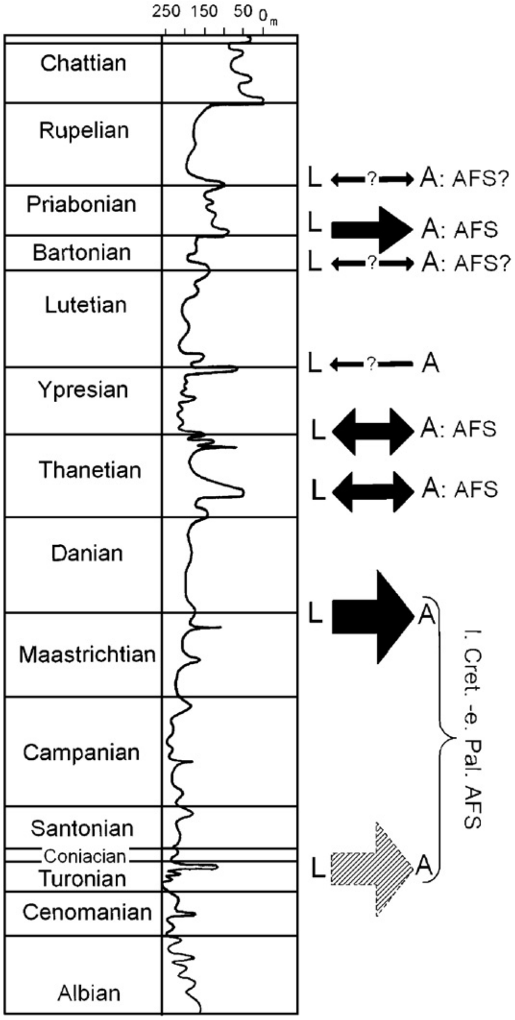


Fig. 4. Correlation between the Dispersal Phases and African Faunal Strata (arrows) of African mammals and major sea-level falls recorded in the eustatic curve of Hallam (1992). Arrows are bi- or unidirectional according to the directions of the dispersals involved in each phase. The thickness of each arrow is proportional to the importance of the Dispersal Phases (i.e., number of involved trans-Tethyan lineages). The Late Cretaceous–Early Paleocene AFS is poorly resolved; it could actually correspond to several dispersal events, of unknown number and ages, spanning the Late Cretaceous–Early Paleocene period. L: Laurasia; A: Arabo-Africa.

DP (base of supercycle TA4, by 37 Ma) and the Late Cretaceous/Early Paleocene DP (at least by the Cretaceous/Tertiary boundary, i.e., the base of supercycle TA1, by 65 Ma). However, other DPs are apparently not coeval with major eustatic events. For example, the Lutetian/Bartonian DP? and Priabonian/Rupelian DP do not correspond to a significant known sea-level fall (e.g., Fig. 4). There is also no major sea-level falls of second order supercycles correlated to the uncertain Ypresian/Lutetian DP and to the prominent Thanetian/Ypresian DP. The Ypresian/Lutetian DP corresponds to a sea-level fall of third order cycle, which however is important (but local?) in Hallam's curve (1992; see Fig. 4); the Thanetian/Ypresian DP does not correspond to an important sea level fall, either of second or third order cycle.

The trans-Tethyan dispersal route first occupied a western place on the Sill — the Alboran and Apulian routes — but, by the Middle Eocene, a second, eastern route — the Iranian route (Gheerbrant, 2001) — occurred on the Iranian block and Arabian Peninsula (Fig. 3). The formation of an eastern trans-Tethyan dispersal route by Middle Eocene times is probably directly related to the progressive closing of the Tethys in the Middle East area, which is consistent with the paleogeographic evolution of the Mediterranean Tethyan Sill as reconstructed by Vrielynck et al. (1995). The Iranian route may indeed have acted as early as the Lutetian, as documented by both paleogeographical (Vrielynck, pers. com. to EG) and paleobiogeographical data (Gheerbrant, 2001; Marivaux et al., 2005). It may explain the early radiation of primitive anthropoids in both Africa and Asia. The Iranian route was the filtering precursor of the definitive connection between Eurasia and Africa.

3.2.7. Summary

Although the above list of taxa that crossed the Tethyan barrier is likely not exhaustive, it clearly shows that interchanges between Africa and Laurasia were not accidental and minor events. They were even more frequent and they affected more taxa than those that took place between Africa and other Gondwanan continents after the Jurassic (Fig. 1). Nevertheless, interchanges between Africa and Eurasia were primarily limited and filtered dispersals.

During the Early Cretaceous, most dispersals apparently took place from the north to Africa. But during the latest Cretaceous (the Cenomanian–Santonian interval is very poorly documented), reptiles from Africa entered southern insular Europe ('Eurogondwana'). The earliest African placental mammals resulted from a dispersal from Laurasia to Africa during the Late Cretaceous or earliest Paleocene. During the Paleogene, several waves of interchanges occurred in both directions, but southward dispersals apparently predominated (Tables 3 and 4b).

More precisely, five to seven trans-Tethyan mammalian Dispersal Phases have been evidenced from the Late Cretaceous to the Eocene/Oligocene boundary (Table 4b). Two of them are doubtful (Ypresian/Lutetian DP? and Lutetian/Bartonian DP?). Three were prominent in terms of numbers of involved taxa: Late Cretaceous/Early Paleocene DP (resulting in the major AFS), Thanetian/Ypresian DP (important AFS), and probably Bartonian/Priabonian DP (significant AFS). The Early Thanetian DP was also significant, although it resulted in an apparently unsuccessful AFS. Major sea-level falls correlate with important DPs by Cretaceous/Paleocene boundary, Early Thanetian, and Bartonian/Priabonian boundary.

It should be emphasized that, aside from a few exceptions, the various groups of Laurasian origins that entered Africa during the Cretaceous and Paleogene did not reach other Gondwanan continents during that period. The only exceptions are some “out-of-Africa” dispersals of mammals toward Madagascar and South America during the Paleogene (see above 2.2).

4. Conclusions

Africa appears to have been the first continent that became isolated in the breakup of Gondwana. The last link that connected Africa to another continent (i.e., South America) was severed by Mid-Cretaceous times (Albian–Aptian); a continuous, terrestrial contact with another continent (i.e., Eurasia, as a part of Laurasia), was not established until the Early Miocene in the Middle East area. Between these two events — a span of at least 75 million years — Africa was isolated. An African faunal province was perhaps already in existence before Africa separated from South America. This is suggested by the presence of endemic mammals (Hahnodontidae multituberculates) in the earliest Cretaceous of Africa, by Late Jurassic and earliest Cretaceous African mammals (Peramuridae, Boreosphenida) that did not reach South America, and by the absence of Australosphenida in Africa.

Isolation was broken intermittently by the establishment of discontinuous, filter routes that linked Africa to other continents. These filters permitted rare interchanges between Africa and some other Gondwanan continents (Madagascar, South America, and perhaps India), but mainly between Africa and Laurasian areas. Interchanges with other Gondwanan continents were nearly all “out-of-Africa” dispersals, while interchanges with Laurasia were bidirectional, although for mammals this was mostly towards Africa.

During isolation, Africa was inhabited by vicariant taxa descended from the former West Gondwanan stock (freshwater fishes, reptiles, perhaps rare mammals such as triconodonts, dryolestoids, and ?sudamericids) that may be regarded as autochthonous or “native” African taxa after the vicariant event, and by some immigrants that succeeded in reaching the continent. Most immigrants, perhaps all identified taxa, came from Laurasia. Thus, at least from a paleobiological point of view, after separation from South America, Africa was more strongly related to Laurasia than to any Gondwanan continent.

Dispersals from Laurasia appear to have reached Africa as early as the earliest Cretaceous, perhaps the Late Jurassic — i.e., nearly by the time of the completion of the Tethys between Laurasia and Gondwana. Except for a proboscidean (Late Oligocene; Antoine et al., 2003), all confirmed trans-Tethyan dispersals took place before the Eocene/Oligocene transition at the latest. Immigrants of Laurasian origin that reached Africa were mainly mammals, and perhaps only mammals during the Paleogene. Aside from rare exceptions, Laurasian immigrants that entered Africa did not subsequently disperse into other Gondwanan continents, except after the closure of the Tethys (e.g., Proboscidea reaching South America). Trans-Tethyan dispersals from Africa to Laurasia were less numerous; they comprised only non-mammalian taxa, mainly reptiles, during the Cretaceous and, apart from rare, but unconfirmed cases, they included only mammals during the Paleogene.

The native Cretaceous African mammals (African dryolestoids and triconodonts) died out before the Paleocene while the history of non-mammalian natives remains poorly known after the Cretaceous.

Despite occasional Cretaceous and Paleogene immigrations, the geographic isolation of Africa was prominent; it resulted in a strong endemicity. Kielan-Jaworowska et al. (2004) noted that the fauna from the earliest Cretaceous of Anoual (Morocco) is marked by a high degree of endemicity but that it nevertheless includes some immigrants. This remark may be extended to the whole Late Cretaceous–Paleogene faunas of Africa.

Another consequence of isolation was the absence, in Africa, of several taxa that widely spread on other continents, including Gondwanan taxa. During the Late Cretaceous–Paleogene interval, Africa was apparently poorly populated, the faunal diversity was low, and ecological niches were free (contrary to other continental provinces), perhaps as a result of the Mid-Cretaceous environmental stress that affected African faunas (Russell and Paesler, 2003). This may account for the success of various mammal groups that came from Laurasia and took roots in Africa, forming there successive ‘African Faunal Strata’ (AFS). All successful and typical African radiations have arisen from these AFSs. Even major, old African clades such as

Paenungulata or the still controversial Afrotheria, originated from Laurasian stem groups. Africa appears to have been an important continental center of origin, a cradle in which a number of major placental clades originated and radiated after arriving from Laurasia. Once in Africa, the opportunities of a favorable environment after the Mid-Cretaceous, including weak competition, promoted the evolution and radiation of endemic lineages.

The success of placental immigrants is a characteristic of the paleobiogeographic history of Africa. Striking African radiations notably include creodonts, hyracoids, and anthropoids; for instance, Paleogene hyracoids show a remarkable diversity and specializations that rival those of several Laurasian ungulate orders. At a larger scale, Africa was at the source of nearly one third of the modern orders of placentals (Tubulidentata, Macroscelidea, Hyracoidea, Sirenia?, Proboscidea, Tenrecoidea), as well as other important extant groups such as anthropoid and possibly strepsirhine primates. The role of Africa, between Gondwana and Laurasia, has been certainly underestimated.

Theoretically, when an isolated area with an endemic fauna contacts a region of less endemism, the former fauna suffers more extinctions. After the establishment of a continuous terrestrial route between Africa and Eurasia during the Early Miocene, the African faunas did not suffer extinctions of major mammalian clades. Several taxa such as anthropoids and proboscideans even diversified widely during the Neogene, spreading out of Africa, and thriving on other continents. This remarkable phenomenon would deserve further examination (for example, by comparison with the history of South America).

As shown by biogeographical relationships, during the period of physical isolation, discontinuous and intermittent routes connected Africa more closely to Laurasia than to other Gondwanan continents. This resulted from the fact that the Mediterranean Tethyan Sill formed a broad, although discontinuous terrestrial route between Africa and Laurasia, while the connections with Gondwanan continents were much more incidental. The Mediterranean Sill was efficient when the sea-level was low; between Africa and Eurasia, it permitted several phases of interchanges that range from the earliest Cretaceous (perhaps the Late Jurassic) to at least the Eocene/Oligocene transition, before the establishment of the definitive contact. It should be noted that the Mediterranean Sill began to permit interchanges between Africa and Laurasia when Africa was still linked to South America (i.e., at the time of the West Gondwanan province).

Trans-Tethyan dispersals first took place between southwestern Europe and Africa on the Alboran and Apulian routes, but, by the Middle Eocene, a second, more eastern route developed — the Iranian route — that involved southeastern Europe and southwestern Asia. The Iranian route appears as the discontinuous forerunner of the definitive connection between Africa and Eurasia.

Finally, the present geographic configuration probably began to take shape as early as the Mid-Cretaceous; at that time the last links between Africa and other Gondwanan continents began to rapidly vanish, while Africa was already connected to Eurasia by a relatively effective (although intermittent) terrestrial route.

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