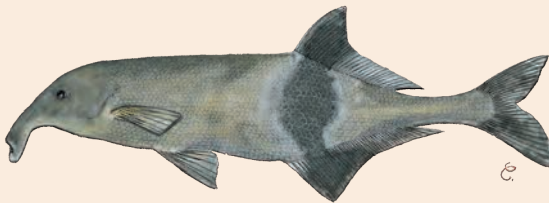


Biogeography and past history of ichthyological faunas

CHRISTIAN
LÉVÊQUE

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Lichthyological faunas established themselves and evolved as a consequence of the history of the aquatic systems they occupy. At various timescales, certain basins were colonized from other basins, and such colonizations were sometimes followed by selective extinctions resulting from geological and/or climatic events. The genesis and continued existence of aquatic habitats depend on two main factors: their morphology, which may change over the long term as a result of erosion or tectonics; and their hydrologic budget, which is dependent on precipitation, evaporation, infiltration, and for which slight changes may lead in the short or medium-term to either the drying out or expansion of the aquatic milieu in question, depending on the basin's shape. Simultaneously, some species were able to give rise to others, and these speciation events often explain the presence of centres of endemism.

Biogeography is the discipline that seeks to explain the distribution of organisms and the relationships between the areas of distribution of different species, by attempting to reconstruct the series of events that led to the present situation. To describe the relationships between the establishment of faunas and the spatio-temporal history of the physical systems, scientists need to draw up the most exhaustive inventories possible for different regions.

How do fish disperse?

Given that the large majority of fishes cannot tolerate exundation, the colonization of new habitats is made possible by the existence of connections between basins. Even if hydrographic systems are currently isolated, such connections may have existed in the past, allowing faunistic exchanges.

Connections between river basins

The great similarity between the faunas of the Nile and Chad Basins is undoubtedly the result of connections that existed between the two basins during a humid period that is difficult to date (Lévêque, 1997a). Meanwhile, a connection still exists between the Chad and Niger basins. When water levels are high, some of the waters of the Logone, a tributary of the Chari, spill westward into the Mayo-Kebi depression, cross the Gauthiot falls, and empty into the Benue, a tributary of the Niger River.

The regressive erosion that led to the capture of certain watercourses was probably the most important means of interbasin exchanges for “primary” fishes. Indeed, there are several known examples of river captures in Africa, and this phenomenon must have been rather common even if it did not always leave identifiable traces. The Boucle du Baoulé, a tributary of the Senegal in Mali, resulted from the capture of the Baoulé – formerly a tributary of the Niger – by a small tributary of the Bakoye, in turn also a tributary of the Senegal (Michel, 1973). The history of the Zambezi is particularly complex, marked by many changes in its course as well as captures that are at the origin of the present-day basin (Skelton, 1994; Thomas & Shaw, 1988).

Certain fish species were also able to colonize other basins using connections that were created via estuaries. As Sydenham (1977) notes, the Ogun River is connected to the Niger by a fine network of lagoons that stretch from Benin to the Niger delta. When several rivers empty into closed lagoons, as is the case on the West African coast, the large drop in salinity that occurs temporarily when water levels are high renders possible the circulation of species that are usually salt-intolerant.

Other means of dispersal

The distribution of a few species could also be explained by variations in seawater levels that led to changes in coastal zones. For example, Bioko island (formerly Fernando Poo), now separated from Africa by a 60-metre-deep narrow sea channel, hosts identical – though more limited – fauna as the continent facing it. Some 18,000 years ago, when the sea level was 110 m lower than today, there was apparently a connection between hydrologic systems, and the island’s current fauna was isolated when the sea level rose (Thys van den Audenaerde, 1967).

It has been suggested several times that birds and mammals could transport fishes from one site to another. Although this has never been truly proved, the resistant eggs of certain Cyprinodontiformes living in temporary ponds can probably be transported by different animals (birds, mammals), in their feet, fur, or feathers. In the same way, some cases of fishes being transported during tornadoes have been reported, and these events are known as “rains of fishes”.

Falls as zoogeographical barriers

Depending on their size, waterfalls can represent impassable barriers for fishes, such that isolated populations upstream remain protected from any competitors. This situation can explain the existence of endemic species in

higher courses, as shown by Daget (1962b) in some watercourses in Guinea. Waterfalls allow species to move downstream, but not upstream (table 6.I). Another example is of the Gauthiot falls on Mayo-Kebi, which connects the Chad basin to the Niger basin. In this case, all the species of the Logone are present in the Benue, and there is no endemic species in the Chad basin. On the other hand, Niger species (*Cromeria nilotica*, *Arius gigas*, *Synodontis ocellifer*, *Citharidium ansorgii*, etc.) that are present in the Benue have never been observed in the Chad basin, as they are unable to pass the Gauthiot falls (Daget, 1988a). A comparable situation can also be seen with the Murchinson rapids on the Shire River connecting Lake Malawi to the Zambezi, which prevent species from the Zambezi's lower watercourses to climb back into Lake Malawi (Banister & Clarke, 1980).

TABLE 6.I

Number of fish species upstream and downstream of falls in upper reaches of the Niger River (Tinkisso) and of the Senegal River (Bafing) in the Fouta-Djalou, Guinea (from Daget, 1962b).

	Tinkisso downstream	Tinkisso upstream	Bafing downstream	Bafing upstream
Mormyridae	1	0	1	0
Alestidae	1	0	0	0
Distichodontidae	3	0	0	0
Cyprinidae	6	3	11	10
Bagridae + Claroteidae	1	0	0	0
Schilbeidae	1	0	0	0
Amphiliidae	0	1	2	1
Clariidae	0	0	2	0
Mochokidae	2	2	2	0
Cyprinodontiformes	2	1	3	2
Cichlidae	2	1	3	1
Eleotridae	0	0	2	2
Total	19	8	26	16

What do we learn with fossils?

African fish fossil remains are scarce and unevenly distributed geographically (with most information coming from the Nile valley.) The information that can be gleaned from investigating the evolution and distribution of species is thus limited, especially considering that the identification of fossil remains rarely goes beyond genus level.

A few major findings should nonetheless be underscored. In particular, the oldest fossils found belong to the genera *Protopterus* and *Polypterus*, both considered very ancient. Fossil remains of *Lates* were also found in sediments from the basins of lakes Victoria and Edward, from which the species had disappeared until its recent reintroduction.

African Alestidae also accounted for a few fossils, most of which were found in deposits from the end of the tertiary (Miocene, Pliocene) or the start of the Quaternary (Upper Pleistocene) (White, 1937; Greenwood, 1972; Greenwood & Howes, 1975). In France, however, in deposits from the lower Tertiary (Eocene) of the Paris and Languedoc basins, several ancient teeth related to the genus *Alestes s.lat.* (Cappetta *et al.*, 1972) were found, which suggests that a tropical fauna could have existed in that latitude and at that time period. As for the Characiformes, while there are no fossil remains, it can be estimated that in the Mesozoic, there were two sub-families, the Characinae (*Alestes junneri*) and the Sarrasalminae (*Sindacharax deserti*, *S. lepersonnei*). The latter went extinct fairly rapidly, while the Characinae continued to evolve, giving rise, among others, to the modern genera *Alestes* and *Brycinus* (Paugy, 1986) (see also chapter *African fossil fish*).

Biogeographical scenario for northern tropical Africa

At the beginning of the Miocene, approximately 20 million years ago, a rather uniform ichthyofauna occupied tropical and subtropical Africa. Some taxa with large distributions in tropical Africa are probably witnesses of this period when the interconnection between drainage basins was probably more extensive: *Schilbe mystus*, *Clarias gariepinus*, *Hydrocynus vittatus*, *Brycinus macrolepidotus*, *Hepsetus odoe*, *Coptodon zillii*, *Sarotherodon galilaeus*. The tectonic events of the Miocene period modified the hydrographic system. One of the major events was the formation of the Rift Valley some 15 million years ago, which resulted in the rise of mountain ranges and the isolation of formerly connected aquatic basins. In West Africa, also during the Miocene, tectonic movements caused the uplift of Fouta-Djalou and the Guinean ridge. Moreover, the Quaternary was a period of great climatic instability with numerous glaciations (21 cycles during the last 2.3 Myrs according to Hamilton, 1988), marked by arid periods in Africa, whereas the interglacial periods were more humid. It resulted in a succession of expansions and regressions of aquatic systems and extinction of fish populations (see box "Refuge zones theory").

The fish inventories carried out in north tropical Africa (Lévêque *et al.*, 1989, 1991; Paugy *et al.*, 1989, 1994; Teugels *et al.*, 1988, 1992) and the search for ichthyological provinces (Hugué & Lévêque, 1994; Paugy *et al.*, 1994) enabled the identification of three ichthyological provinces (Nilo-Sudan, Upper Guinea, Lower Guinea) as well as two large groups of fish species (Lévêque, 1997a):

- species that colonize most of the Nilo-Sudan basins and which, for the most part, are absent from the Congo basin;
- species that are essentially represented in the coastal basins of Upper and Lower Guinea, and which have many similarities with the Congo fauna.

The current Nilo-Sudanian fauna has a pan-African fauna origin that existed during the Pliocene (between 2 and 5 Myrs) when the Congo and Chad basins

REFUGE ZONES THEORY

The refuge zones theory was initially developed for forest environments (Haffer, 1982), then applied to organisms such as birds or fishes. It was based on the observation that the distribution of organisms is not solely explained by current ecological conditions, but is also accounted for by climate changes during the Quaternary, characterized by alternating dry and humid periods. This resulted in a series of extensions and regressions of the forest which, during dry periods, would only be confined to limited zones where forest species could survive. These refuge zones functioned as allopatric speciation centres from which species could recolonize new areas

when conditions became favourable once more. The dispersal rate varies depending on the species and if the last regression phase is not yet too old, some of the species still remain confined to the refuge zone or its neighbouring zones. These zones would then be characterized by a high degree of endemism. By analogy, this theory can be applied to aquatic organisms, given that forest refuge zones were apparently sufficiently humid to allow the existence of aquatic biotopes where fishes could survive. This, of course, does not preclude the possibility that other refuge zones such as lakes may have existed for fishes during dry periods.

were not isolated. In many respects, this fauna is close to the Congolese one. In another way, at an unspecified time, exchanges took place between the Nile and the Chad basin, whose fauna is very similar. However, the Chad basin is still in contact with the Niger via the Mayo-Kebi and the Niger itself was probably a refuge zone which served as a reservoir for the recolonization of the Senegal, Gambia, Bandama, Sassandra and Comoé, Volta and Ouémé basins, after long periods of aridity during which these rivers were partially dry. Studies of genetic variability of the populations of *Oreochromis niloticus* for example have indicated that this species drew its origins from the Nile basin and then dispersed into West and East Africa (Pouyaud & Agnès, 1995).

Species from the Upper and Lower Guinean provinces have different origins. The coastal basins of Upper Guinea were isolated from the Nilo-Sudanian basins during the Miocene with the uplift of the Guinean ridge and Fouta-Djalon, and several species are vicarious forms of Sudanian species. But another group of fishes colonized coastal rivers by northwards migration from the Congo basin, along the West African coast (figure 6.1). This colonization of the coastal basins occurred gradually and probably involved waves of migrations. The presence of species in common or that are very closely related between the Upper and Lower Guinean provinces, with affinities to Congolese fauna, support this shared origin. For example, *Ichthyborus quadrilineatus* of Upper Guinea is close to *I. monodi* of Lower Guinea and *I. ornatus* of the Congo basin. *Sarotherodon melanotheron* has a continuous distribution along the coast from the Democratic Republic of the Congo to Mauritania. Other species such as *Mormyrus tapirus*, *Marcusenius mento*, *Brienomyrus brachyistius* and *Mormyrops caballus* are present in the Upper and Lower Guinean provinces, and several other species are observed in a more or less sporadic way on the West African coast (Lévêque, 1997a).

According to palynological data (Maley, 1989), part of the provinces of Upper Guinea and Lower Guinea were forest refuge zones during the last dry periods (figure 6.2). They could also have served as refuge zones for fishes, which would explain the great wealth and endemism in these zones. Some observations also suggest that a refuge zone may have existed for fishes on the southern border of Ghana and Côte d'Ivoire.

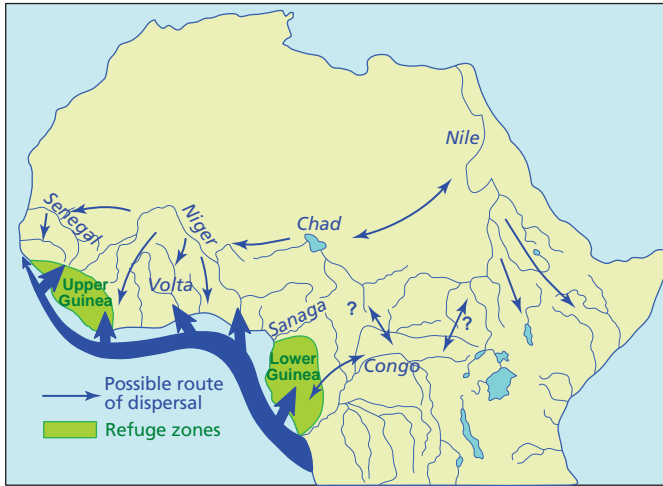


FIGURE 6.1.
Possible post-Miocene biogeographic scenario for fish assemblages of north tropical Africa (redrawn from Lévêque, 1997).

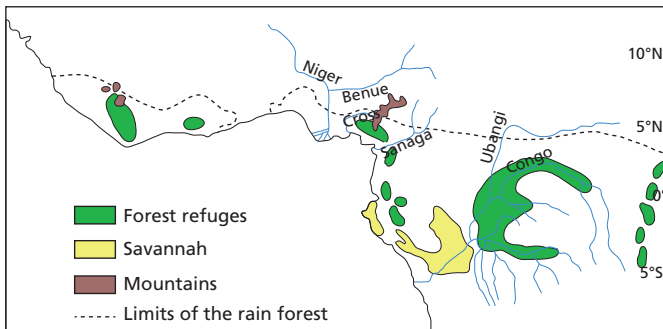


FIGURE 6.2.
Distribution of the main lowlands forest refuges in equatorial Africa during maximum of the last arid phase (about 18,000 years BP (from Maley, 1991). The modern conditions (forest boundary, included savannah) are adapted from White, 1983.

Biogeographical scenario for North Africa

At a more recent time period, the presence of ichthyological fauna with tropical affinities in the Sahara (see box "Fish of the Sahara: witnesses of a wetter past") is explained by climate fluctuations during the recent Quaternary (table 6.II). Once again, the presence of such fauna is accounted for by the existence of physical connections with basins in the south.

TABLE 6.II

Occurrence of fish species in different regions of the Sahara (from Lévêque, 1990).

1: Adrar (Mauritania); 2: Tunisia and South Algeria; 3: Hoggar; 4: Tassili N'Ajjer; 5: Ghat; 6: Tibesti; 7: Ennedi; 8: Borkou.

Regions	Adrar Mauritania	Tunisia and South Algeria	Ahaggar Algeria	Tassili Algeria	Ghat Libya	Tibesti Chad	Ennedi Chad	Borkou Chad
Polypteridae								
<i>Polypterus senegalus</i>								●
Cyprinidae								
<i>Barbus apleurogramma</i>							●	
<i>Barbus occidentalis</i>			●	●	●	●		
<i>Barbus callensis</i>	●		●			●	●	
<i>Barbus macrops</i>	●					●	●	
<i>Barbus pobeguini</i>	●							
<i>Labeo niloticus</i>						●		
<i>Labeo parvus</i>						●	●	
<i>Raiamas senegalensis</i>						●		
Clariidae								
<i>Clarias anguillaris</i>	●			●				
<i>Clarias gariepinus</i>				●		●	●	
Nothobranchiidae								
<i>Epiplatys spilargyreus</i>								●
Poeciliidae								
<i>Poropanchax normani</i>								●
Cichlidae								
<i>Hemichromis bimaculatus</i>		●		●			●	●
<i>Sarotherodon g. galilaeus</i>	●							
<i>Sarotherodon g. borkuanus</i>						●	●	●
<i>Coptodon zillii</i>		●	●	●		●	●	

The Maghreb province, found between the African and European tectonic plates, plays host to families with a tropical distribution (Cichlidae, Clariidae), and others of holarctic origin (Salmonidae, Cobitidae). For Doadrio (1994), three biogeographic zones can be distinguished in Africa (figure 6.3):

- the Atlantic zone in the north-west, characterized by the presence of Cyprinidae such as *Labeobarbus* and *Varicorhinus*, and Cobitidae;
- the Mediterranean zone characterized by the Cyprinidae *Pseudophoxinus* and *Barbus* s.s. as defined by Howes (1987), which are absent from the rest of Africa;
- the tropical zone in the east, including the artesian wells of the Sahara (see also chapter *Fish communities in small aquatic ecosystems: caves, gueltas, crater and salt lakes*), where one finds Cichlidae (*Haplochromis*, *Hemichromis*, tilapias) and Clariidae (*Clarias*).

According to Doadrio (1994), the North African region could have had connections with Asian faunas and the Iberian peninsula during the Cenozoic. The fish fauna is different from that of Europe, and the presence of African taxa that

are similar to Asian forms such as *Pseudophoxinus* and *Barbus s.s.* (*Barbus callensis* for example) could suggest an Asian connection during the Oligocene and (or) lower Miocene. Connections with the Iberian peninsula could be more recent and date back to the upper Miocene, when the Mediterranean dried up. Moreover, some species of the Iberian peninsula and Greece are closer, from a phylogenetic standpoint, to north African (*Barbus callensis*) and Asian species than to European *Barbus* species (Doadrio, 1990).

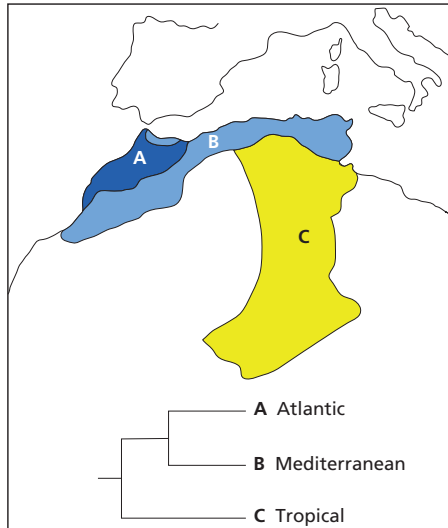


FIGURE 6.3.
Biogeographical zones in North Africa (redrawn from Doadrio, 1994).

The existence in North Africa of four endemic species from the genus *Labeobarbus*, similar to the large *Barbus* of West Africa, seems to argue in favour of an ancient origin with African roots for this genus.

FISH OF THE SAHARA: WITNESSES OF A WETTER PAST

Several tropical fish species have been collected in the ponds of central Sahara (Lévêque, 1990). The most varied fauna is found in the region of Borkou-Ennedi-Tibesti, similar to that found in the Nile and Chad basins (*Barbus bynni occidentalis*, *Barbus macrops*, *Labeo niloticus*, *Labeo parvus*, *Raiamas senegalensis*, *Clarias gariepinus*, *Hemichromis bimaculatus*, *Sarotherodon galilaeus*, *Coptodon zillii*). It has now been shown that during the first wet period of the Holocene, the Chad basin extended to the foot of the Ennedi-Tibesti, whose then-functional hydrographic systems emptied into the Chad (Talbot, 1980). The region's fauna is thus a remnant of the Chad basin's ichthyofauna which persisted in precarious conditions after the deterioration of the climatic situation. Populations were probably isolated around 5,000 to 6,000 years ago, which was not enough for them to become differentiated.

The much poorer fauna of the Hoggar is thought to be the relict of the Niger fauna, given that this part of the Sahara was well-irrigated during the Holocene by a dense network of rivers that have now dried out.

At the start of the Holocene there were even large tropical lakes in central Sahara (Riser & Petit Maire, 1986) and numerous fish fossil remains have been found (Daget, 1959b, 1961; Gayet, 1983). It appears that the poverty of modern ichthyological fauna is the result of a lack of sufficient aquatic habitats that could serve to a certain degree as refuge zones.

The presence of *Barbus pleurogramma* in the Ennedi is surprising, as this species is only known today in Lake Victoria and its tributaries. It is possible that it may be the relict of a more ancient fauna, some of whose representatives could have then disappeared from Nilo-Sudanian rivers.

Biogeographical scenario for Central Africa

The Congo basin, which covers approximately 4 million km², appears to have existed long before the Pleistocene. During the Mesozoic, it was invaded by marine water which left behind sediments and fossils. From the end of the Miocene to the beginning of the Pliocene, the Congo basin became endorheic and a large lake occupied the central basin. Then, before the beginning of the Pleistocene, the basin was captured (most probably in the area around Kinshasa or Brazzaville) by a coastal river flowing into the Atlantic and became the lower Congo. The marshy zones of the western half of the basin where lakes Tumba and Mai-Ndombe are located are possibly the remains of this large lake (Beadle, 1981).

At different periods, there were connections between the Congo basin and adjacent basins. As such, a tributary of the Nyong could have been captured by the Dja, a tributary of the Sangha River (Congo basin). There could also have been temporary and difficult-to-date connections with other coastal rivers of the 'Lower Guinea' province such as the Ogowe River, as well as with Angolan rivers (Cuanza, Cunene) by the Kasai River. Likewise, the Ivindo, the main tributary of the left bank of the Ogowe River, appears to have had been in contact with the Ntem River before being captured by the Ogowe River.

Interactions within the Chad basin may have taken place during very wet periods. Species such as *Coptodon zillii* and *Sarotherodon galilaeus* (Thys van den Audenaerde, 1963) or *Clarias albopunctatus* (Teugels, 1986) may have colonized the upper sections of the Chad basin via tributaries of the Ubangi River.

Biogeographical scenario for South Africa

The tropical freshwater dispersant fishes of East and Southern Africa comprise a similar assemblage of relatively low diversity. The fauna is dominated by barbin cyprinids with aplocheiloid killifishes and tilapine cichlids being notable elements of the East Coast and eastern Zambezian Rivers. A radiation of serranochromine cichlids highlights the Zambezian fauna. In the East Coast Province, centres of elevated biodiversity include the Ruaha basin and the north-Tanzanian coastal catchments.

Skelton (1994) provided a biogeographical scenario for South Africa based on a reconstructed history of hydrographic development (figure 6.4) and on the basis of the current distribution of species. The model proposes that the fauna developed in two main arenas (eastern and western) and that drainage development within these arenas resulted in modern day faunal composition.

At the beginning of the Tertiary period (stage a), three large hydrographical systems existed. The Western basin corresponded to the upper course of the

FIGURE 6.4.

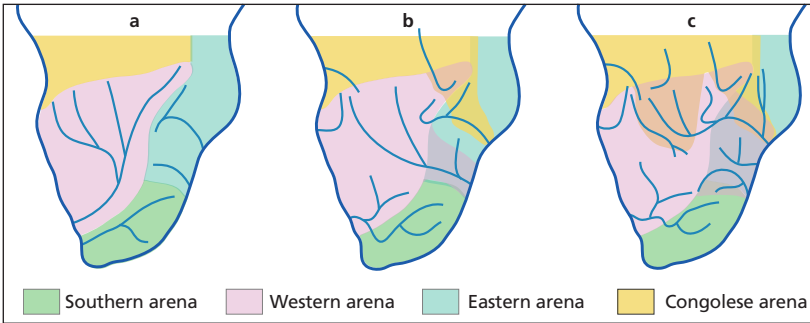
Biogeographic model for Zambezan freshwater dispersant fishes.

(a) Early Tertiary; (b) Mid-Tertiary; (c) Late Tertiary (redrawn from Skelton, 1994).

(a): in the early Tertiary the freshwater fish faunas of southern Africa became established in four evolutionary arenas;

(b): by the mid-Tertiary there were infusions of western and Congolese fauna into the eastern arena, and marginal infusions of Congolese and southern fauna into western arena;

(c): by the late Tertiary there was a second infusion of western fauna into the eastern arena and further infusion of Congolese fauna into the western arena. Minor faunal infusions occur along contact zones of the faunal arenas e.g. western/eastern elements into the southern arena (redrawn from Skelton, 1994).



Zambezi, Cunene, Kafue, and the Okavango basin, which were the tributaries of a river that at the time flowed southwards and discharged on the Western coast of Africa. Its mouth corresponded to the current mouth of the Orange River. The southern basin corresponded to the current upper course of the Orange River. The Eastern basin, which included the mid- and lower Zambezi, Limpopo and Shire River, was then in communication with the Congo basin until the formation of the Rift Valley lakes. Fauna of the Western, Southern and Eastern basins thereafter evolved independently for several million years and then differentiated.

During the mid-Tertiary Period (stage b) the Western basin was divided due to river captures and tectonic movements, and its course was diverted towards the east coast of the upstream reservoir whose fauna attests to its past connection with what is the current Limpopo basin. In the south, the hydrographical system of the Orange River was reconstructed by a merger with southern sections of the lower course of the precedent western basin, causing a mixture of fauna. Connections were also established between the Congo basin and the northern part of the eastern basin.

At the end of the Tertiary period (stage c), intrusions of species of the Congo basin were accentuated, even in the western sector. The capture of the upper Zambezi by the middle course of the Zambezi during the Plio-Pleistocene caused an extension of the western fish fauna towards the east, and an isolation of the Okavango basin which is currently endorheic. The Limpopo and Save basins separated in the eastern sector and their fish fauna is currently a mixture of Western and Eastern elements.

Madagascar

Madagascar's freshwater fish fauna contrasts with that of continental Africa (Sparks & Stiassny, 2003). Of a total of 135 native fish species, 84 are endemic to the island itself. Many new species have been described during the last decade and many more are awaiting identification.

The origin of the freshwater fish fauna remains unclear. The fish fauna is deprived of Cypriniformes, several Siluriformes as well as important Afro-Asian families such as Notopteridae, Anabantidae, and Channidae. Ancient groups such as *Polypterus*, *Protopterus* and Arapaimidae are also missing (De Rahm, 1996). Most of the species belong to widely distributed peripheral families. Many of the major groups of freshwater fish present in Africa, as well as those present in Africa and Asia (anabantids, bagrids, clariids, mastacembelids, notopterids, etc.), are absent in Madagascar (Stiassny & Raminosoa, 1994). Noteworthy is the absence of primary freshwater families such as the cyprinids, characins and mormyrids. Only three secondary freshwater families (Aplocheilidae, Cichlidae and Poeciliidae) have been recorded from the island. Many Malagasy species are phylogenetically basal within their respective families, and the ichthyofauna is apparently of relict nature.

The inclusion of Madagascar in the African region is hence mainly a function of geographical propinquity, as its ichthyofauna has more in common with those of Australasia and India than with those of mainland Africa.

Thus, the family Aplocheilidae and the cichlid subfamily Ectoplineae are common to Madagascar and India (Murphy & Collier, 1997; Stiassny *et al.*, 2001; Sparks, 2008). The remaining Malagasy cichlids have no obvious sister-group relationship to the family's currently recognized lineages and are regarded as the plesiomorphic sister-group of all other cichlids (Stiassny & Sparks, 2006). The sister taxa of the endemic atheriniform family Bedotiidae are the Australasian families Melanotaeniidae and Pseudomugilidae (Stiassny, 1990; Sparks & Smith, 2004). It cannot be decided on the basis of available evidence whether the closest relatives of the endemic siluriform family Anchariidae are to be found on the mainland of Africa or in India (Mo, 1991; Ng & Sparks, 2005). Madagascar's nominal *Pantanodon* species are the only freshwater fishes whose nearest relatives are of African provenance. In light of these data and given the generally recognized basal nature of Madagascar's endemic freshwater fishes, the island is clearly host to a relict Gondwanan ichthyofauna. Most of the island's freshwater fishes are diadromous or peripheral taxa, many of them widely distributed throughout the Indian Ocean region. The most mysterious aspect of the Malagasy ichthyofauna is the absence of lungfish and osteoglossoids. It is clear from the fossil record that both lineages were present on the Indo-Malagasy island prior to its scission in the late Cretaceous and it is difficult to envisage a scenario that would account for their selective extinction and the survival of the teleost lineages currently present on Madagascar. The absence of the lineages that dominate the ichthyofaunas of mainland Africa from Madagascar is most parsimoniously explained by their relatively recent invasion of Africa [Cyprinidae; Mastacembelidae; Anabantidae] or their absence from the region of Gondwana that ultimately gave rise to India, Madagascar and Australasia.

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