Geographical distribution and affinities of African freshwater fishes

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The present day composition and distribution of the fish fauna are the result of a long and complex history. They have been shaped by millions of years of changes in the global water cycle and the dynamics of freshwater systems. The dual processes of speciation and extinction have interacted with climatic and geological events that have isolated fish populations and/or provided opportunities for migrations and colonization of new habitats.

The understanding of the zoogeography of African fish has prompted several surveys since the beginning of the century. Ideas have evolved substantially according to progress made in regional inventories and taxonomic information (see chapter *General characteristics of ichthyological fauna*). However, some fundamental questions remain challenging. What are the driving factors responsible for the colonization of the continent and the differentiation of the fish fauna in several provinces (biogeography)? What are the affinities of the African ichthyofauna with the other continental faunas? Ichthyologists try to answer these and many other puzzling questions with unflagging pleasure!

Patterns of fish distribution and ichthyological provinces

At the continental level, African ichthyofauna is not distributed homogeneously and the current distribution is a result of:

• the climatic history and geological events that have shaped the current hydrographic systems. In the past, they permitted interconnections between river basins, as well as the temporary or permanent isolation of certain aquatic systems;

• the process of speciation which depends on the duration of hydrographic isolation and of the evolutionary potential of species;

• the ability of fish to disperse and the existence of refuge zones during drought period;

• the size of the catchment area and the diversity of aquatic habitats available for fish which subsequently determine the composition of the communities observed;

• the consequences of diseases that may have affected fish population, even if this type of impact is still very poorly documented.

TABLE 5.I

Presence/absence of families of fish in the African ichthyologic provinces (shown on figure 5.1) belonging to "primary" and "secondary groups ".
Abbreviations for provinces: Maghreb (Mag); Nilo Sudan (NS) including sectors Eburneo-Ghanaian (EG), nilotic (Nilo), Abyssinian (Aby); Upper Guinea (UG); Lower Guinea (LG); Congo (Con); Zambezi (Zam); Angola (Ang); Eastern coast (East); Ethiopian area (Ethio), including Ethiopian Rift Valley (ERV), Lake Tana (Tan), Coastal Red Sea (CRS) and Nilotic group (Nilo); Karroid (Kar); Cape (Cape); Madagascar (Mad).

Families	Mag	NS		UG	LG	Con	Zam	Ang	East	Ethio				Kar	Cape	Mad
		EG	*Nilo*							*ERV*	*CRS*	*Tan*	*Nilo*			
Protopteridae		●	●	●	●	●	●		●				●			
Polypteridae		●	●	●	●	●							●			
Denticipidae					●											
Arapaimidae			●		●								●			
Pantodontidae					●	●										
Notopteridae		●	●	●	●	●										
Mormyridae		●	●	●	●	●	●	●	●				●			
Gymnarchidae			●										●			
Kneriidae			●		●	●	●	●								
Phractolemidae					●	●										
Hepsetidae		●	●	●	●	●	●	●	●							
Alestidae		●	●	●	●	●	●	●	●				●			
Distichodontidae		●	●	●	●	●	●	●	●				●			
Citharinidae		●	●		●	●			●				●			
Cyprinidae	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	
Cobitidae	●															
Balitoridae												●	●			
Bagridae		●	●	●	●	●	●	●	●				●			
Claroteidae		●	●	●	●	●	●	●	●				●			
Auchenoglanididae		●	●	●	●	●	●	●	●				●			
Austroglanididae														●	●	
Schilbeidae		●	●	●	●	●	●	●	●				●			
Amphiliidae		●	●	●	●	●	●	●	●				●			
Clariidae	●	●	●	●	●	●	●	●	●	●		●	●	●		
Malapteruridae		●	●	●	●	●	●						●			
Mochokidae		●	●	●	●	●	●	●	●				●			
Cyprinodontiformes	●	●	●	●	●	●	●	●	●	●	●		●			●
Bedotidae																●
Channidae		●	●	●	●	●										
Latidae			●			●							●			
Synbranchidae				●												
Nandidae		●		●	●											
Cichlidae	●	●	●	●	●	●	●	●	●	●	●	●	●	●		●
Anabantidae		●	●	●	●	●	●		●					●	●	
Mastacembelidae		●	●	●	●	●	●	●	●							
Tatraodontidae		●	●		●	●							●			
Number of families	**5**	**24**	**27**	**23**	**29**	**27**	**19**	**16**	**18**	**4**	**3**	**4**	**22**	**5**	**3**	**3**

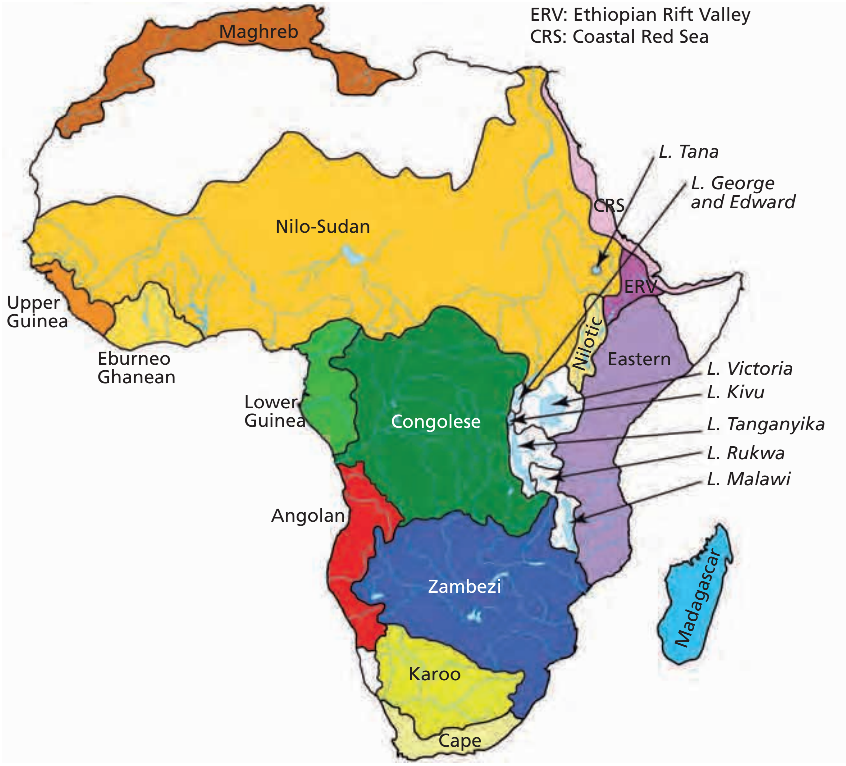


FIGURE 5.1.
The main ichthyological provinces of Africa (from Lévêque, 1997a and Paugy, 2010b).

On the basis of the distribution of the various families and fish species (table 5.I), ichthyologists have currently recognized the existence of ten large ichthyological provinces, inhabited by particular fish communities (Lévêque, 1997a; Paugy 2010b) (figure 5.1):

- Maghreb province has a depauperate fish fauna which has little affinity to tropical fauna and is primarily made up of Cyprinidae (Doadrio, 1994);
- Nilo-Sudan province extends from the Atlantic up to Ethiopia. It includes the major river basins of the Sahelian zone: Nile, Chad, Niger, Volta, Senegal, Gambia, and Cross Rivers in the south-west (Lévêque *et al.*, 1991; Paugy *et al.*, 2003a; b). Historically, Lake Victoria was also included into this province which is characterized by the presence of a great number of families. It can contain two sub-provinces: Eburneo-Ghanean to the west, characterized by a couple of endemic species (Teugels *et al.*, 1988), and Nilotic (Paugy, 2010b) to the east which is impoverished compared to the others (Hugueny & Lévêque, 1994; Paugy *et al.*, 2003a, b and Paugy, 2010b);
- Upper Guinea includes coastal basins from Kogon River in Guinea to Nipoué River at the border of Ivory Coast and Liberia. The families of fish represented are more or less similar to the Nilo-Sudan province, although species composition is very different. Many taxa are endemic to that area which exhibits affinities with the Lower Guinea and Congo (Lévêque *et al.*, 1989; Paugy *et al.*, 2003a; b);

- **Lower Guinea** covers the region from the coastal rivers of Cameroon and Gabon to the mouth of Congo and comprises a rich and diverse fauna (Teugels *et al.*, 1992; Mamoneke & Teugels, 1993; Stiassny *et al*. 2007a; b);
- **Congolese province** includes the entire Congo River basin that is the largest in Africa. Fish faunas of Lakes Kivu and Tanganyika are sometimes in this province. Its fauna is the richest in the continent, although rather poorly known in regards to systematics and distribution of species;
- **Angolan province** includes the coastal drainages of Angola which are inhabited by a characteristic ichthyofauna (Poll, 1967). Currently, this is probably the most poorly-known province;
- **Zambezi province** including the Zambezi and the Okavango basins has a moderately rich fish fauna (Jackson, 1986; Skelton, 1994);
- **East coast province** extends from coastal basins flowing towards the Juba River to the Zambezi (Eccles, 1992; Skelton, 1994);
- **Ethiopian Rift Valley (ERV) or Oromo province** includes all the central and northernmost lakes of the ERV and the Awash River (including Lake Abbe) (Paugy, 2010b);
- **Coastal Red Sea (CRS) province** includes the small coastal basins that flow into the Red Sea. Its fauna, very poor, is close to that of the Near East (Paugy, 2010b);
- **Cape province**, restricted to the rivers of the Cape Fold Mountains, the Amatolas and the Drakensberg, has a rather poor fauna with predominance of Cyprinidae (Skelton, 1994);
- **Karroo province**, centred upon the Orange basin, mainly includes Cyprinids (*Barbus* and *Labeo umbratus* group), as well as southern rock catfishes (*Austroglanis* species) (Skelton, 1993);
- **Malagasy province** remains an enigma for biogeographers. The fauna (135 species, predominantly endemic) is moderately rich. Most of the species belong to widely distributed peripheral families having affinities with Indian Ocean marine province. (Stiassny & Raminosoa, 1994; Sparks & Stiassny 2003).

Finally, due to their endemicity, we consider all the great lakes of East Africa as separate provinces. In most of them, the main fish fauna is constituted by species flocks (Cichlids in Lakes Victoria, Kivu, Tanganyika, Malawi, etc. and Cyprinids in Lake Tana).

In regards to species richness and diversity, the composition of the ichthyofauna within these ichthyoprovinces (table 5.II) has shown that some families have a wider distribution and a greater relative importance than others. That is the case, namely, for Mormyridae, Cyprinidae, Mochokidae, Cichlidae.

The East African Lakes (Victoria, Tanganyika, Malawi, Kivu) and to a lesser extent the lakes of the Rift Valley are inhabited by species that are unique to each lake. The term species flock is sometimes used for these monophyletic groups of species coexisting in the same environment. These large lakes are unique

TABLE 5.II

The composition of the ichthyofauna in representative rivers of the major ichthyological provinces. Nile, Chari and Lake Chad (Cha), Niger and Volta according to Lévêque *et al.*, 1991; Konkouré (Konk) according to Lévêque *et al.*, 1989; Jong according to Paugy *et al.*, 1990; Sassandra (Sass) and Bandama (Band) according to Teugels *et al.*, 1988; Ogowe according to Stiassny *et al.*, 2007a, b; Awash according to Paugy, 2010b; estimates for Sanaga (Sana), and Congo according to CLOFFA (Daget *et al.*, 1984, 1986a, 1991); Ruaha according to Eccles, 1992; Zambezi (Zamb) according to Jackson, 1986; Orange-Vaal (Oran) according to Skelton, 1986. Provinces NS: Nilo-sudan; UG: Upper Guinea; EG: Eburneo-Ghanean; LG: Lower Guinea; EC: Eastern; ERV: Ethiopian Rift Valley; Co: Congolese; Zz: Zambezi.

Basins ***Provinces***	**Nile** *NS*	**Chad** *NS*	**Niger** *NS*	**Volta** *NS*	**Konk** *UG*	**Jong** *UG*	**Sass** *EG*	**Band** *EG*	**Sana** *LG*	**Ogowe** *LG*	**Rufiji** *ET*	**Awash** *ERV*	**Congo** *CO*	**Zamb** *ZZ*	**Oran** *KA*
Dasyatidae			1						1				1		
Protopteridae	2	1	1	1				1		1			3	1	
Polypteridae	3	3	4	3	1		1	1	1	1			9		
Anguillidae	1										1			4	
Denticipidae			1												
Clupeidae	1		5	3			1	1	1	3			13	3	
Arapaimidae	1	1	1	1									1		
Pantodontidae			1						1	1			1		
Notopteridae	1	1	2		1	2		1	1	1			2		
Mormyridae	15	14	27	16	10	13	8	10	16	21	6		109	10	
Gymnarchidae	1	1	1	1											
Kneriidae	1		1	1						2			15	4	
Phractolaemidae			1										1		
Hepsetidae		1	1	1	1	1	1	1	1	1			1	1	
Alestidae	8	11	16	15	4	7	7	8	12	18	6		55	8	
Distichodontidae	7	10	14	8	1	4	3	4	7	11	3		48	2	
Citharinidae	2	3	4	3			1	1			1		3	4	
Cyprinidae	25	23	35	24	16	13	17	18	39	28	16	6	128	45	8
Cobitidae	1														
Bagridae	2	2	3	3					2		2		3	1	
Claroteidae	5	6	13	4	4	6	4	3	7	9			26	1	
Austroglanididae															1
Schilbeidae	5	5	5	6	2	2	2	3	5	3	3		13	3	
Amphiliidae	1	1	5	3	4	2	1	1	3	8	1		25	1	
Clariidae	7	8	14	7	4	5	3	7	8	16	1	1	28	8	1
Malapteruridae	1	1	2	1	1	1	1	1	1	1			2	1	
Mochokidae	15	12	26	13	8	5	5	3	7	15	6		82	10	
Ariidae			3	1											
Cyprinodontiformes	7	8	23	9	8	8	6	10	20	52	5	2	59	8	
Channidae	1	1	2	1		1	1	1	1	2			2		
Latidae	2	1	1	1	1	1	1	1	1				1		
Polycentridae			1							1					
Gobiidae			3	?		1	1	3	2	2	1		3	2	
Eleotridae	1	1	5	1	3	3	1	1	1	2	1		4		
Cichlidae	10	10	17	9	15	16	8	9	7	23	3	1	90	28	2
Anabantidae	2	4	4	1	1	1	1	1	3	3			15	2	
Mastacembelidae		1	3	1	1	3	1	1	4	2	1		23	2	
Tetraodontidae	1	1	1	1									4	?	
Cynoglossidae			1						1	1			1		
Soleidae			1												
Number of families	**28**	**26**	**37**	**29**	**19**	**20**	**22**	**25**	**26**	**26**	**16**	**4**	**32**	**23**	**4**
Number of species	**129**	**131**	**249**	**139**	**86**	**95**	**75**	**91**	**153**	**228**	**57**	**10**	**771**	**149**	**12**

and exceptional sites for the study of speciation. They have been compared to natural laboratories. No equivalent situation exists in South America where the family Cichlidae is also well represented.

Moreover, these East African Lakes are inhabited by a diversified ichthyological fauna (table 5.III) whose origin depends on the hydrographical systems to which they were previously associated: the Nile for Lake Victoria, the Congo for Lake Tanganyika and the Zambezi for Lake Malawi. In Lake Tanganyika, species flocks also exist for groups other than Cichlidae: Mastacembelidae, Claroteidae (*Chrysichthys*) and Mochokidae (*Synodontis*) (De Vos & Snoeks, 1994). In Lake Malawi there is also a species flock for Clariidae (*Bathyclarias*) (Anseaume, 2007).

TABLE 5.III

Composition of the ichthyofauna of the East African Great Lakes (int.: introduced).
Data for Cichlidae drawn from CLOFFA IV (Daget *et al.*, 1991).
For other species: Coulter, 1991 (Lake Tanganyika); Ribbink & Eccles, 1988 (Lakes Malawi and Victoria); Lévêque *et al.*, 1991 (Lake Turkana).

Lakes	**Tanganyika**		**Malawi**		**Victoria**		**Kivu**		**Turkana**	
Families	Species	Genera	Species	Genera	Species	Genera	Species	Genera	Species	Genera
Protopteridae	1	1	1	1	1	1			1	1
Polypteridae	2	1							1	1
Anguillidae			1	1						
Clupeidae	2	2					1 int.	1 int.		
Arapaimidae									1	1
Mormyridae	6	6	9	7	8	6			2	2
Gymnarchidae									1	1
Kneriidae	2	1								
Alestidae	7	5	2	2	5	2			9	4
Distichodontidae	3	1							1	1
Citharinidae	1	1							1	1
Cyprinidae	35	8	16	5	22	5	5	2	12	6
Auchenoglanididae	1	1							1	1
Bagridae	1	1	2	2	2	1			2	1
Claroteidae	15	7							1	1
Schilbeidae	2	1			2	3			1	1
Amphiliidae	2	2	1	1	3	2	1	1	1	1
Clariidae	9	4	15	3	6	3	2	2	2	2
Malapteruridae	1	2							2	1
Mochokidae	13	2	2	2	3	2	1	1	3	2
Cyprinodontiformes	2	2	3	3	8	5			2	1
Latidae	4	1			1 int.	1 int.			1	1
Cichlidae	250+	54	800+	59	500+	15	17	2	9	5
Anabantidae	1	1			1	1				
Mastacembelidae	13	1	1	1	1	1				
Tetraodontidae	1	1							1	1
TOTAL	**374+**	**106**	**853+**	**87**	**563+**	**48**	**27**	**9**	**55**	**36**

Intercontinental affinities of African fish

The precise number of extant fish species remains to be determined. However, since Linnaeus' listing of 478 species of teleost fish in 1758, our knowledge has increased considerably and some global estimates are available. The Catalog of Fishes established by Eschmeyer (2005) provided an estimate of 27,300 valid fish species, with a prediction of about 31,500 species when all inventories are completed (Berra, 2001). In September 2005, 28,900 species were already listed in FishBase. Nelson (2006) suggested a total of almost 28,000 species (freshwater and marine), which is 51% of the 54,711 then recognized living vertebrate species. The eventual number of extant fish species may be projected to be close to, conservatively, 32,500 (Nelson, 2006). At the global scale, the fresh and brackish water fish belong to 207 families, 2,513 genera and approximately 15,100 species (table 5.IV).

TABLE 5.IV.
Fresh and brackish water fish species richness by continents or large sub-continental units (from Lévêque *et al.*, 2008).

	Freshwater		Brackish water		Total	
	Families	Species	Families	Species	Families	Species
Africa	48	2,945	66	295	89	3,240
Asia	85	3,553	104	858	126	4,411
Europe	23	330	36	151	43	481
Russia	28	206	28	175	40	381
Oceania	41	260	74	317	85	577
North America	74	1,411	66	330	95	1,741
South America	74	4,035	54	196	91	4,231
Total		**12,740**		**2,322**		**15,062**

African ichthyofauna has close affinities with that of South America (Characiformes, Cyprinodontiformes) and Southeast Asia (Notopteridae, Bagridae, Clariidae, Schilbeidae, Channidae). Why do certain families of fish exhibit a vast distribution and occur on continents that have been long separated from each other? This geographical distribution can be explained both by geological events and the evolutionary history of fish.

At the end of the Triassic period, approximately 200 million years ago, all continents were joined in a "super-continent", Pangea, referred to as Gondwana in the south and Laurasia in the north (figure 5.2). In the mid-Jurassic (approximately 150-160 million years), Gondwana began to separate in two parts: an Eastern part (Madagascar, the Indies and Australia) and a Western part (Africa and South America). In the Lower Cretaceous (125 million years) South America started to separate from Africa, but this separation was not completed until the Late Cretaceous (approximately 100 million years). At the beginning of the Eocene epoch, 40 million years ago, Africa, still joined to Arabia had become an island. India was encroaching upon the Asian continent during the Eocene, pushing up the Himalayas. Finally, in the Miocene, approximately 17 million years ago, Africa and Arabia came into contact with the Asian continent at the vicinity of Turkey and Iran.

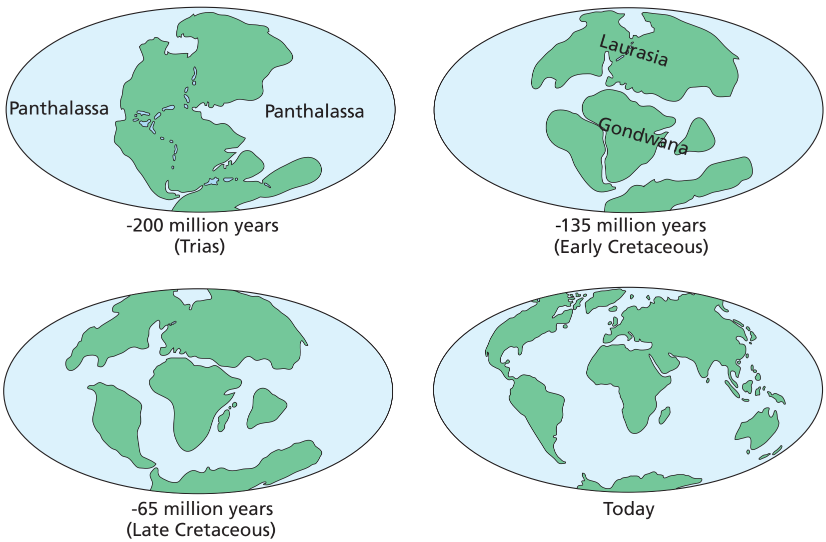


FIGURE 5.2.
Reconstitution of the location of the continental masses from early secondary era (according to Cloud, 1978).

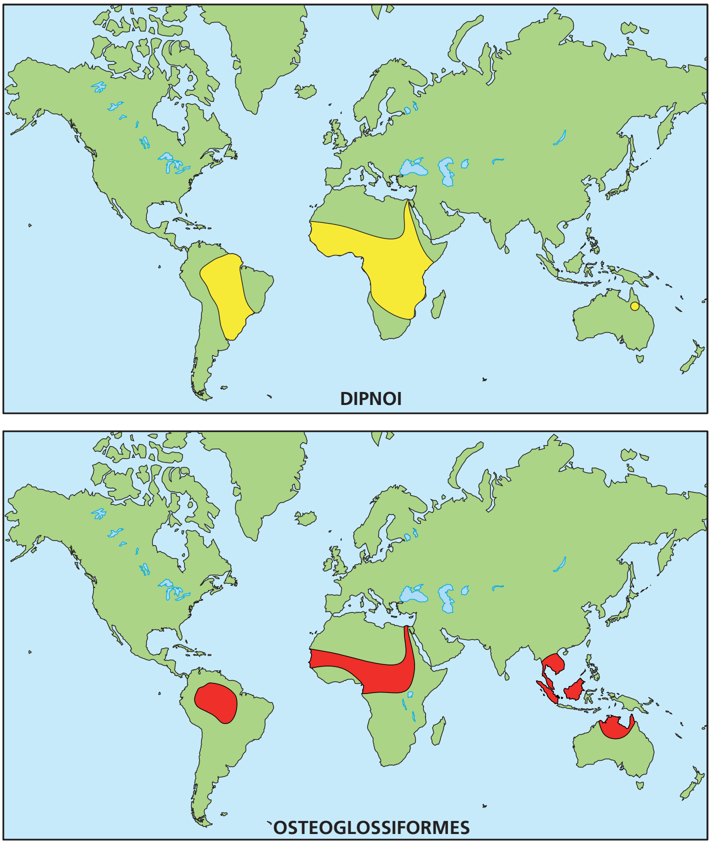
For many ichthyologists the majority of the larger groups of taxa (order and family) which make up the current African ichthyofauna were already established at the end of the Cretaceous (see chapter *African fossil fish*). Actually, South America and Africa have great taxonomic affinity even though their fauna had a different history after isolation (Maisey, 2000). The study of fossils provided evidence that part of the African ichthyofauna was already differentiated in the mid Jurassic *i.e.*, at the beginning of the fragmentation of Gondwana. Representatives of certain fish families in the formerly united continents could thus subsist and evolve independently. This is one of the explanations for the existence of families with a worldwide distribution.

Several fish lineages appear to have a Gondwanan origin *i.e.,* members of the lineage were present on Gondwana prior to fragmentation. Consequently, they have widespread distribution with living representatives and/or fossils present on different continents.

The order Osteoglossiformes is one of the best-known example of widespread distribution among freshwater fish (figure 5.3). It is now represented by one African species (*Heterotis niloticus*), three South American species (*Arapaima gigas*, *Osteoglossum bicirrhosum* and *O. ferreirai*), and by a genus (*Scleropages*) occurring in Australia (*S. jardinii* and *S. leichardti*) and in Southeast Asia (*S. formosus*). Fossils belonging to this family were also discovered in Asia and North America

Dipnoi (lungfishes) (figure 5.3) is a monophyletic group that first appeared in the Devonian and diversified in the Mesozoic (Lundberg *et al.*, 2000). It is now represented by the family Protopteridae with four living species of *Proptopterus* in Africa. The family Lepidosirenidae from South America is closely related and is represented by the genus *Lepidosiren* (one species, *L. paradoxa*). This group is also closely related to Neoceratodontidae today

FIGURE 5.3.
Global distribution of Dipnoi and Osteoglossiformes.



represented by one living Australian species (*Neoceratodus forsteri*). Several fossils of Dipnoi especially those of *Protopterus* have also been discovered in various parts of the world, particularly in South America and Africa.

The Polypteridae (bichirs and reedfishes or ropefishes) also had a large distribution. Today, however, living species occur only in Africa while fossils have been identified in South America (see box "Polypterids").

The distribution of the Cichlids in Africa, Madagascar, India, South and Central America (figure 5.4) may also be explained by a Gondwanan origin. Fossil remains of this group have also been found in Europe. The order Characiformes is generally regarded as the most primitive among Ostariophysi with four families known in Africa and 15 in South America (figure 5.5). Fossils of Characiformes have been uncovered in Europe (Serrasalmidae), but it is not known why they did not survive or spread into Asia or North America.

The Otophysi (superorder Ostariophysi) is a monophyletic group that includes very speciose families in freshwater: the Siluriformes (catfishes), Gymnotiformes (knifefishes), Cypriniformes (minnows) and Characiforms (characins) whose current distribution present some interesting contrasts (figure 5.5). They do not

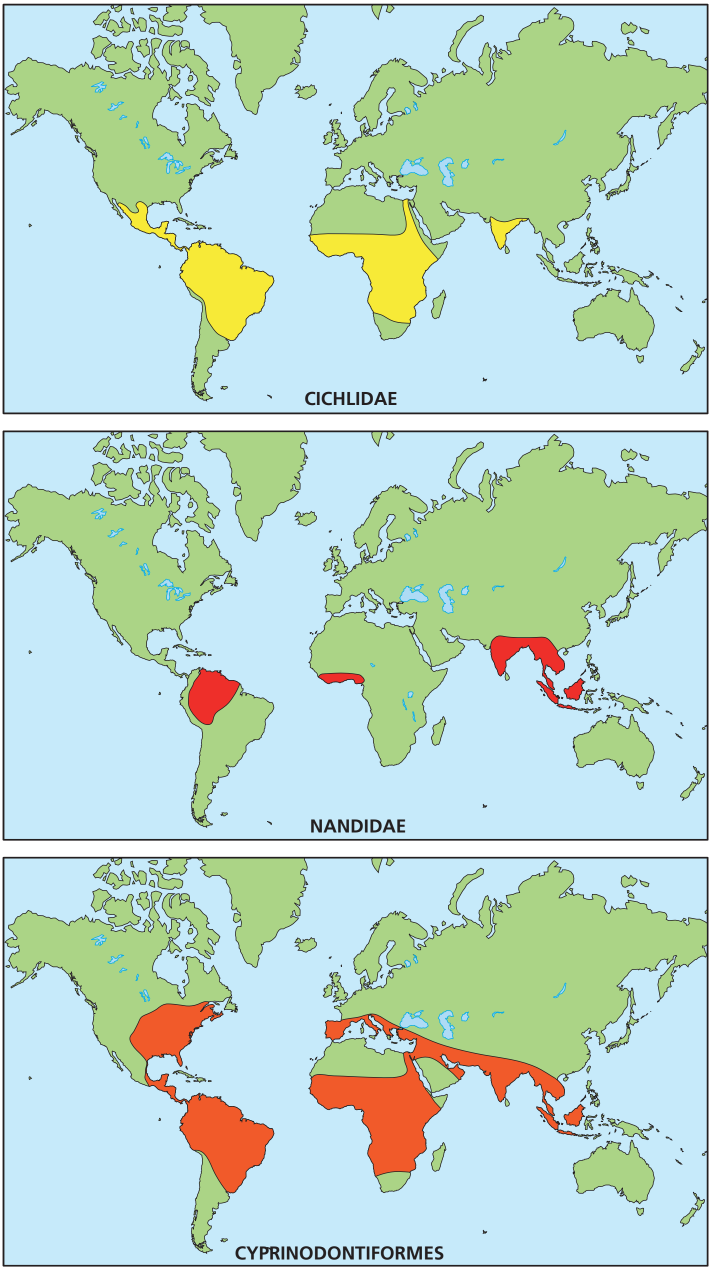


FIGURE 5.4.
Global distribution of Cichlidae, Nandidae and Cyprinodontiformes.

occur in Australia, Madagascar or the West Indies. Recent molecular studies supported the hypothesis that Cypriniformes are the sister group to the remaining three orders (Saitoh *et al.*, 2003). The divergence time of cypriniforms from the otophysan stock has been estimated at 250 Myrs ago (Kumazawa *et al.*, 1999).

Polypterids

François Meunier

American polypterids!

Of uncertain origin (but probably close to the Palaeonisciformes), Polypterids have long been considered typically African fishes, and modern species are related to the continent's tropical regions. Moreover, the somewhat ancient Polypterid fossils were limited to scattered and unconnected remains (scales, vertebrae and finlet rays, skull fragments). Up to the late 1980s, they had only been found in different beds dating from the Tertiary and mid Cretaceous (Greenwood, 1972, 1984) that cover their current zone of geographic distribution; only a single mention, in Tunisia (Greenwood, 1974), was clearly located outside this area. The single known complete Polypterid fossil in Africa was found a short time ago in Chad, in a recent fossil bed of about 7 million years of age (Otero *et al*., 2006). Owing to the paucity of the fossil record, the origin of this group of fishes as well as their geological history thus long remained a mystery.

In fact, recent studies based on palaeohistological techniques and scanning electron microscopy on one hand, and the collection of more or less complete new fossils on the other hand, have revolutionized these traditional views. First, in 1986, scales, vertebrae, and finlet rays were described in a Niger bed in In Becetem from the Senonian, *i.e.,* some 75 million years, which places them significantly earlier (as most of the then-known fossil remains came from the end of the Tertiary). The greatest surprise came from the discovery in 1991, in several fossil beds in Bolivia (South America) dating from the late Cretaceous/early Tertiary, of scattered remains that were incontestably from Polypteridae. They consisted of scales whose structure was comparable on all points to those of modern Polypterids or African fossils, with the presence in particular of a characteristic orthogonal structure between the dentin and the bony basal plate. In addition, these scales are accompanied by finlet rays and vertebrae whose morphology and histological characteristics are typical of Polypteridae. As these beds were located outside the western zones of the Brazilian Shield, there remained an enormous gap between these sites and the African provinces. The gap was bridged in 2001 with the discovery of Polypterid scales, finlets, and vertebrae (Dutra & Malabarba, 2001), in eastern Brazil, more precisely in an Albian-Cenomanian bed (100 million years) in the state of Maranhão, east of the mouth of the Amazon.

An American or African origin?

As Polypterids are typically freshwater species and the Bolivian remains were found in continental sediments, this discovery implies that the origin of this Osteichthyes family predates the opening of the southern Atlantic ocean, when South America and Africa were still connected, *i.e.,* more than 110 million years ago (figure 5.2). Moreover, at this time, the morphology of American Polypterids was probably similar to that of modern Polypterids, as the Bolivian species also had finlets. Alas, none of the American fossils, nor most of the African ones, have connected skeletal elements, and the cranial bones are too rare or incomplete to permit reconstruction. Nonetheless, it is possible to imagine that the ancestors of the Polypteridae family may have been "American"!

Siluriformes (figure 5.5) are present on the various continents, but whereas three families (Bagridae, Clariidae and Schilbeidae) (figure 5.6) are common to Africa and Asia, there are no families in common between Africa and South America. Their origin, as that of Cypriniformes (figure 5.5) is still debatable.

Actually, the understanding of Otophysan biogeography has been a matter of debate since the beginning of the 20th century. Asia, where the group is the most speciose, was long considered to be the centre of origin of the Cypriniformes. However, current evidence argues for a hypothesis that the Cypriniformes, and probably also the Siluriformes, originated in South America and migrated to Asia in the late Jurassic (ca 150-160 Myrs ago) along the northern shore of the Thethys sea (Briggs, 2005). Diogo (2004) also supported the

That said, several relatively well-preserved fossils (Sereno *et al.*, 1996) composed of articulated skeletal elements were found in a fossil bed aged 93 million years in Morocco.
A first fossil, named *Serenoichthys kemkemensis* (Dutheil, 1999), whose head is not known, as well as a second species currently being described, with bodies that are shorter than modern Polypterids, allow reconsideration of the region of origin of these animals. Africa has the advantage once again, more so given that the Polypteridae family appears to have diversified further there compared with America, at least based on current palaeontological knowledge!

A Polypteriform fish named *Bawitius* is known from various isolated bones (maxillae, ectopterigoid and many scales) from the Kem Kem beds or Bahariya bed (Grandstaff *et al.*, 2012; Cavin *et al.*, 2015).
Some histological characteristics of scales allow a closed linking of *Bawitius* to the Polypteridae family. But it cannot be considered as a true Polypteridae because of the discontinuous ganoine layer of its scales (Meunier *et al.*, 2016).
Nevertheless this taxonomic proximity is an argument to favour an African origin of the polypterid family.

Peculiar Polypterids!

Indeed, two African fossil beds from the end of the Cretaceous, 87 million years for In Becetem in Niger (Gayet & Meunier, 1996) and 95 million years for Wadi Milk in Sudan; (Werner & Gayet, 1997), contain many disarticulated Polypterid bones, particularly scales and most especially spiny rays from finlets. Analysis of theses rays show that some are rather similar in form to existing species, while others are very different.
Some of these rays are clearly asymmetrical, which implies that they did not move in the animal's plane of symmetry.
Rather, they probably deviated from this plane, as is the case today with the 'pinecone fish', a Pacific marine species. Unfortunately, since no complete fossil (with articulated bones) has been found, it is difficult to draw the precise "portrait" of this animal, other than a hypothetical frontal view (Gayet *et al.*, 1997).
In fact these asymmetric bony rays have been misinterpreted; they probably are pectoral rays (as siluroid spiny pectoral rays) that could belong to a short non-anguilliform polypterid!
In any case, the presence of these rays with highly varied morphologies implies that at the end of the Secondary era, Polypterids showed significant diversification in Africa that is much greater than that observed today.

Parallel histories

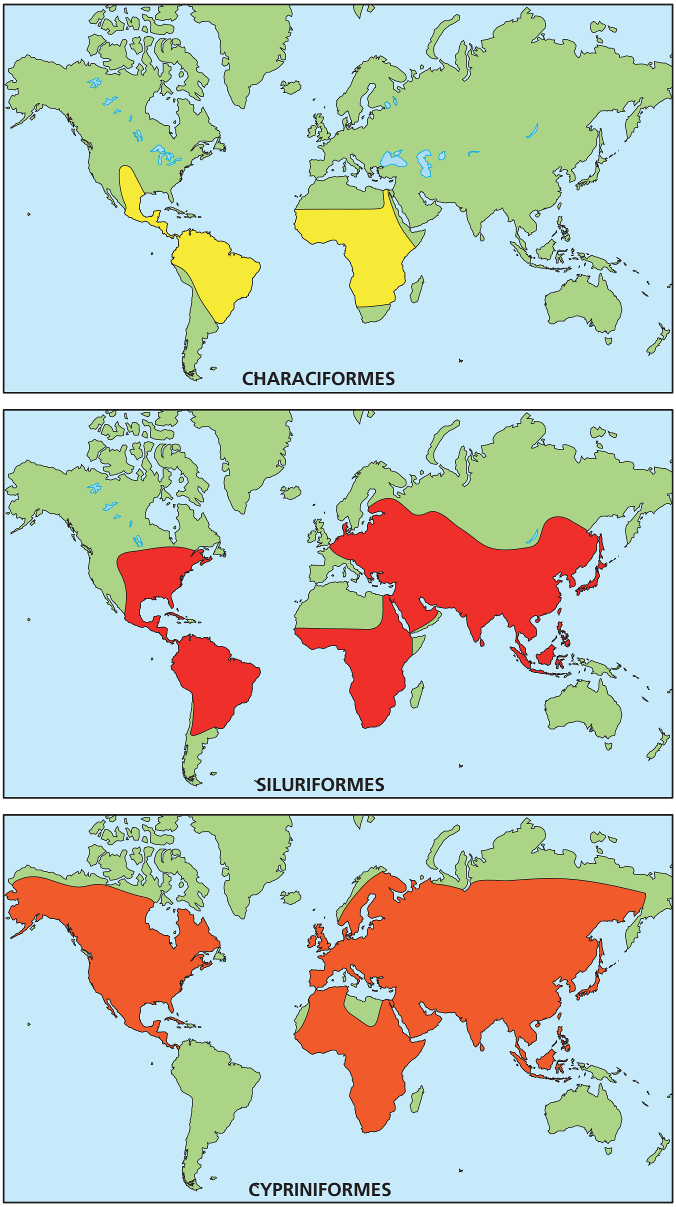
At the end of the Cretaceous, the rivers of the clearly separated South America and Africa hosted a second group of "primitive" fishes, the Lepisosteids. The latter are undoubtedly of slightly more recent origin than the Polypterids. Curiously, Lepisosteids have totally disappeared from Africa but remain present in North and Central America. Meanwhile, as we have seen earlier, Polypterids only remain in Africa and have disappeared from Latin America.
What are the biogeographic events that are behind these two histories from the start of the Tertiary (Gayet *et al.*, 2002)? The discovery of new fossils may provide answers to this question.

origin of catfishes in the South American region during the late Cretaceous period, at a time when there were still some remaining Pangean connections between Gondwana and Laurasia. Then catfishes would have dispersed to other areas with some subgroups migrating via predrift dispersion to Laurasian regions. (Sullivan *et al.*, 2006)

Continental drift explains why the ichthyological fauna of the Indian sub-continent is very similar to that of Africa and why certain groups have very strong morphological resemblances. It is observed in particular that the family of Notopteridae (figure 5.6) is represented in Africa by two species with broad distribution: *Xenomystus nigri* and *Papyrocranus afer*; the latter is close to the Asian genus *Notopterus* which is represented by four species in South Asia.

FIGURE 5.5.

Global distribution of Characiformes, Siluriformes and Cypriniformes.



Other families have a distribution limited to Africa and India. These include families belonging to the orders Siluriformes (Bagrids, Schilbeidae, Clariidae); Mastacembelidae, also referred to as spiny eels (figure 5.6); certain groups of Cyprinidae; Perciformes such as Channidae with the genus *Parachanna* in Africa and the genera *Channa*, *Micropletes* and *Ophicephalus* in Southern Asia; Anabantidae, with the African genera *Ctenopoma* and *Sandelia* and the Asian species of the family Belontiidae.

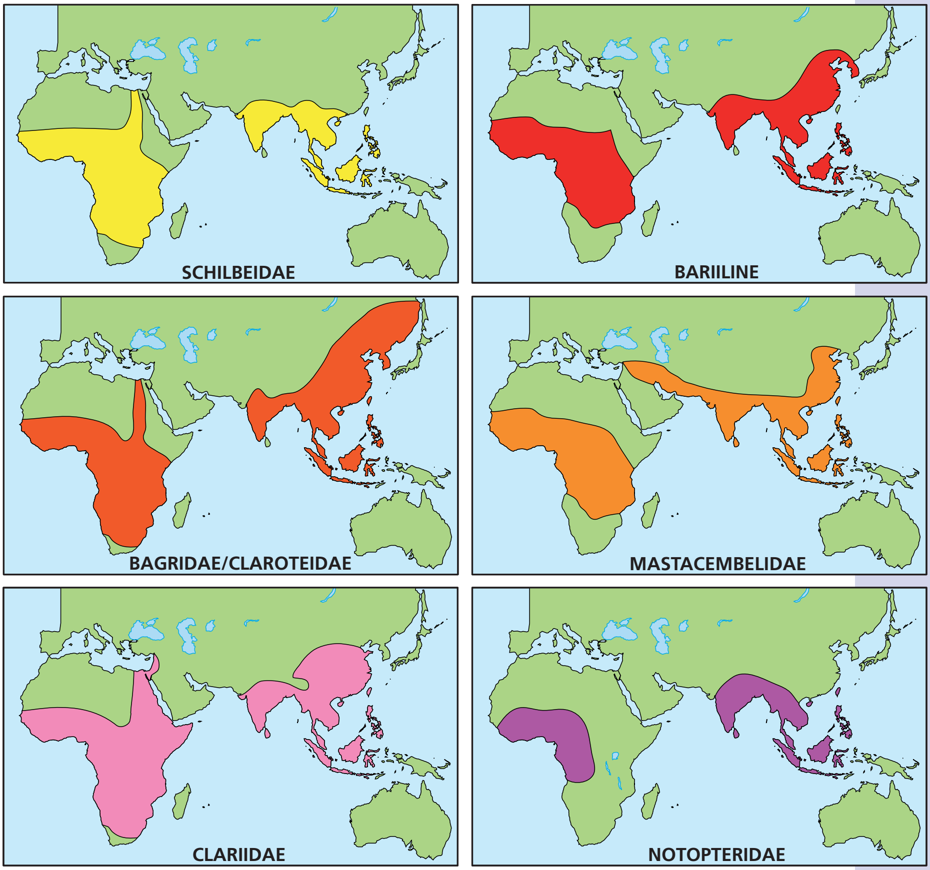


FIGURE 5.6.
Global distribution of Schilbeidae, Bariiline, Bagridae/Claroteida, Mastacembelidae, Clariidae and Notopteridae.

What can we learn from fossils?

African fish fossil remains are very few and are unequally distributed geographically (most are from the Nile valley). However, a certain number of rich and relatively ancient (Cretaceous) fossiliferous layers have enabled to a certain extent the demarcation of the ichthyological history of Africa (Egypt, Sudan, Niger, and Morocco). Western Africa and Southern Africa remain very poor in fossil remains and thus the available information for deduction of evolution and distribution of African species is reduced. Moreover, identification of fossil remains in general does not go beyond the genus level.

Fish fossils are often found during excavations targeting reptiles or mammals and are thus maintained in certain anonymity, particularly for Africa and Asia. The materials are often fragmented and incomplete and remain insufficiently studied whereas they deserve to be re-examined in the light of new palaeo-ichthyology techniques, which would undoubtedly make it possible to infer the palaeobiogeography of higher taxa. It should be noted that Pleistocene fossil remains are the most numerous remains collected for Africa in comparison to other continents. This is may be due to several studies that have been carried out from this period for the reconstruction of primate history (see chapter *African fossil fish*).

One of the difficulties faced by palaeo-ichthyologists has been to decipher fossilized material due to the fact that fossils are generally dislocated from the layers of their continental origin (after their death, the animals are transported, furled and, after the destruction of non-mineralised tissue, the bones are dispersed and found in detrital accumulation). Moreover, it is often difficult to attribute an isolated bone, even a fragment, to a precise species, genus, or even family. Museums therefore possess abundant, unstudied disparate material. However, in a certain number of cases, the bones are sufficiently characteristic for a more precise systematic positioning either by their morphology (jaw of lungfish, finlet of bichir), or their histology (scales of *Polypterus*).

Some important results deserve mention. In particular, the most ancient fossils (table 5.V) belonging to the genera *Protopterus* and *Polypterus* (from the beginning of the Cretaceous for the former and mid Cretaceous for the latter). Incidentally, remains of *Lates* have been found in sediments belonging to Lakes Victoria and Edward basins, where the species was no longer present until its recent reintroduction.

Remains of Osteoglossiformes, such as Mormyridae, are rare and belong to the late Miocene era. Cyprinidae of the genera *Labeo* and *Barbus* date beyond the mid Miocene. Characiformes fossils are represented by several genera within three families; one of these Characidae comprises 6 genera of which *Alestes* and *Brycinus* are the only living representatives while the others are completely extinct. *Sindacharax* and *Bunocharax* have however been excavated from the lower Miocene.

Among Perciformes, the family Latidae occupies an important place in African continental fauna. The first Latidae goes back to the beginning of the Miocene, from around the large lakes, in Libya and near the Nile delta. Cichlidae is widespread and comprises two subfamilies in Africa (Tilapinae and Haplochrominae). Their fossils are difficult to link to current forms although the first species date back to the lower Miocene from Uganda and Kenya. Another group of highly specialized osseous fish, Tetraodontidae (puffer fish) was described from the lower Pliocene from the Great Lakes region. Last but not least, a fauna of diversified freshwater fish possessing strong affinities to that of tropical northern Africa has been uncovered in deposits from the end of the Miocene from Tunisia, (Greenwood & Howes, 1975). Fossil remains of the genera *Lates*, *Clarias*, *Heterobranchus* and *Polypterus* were also identified in sediments from the beginning of the Eocene from the southern slope of the Algerian Atlas (Mahboudi *et al.*, 1984). These observations thus affirm that at a certain time tropical ichthyofauna reached the banks of the Mediterranean, whereas at present fish fauna is very poor in the Maghreb. In fact, it is possible to show the existence of a dense forest as well as mangroves along the northern coast of Africa at the beginning of the Eocene, 60 million years ago, a time at which the equator was located 10° to 15° higher than at present. Remains of Cichlidae similar to certain known species from West and Central Africa dating from the end of the Miocene (5 to 10 million years) were also discovered in Algeria (van Couvering, 1982), which shows that tropical fauna was previously present in North Africa.

TABLE 5.V

Fossil remains from African fish observed from various geological times
(summarized from results of Lévêque, 1997a; Murray, 2000 and Stewart, 2001).(Myrs: million years).

Geological era Myrs ago	**Eocene** 54-36	**Oligocene** 36-23	**Miocene** 23-6	**Pliocene** 6-1.8	**Pleistocene** 1.8-0.01	**Holocene**
Orders/Families						
Alestidae	●	●	●	●		
Bagridae					●	
Cichlidae		●	●	●	●	
Clariidae			●	●	●	
Cyprinidae					●	
Cyprinodontiformes		?				
Mochokidae			●			
Mormyridae					●	
Genera/Species						
Alestes deserti				●		
Alestes junneri					●	
Alestes sp.		?	●	●	●	●
Anguilla anguilla					●	
Arius sp.					●	
Auchenoglanis sp.			●	●	●	
Bagrus docmak				●		
Bagrus sp.			●	●	●	
Barbus altianalis					●	
Barbus bynni					●	
Barbus sp.			●	●	●	●
Bunocharax sp.				●	●	
Chrysichthys macrotis				●	?	
Chrysichthys sp.					●	●
Citharinus sp.					●	
Clarias gariepinus					●	
Clarias lazera					●	
Clarias mossambicus					●	
Clarias sp.			●	●	●	●
Clarotes laticeps				●	●	
Clarotes sp.			●	●	●	
Dasyatis africana				●	●	
Distichodus sp.			●	●	●	
Eaglesomia eaglesomei	●					
Gymnarchus niloticus				●	●	
Gymnarchus sp.			●	●	●	
Heterobranchus sp.			●	●	●	●
Heterobranchus bidorsalis				●		
Heterotis sp.			●	●	●	
Hydrocynus sp.				●	●	
Hyperopisus sp.				●	●	
Kalyptochromis hamulodentis			●			
Labeo sp.			●	●	●	
Lates karungae			●			

TABLE 5.V (CONT.)

Geological era Myrs ago	Eocene 54-36	Oligocene 36-23	Miocene 23-6	Pliocene 6-1.8	Pleistocene 1.8-0.01	Holocene
Genera/Species						
Lates niloticus			●	●	●	
Lates rhachirhincus			●	●	●	
Lates sp.			●	●	●	●
Lepidosiren paradoxa				●		
Macfadyena dabanensis		●				
Nderechromis cichloides			●			
Nkondobagrus longirostris				●		
Oreochromis harrisae				●		
Palaeochromis rouselleti			●			
Palaeochromis darestei			●			
Palaeodenticeps tanganyikae	●					
Palaeofulu kuluensis			●			
Parachanna sp.				●	?	
Polypterus bichir ornatus					●	
Polypterus sp.	●		●	●	●	
Protopterus aethiopicus					●	
Protopterus polli			●			
Protopterus sp.	●	●	●	●	●	●
Sarotherodon martyni			●			
Sarotherodon sp.					●	
Semlikiichthys rhachirhinchus			●	●		
Schilbe sp.			●			
Sindacharax deserti				●	?	
Sindacharax greenwoodi				●	●	
Sindacharax howesi				●		
Sindacharax lepersonnei			●	●		
Sindacharax lothagamensis			●	●		
Sindacharax mutetii				●		
Sindacharax sp.			●	●	●	
Singida jacksonoides	●					
Synodontis frontosus					●	
Synodontis schall					●	
Synodontis sp.			●	●	●	●
Tetraodon sp. nov..				●		
Tetraodon sp.				●	●	
Tilapia crassispina					●	
Tilapia fossilis					●	
Tilaîa melanopleura					●	
Tilapia nigra					●	
Tilapia sp.			●	●	●	●

Scientific editors

Didier Paugy Christian Lévêque Olga Otero

The Inland Water Fishes of Africa

Diversity, Ecology and Human Use

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