

Chapitre 5

BROAD CHARACTERISTICS OF THE ICHTHYOFAUNA

CARACTÉRISTIQUES GÉNÉRALES DE L'ICHTHYOFAUNE

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1 - COMPOSITION OF AFRICAN FRESHWATER FISH FAUNAS.

Africa has over 2000 known species of indigenous freshwater fishes. The families these represent are listed in Table 1, indicating the approximate number of genera and species at present known (see Daget *et al.* 1984). These figures are only very provisional as in some families, especially the Cichlidae, many new ones have yet to be described.

Throughout the world, freshwater fish faunas are dominated by Ostariophysan fishes, and the riverine faunas of Africa are no exception to this. But in addition African rivers and swamps harbour an extraordinary assortment of archaic and phylogenetically isolated fish groups, mostly endemic, while the lacustrine faunas present the most spectacular examples of adaptive radiations, mainly amongst the cichlid fishes.

Ostariophysans and most of the archaic groups are primary division fishes, obligatory freshwater fishes, physiologically intolerant of seawater, the distributions of which provide strong evidence of former connections of the landmasses. The cichlids are among the secondary division freshwater fishes, those that live almost exclusively in freshwater but are able to tolerate seawater well enough to disperse through it. The fishes of marine origin, peripheral division fishes of Roberts (1975), can live readily in freshwater or seawater, so the sea serves as a highway for dispersal. Within this group many freshwater species have evolved, but it also includes diadromous fishes which spend part of the life cycle in freshwater (as do the catadromous *Anguilla* eels), and sporadic visitors, euryhaline fishes moving upriver from estuarine regions. These peripheral fishes are generally more abundant in faunas which lack a rich diversity of primary and secondary freshwater fishes. In Africa the richness of these latter groups means that there has been little opportunity for peripheral fishes to move in. Furthermore, the general height of the African landmass, with rapids near the coast of some rivers, militates against their entry. While riverine faunas are dominated by primary division fishes, it is the secondary division fishes (particularly the cichlids) and those with marine affinities (such as clupeids and centropomid *Lates*) which have come to dominate the lacustrine faunas.

The most striking feature of the African freshwater fish fauna is the high degree of endemism. Table 5.1 shows that 18 of the families are endemic to Africa, and that this endemism at family level occurs amongst the less advanced (pre-acanthopterygian) fishes viz : lungfish Protopteridae, brachypterygian Polypteridae, clupeomorph Denticipitidae and Congothriidae, osteoglossomorph Pantodontidae, Mormyridae and Gymnarchidae, ostariophysan anotoophysan Kneriidae, Cromeriidae, Grasseichthyidae and Phractolaemidae, and otophysan characiform Hepsetidae, Distichodontidae, Citharinidae, siluriform Amphiliidae, Mochokidae and Malapteruridae, also the cyprinodontiform Aplocheilichthyinae. At the generic level, almost all genera are endemic to Africa with the exceptions of some euryhaline fishes of marine origin, and a few genera shared with the Oriental region, including the cyprinids *Barbus*, *Garra*, *Labeo*, *Raiamas* and *Nemachilus*, and the catfish *Clarias*.

Table 1 : Fish families indigenous to African freshwaters, indicating their range outside Africa in the Neotropical Region (N), Oriental Region (O), in marine communities (M), or endemic to African freshwaters (E). Excluded are introduced species as well as marine families only sporadically represented in the lower courses of rivers.

FAMILY	RANGE	GENERA (approximate numbers)	SPECIES	COMMENTS ON DISTRIBUTION
ELASMOBRANCHII				
Carcharinidae	M	1	1	lower reaches
Pristidae	M	1	1	lower reaches
Dasyatidae	M	1	4	
DIPNOI				
Protopteridae	E	1	4	swamps, rivers, lakes
BRACHIOPTERYGII				
Polypteridae	E	2	10	swamps, rivers, lakes
TELEOSTEI				
ELOPOMORPHA				
Elopiformes				
Elopidae	M	1	3	lower reaches
Megalopidae	M	2	2	lower reaches
Anguilliformes				
Anguillidae	M	1	6	mainly eastern rivers
Ophichthidae	M	2	5	
CLUPEOMORPHA				
Clupeiformes				
Clupeidae	M	20	38	
Denticipitidae	E	1	1	streams, W. Africa
Congothriissidae	E	1	1	Zaire
OSTEOGLOSSOMORPHA				
Osteoglossiformes				
Osteoglossidae	N/O	1	1	shallow waters
Pantodontidae	E	1	1	
Notopteridae	O	2	2	
Mormyridae	E	18	198	
Gymnarchidae	E	1	1	
PROTACANTHOPTERYGII				
Salmoniformes				
Salmonidae	M	1	1	indigenous N. Africa
Galaxiidae	M	1	1	South Africa
OSTARIOPHYSII				
Anotophysii				
Gonorynchiformes				
Chanidae	M	1	1	eastern, lower reaches
Kneriidae	E	2	24	streams
Cromeriidae	E	1	1	
Grasseichthyidae	E	1	1	
Phractolaemidae	E	1	1	swamps, Niger, Zaire
Otophysi				
Characiformes				
Hepsetidae	E	1	1	
Characidae	N	18	109	
Distichodontidae	E	17	90	
Citharinidae	E	3	8	

FAMILY	RANGE	GENERA (approximate numbers)	SPECIES	COMMENTS ON DISTRIBUTION
OSTARIOPHYSII				
Cypriniformes				
Cyprinidae	O	23	475	Ethiopian highlands
Cobitidae	O	2	2	
Siluriformes				
Bagridae	O	16	100+	
Schilbeidae	O	8	40+	
Clariidae	O	14	100+	
Amphiliidae	E	8	50	
Malapteruridae	E	1	2	
Mochokidae	E	10	155	
Ariidae	M	1	1	
Plotosidae	M	1	1	lower reaches
ACANTHOPTERYGII				
Atherinomorpha				
Cyprinodontiformes				
Aplocheilidae	O/N	6	255+	shallow pools
Poeciliidae	N	8	75+	
Cyprinodontidae	O/N	1	2	North Africa
Percomorpha				
Gasterosteiformes				
Syngnathidae	M	4	10	
Perciformes				
Centropomidae	M	1	6	
Nandidae	O/N	2	2	
Cichlidae	N/O	ca.100	ca.700+	species flocks lakes
Gobiidae	M	4	26?	lower reaches
Channidae	O	1	3	swampy places
Anabantidae	O	2	29	
Mastacembelidae	O	1	38+	
Synbranchiformes				
Synbranchidae	M	2	2	
Pleuronectiformes				
Cynoglossidae	M	1	1	endemic Benue R.
Tetraodontiformes				
Tetraodontidae	M	1	6	

Classification based on Greenwood (1975); updated by reference to Vari (1979), Fink & Fink (1981), Parenti (1981); some data from Roberts (1975), Bowmaker *et al.* (1978), Travers (1984) and Daget *et al.* (1984).

Families shared (but not exclusively) with the Neotropical zoogeographical region include the Osteoglossidae (also present in Southeast Asia), the Characidae and Poeciliidae *sensu* Parenti, 1981 (both confined to Africa and the Neotropics), the Cichlidae (which also has a few species in Madagascar, southern India and Ceylon), the Nandidae (also present in the Oriental region), and the Cyprinodontidae (in most continents except Australia). These groups probably all pre-date the final breakup of Gondwanaland. Families shared solely with the Oriental region include the Notopteridae, the catfish families Bagridae, Clariidae and Schilbeidae, also the Channidae, Anabantidae and Mastacembelidae, with, as mentioned above, some shared genera. Problems concerning the places of origin of these families and dispersal routes remain unresolved (see Howes, 1980, for discussion of bariliine distribution and dispersal tracks, and Figure 1) Africa is the only major continental area where the three groups Cypriniformes, Characiformes and Siluriformes all occur, and it seems clear that the Ostariophysi must have originated in Gondwanaland prior to the separation of Africa and South America.

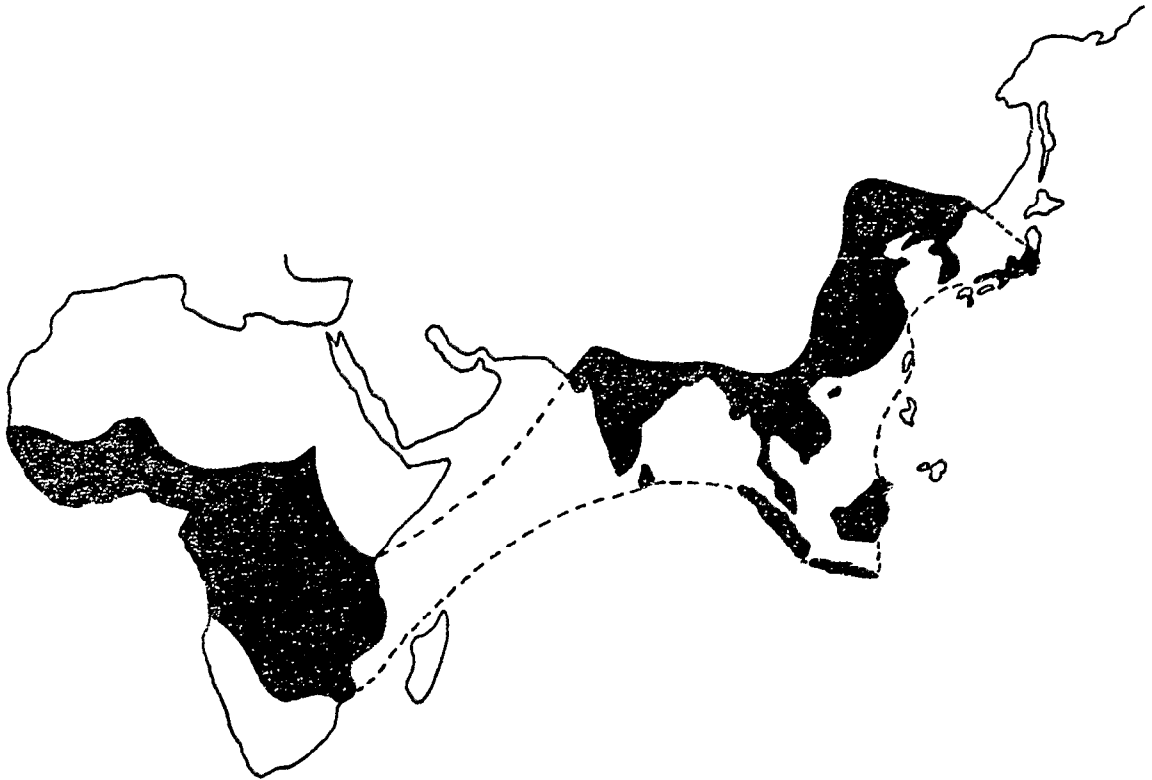


Figure 1 : Map showing distribution of bariliine genera (dark grey) and dispersal track (broken line). Blanket coverage is given to Sumatra, Java and Borneo although the actual distribution of bariliines on these islands is still to be ascertained (after Howes, 1980).

The affinities of African freshwater fishes have long suggested that there have been land connections between Africa and South America, and between Africa and Asia; evidence from fish parasites also supports this view (Manter, 1963). Figure 2 compares the relative composition of African freshwater fish faunas from rivers, and lakes) with faunas from South America (Brazil) and tropical Asia (Thailand). This shows clearly that characiforms and siluriforms are dominant groups in South America, cypriniforms and siluriforms in Asia (where there are also many 'other species', often of marine origin), while African riverine faunas have important cypriniform, characiform and siluriform components, plus significant numbers of endemic Mormyridae. Figure 2.2 also shows clearly that the cichlid fauna (shared with South America) is less important in the rivers than in the lakes of Africa.

The separation of Africa from South America probably began in the Lower Cretaceous (ca.125 m.y. BP) but was not completed until the Upper Cretaceous (90-80 m.y. BP) (Howarth, 1981). Much later, Africa was broadly connected with the Arabian peninsular over a long period of time (including the Miocene, 25 m.y. BP), though when this whole landmass joined Eurasia is uncertain. Possible dispersal routes between Africa and Asia through the Arabian peninsular are discussed by Banister & Clarke (1977). India was, however, also a part of Gondwanaland until it separated, together with Madagascar, probably in the Lower Cretaceous. Stocks of some fishes could therefore have found their way to Asia with the Indian landmass. Until more is known about Cretaceous freshwater fishes we can only speculate. Madagascar lacks characiform fishes and has none of the characteristic freshwater fishes of Africa except a few cichlids; from this Regan long ago concluded that the separation of Madagascar from Africa must be very ancient, a hypothesis now supported by geophysical studies.

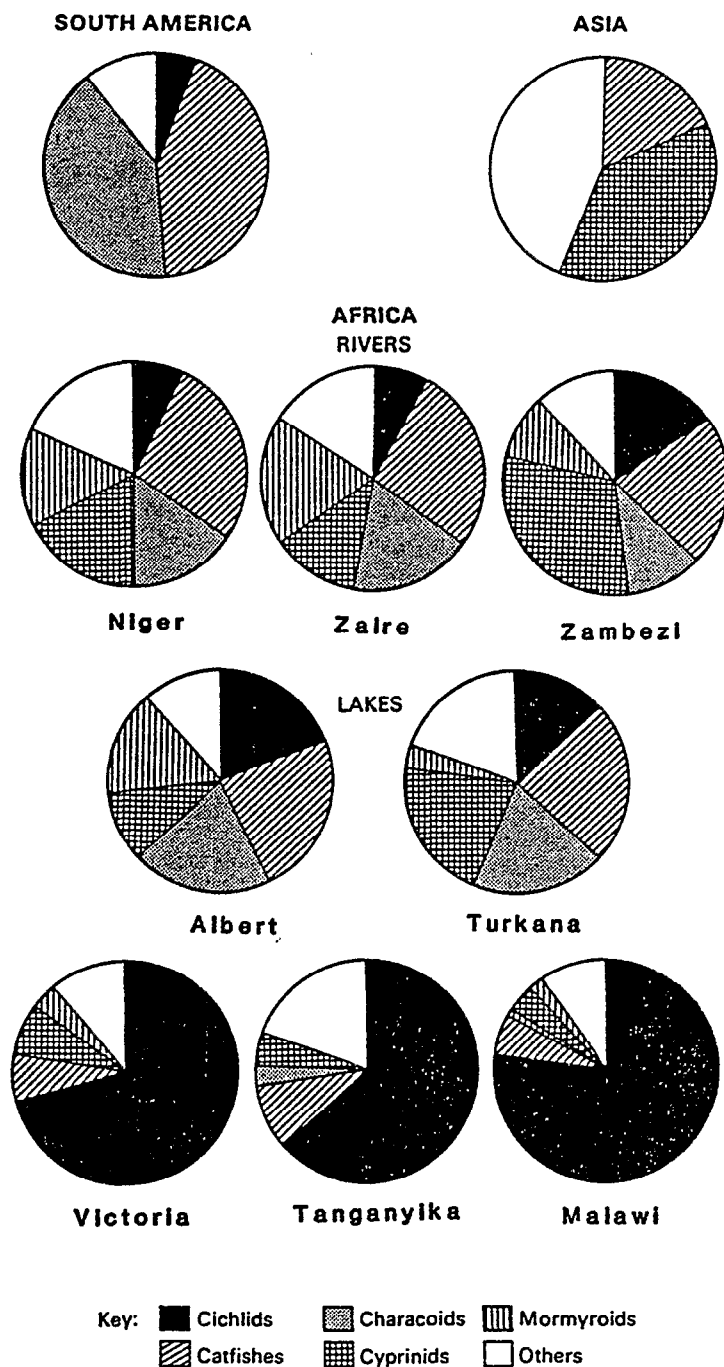


Figure 2 : The proportional composition of the freshwater fish faunas of South America (Brazil), Asia (Thailand), African rivers and African Great Lakes. Numbers of species expressed as a percentage of the known fauna (1 per cent = 3.6°). Note relative importance of Cichlidae in African lakes and cypriniform fishes (Characoidei and Cyprinidae) in rivers (after Lowe-McConnell, 1969).

To sum up : the African freshwater fish fauna now consists of :

- a) remnants of archaic elements of wide distributions such as the dipnoan lungfish and the osteoglossid *Heterotis niloticus*, which have living relatives in South America and Australia, and South America and Southeast Asia respectively;
- b) endemic families which have evidently evolved within the African landmass;
- c) elements shared with South America, indicating their Gondwanaland origin;
- d) elements shared with the Oriental region, some of which may have Gondwanaland ancestors, others, as indicated by the shared genera, resulting from much more recent faunal exchanges;
- e) marine immigrants, from which freshwater species have evolved and others moving from sea to freshwater either seasonally, during the life cycle, or sporadically.

The families shown in Table 1 are very unequally represented. The families Cichlidae and Cyprinidae have by far the most species, cichlids with at least 700, mainly in lakes, cyprinids with some 475 species (see Daget *et al.*, 1984), mainly in rivers, followed by the endemic family Mormyridae with nearly 200 species (Taverne, 1972; Daget *et al.*, 1984) and the endemic siluriform family Mochokidae with ca. 155 species. African characiforms number over 200 species when the ca. 109 characids (a mixed group of small species, see Poll & Gosse, 1963; Poll, 1967; Daget *et al.*, 1984) are added to the 90 distichodontid and 7 citharinid species (genera revised by Vari, 1979). Over 100 species each of bagrid and clariid catfishes occur in Africa. At the other end of the scale, many families are represented by only one or two living species : the freshwater families Denticipitidae, Osteoglossidae, Pantodontidae, Notopteridae, Gymnarchidae, Cobiidae, Malapteruridae, Nandidae, and the freshwater members of the marine families Carchariidae, Pristidae, Dasyatidae, Elopidae, Megalopidae, Galaxiidae, Ariidae, Synbranchidae, Cynoglossidae, (Poll, 1973; Roberts, 1975).

Cichlids spawn in still waters so were preadapted, in this way as in others, to colonize lakes. There are only about 22 cichlid genera in African rivers, but adaptive radiations have produced very numerous endemic genera and species in the Great Lakes. For example, 33 of the 37 cichlid genera in Lake Tanganyika are endemic, and 20 of the 23 cichlid genera in Lake Malawi (see Chapter 2). The relationships between cichlid genera are being studied (Greenwood, 1978, 1979, 1980, 1981; Liem, 1980, 1981; Stiassny, 1981), as is their ecology, for example in Lake Victoria (Van Oijen *et al.*, 1981), Lake Malawi (Ribbink *et al.*, 1983), and Lake Tanganyika (Brichard, 1978; and the Japanese/Zaire team, Kawanabe, 1983, Hori *et al.*, 1983). The tilapias, now so important as food fishes throughout the tropics, are cichlids endemic to Africa, although they have been distributed to other continents for fish culture. Trewavas (1983) now recognizes four genera : *Tilapia*, in which both parents share guarding duties but do not mouth-brood, *Sarotherodon* (mainly in West Africa) in which both parents share mouth-brooding of eggs and young, *Oreochromis*, the maternal mouth-brooders so important as food fishes in the Great Lakes, and *Danakilia* (restricted to Danakil desert springs). Data on the biology of tilapias in natural waters and in culture were collated by Pullin & Lowe-McConnell (1982).

Another percoid family, the Centropomidae, is represented in African freshwaters by the predatory *Lates niloticus*, which grows to 120 kg. Widely distributed from West Africa to the Nile system, its ecology has been studied in Lake Chad by Hopson (1972) and Loubens (1979). Offshore forms of *Lates* have evolved in Lakes Albert and Turkana, and Lake Tanganyika has a species flock of four endemic species (Greenwood, 1976 a), whose biology has been studied by Coulter (1976). *L. niloticus* was introduced to various lakes including Victoria and Kyoga in the 1950s where it rapidly became established (Gee, 1969); it has since had a profound effect on the cichlids of the waters of Lake Victoria (Barel *et al.*, 1985).

The African ostariophysian fishes include very numerous cyprinids (475 species in 23 genera, Daget *et al.*, 1984), mostly feeders on benthic invertebrates and vegetable debris. The immense genus *Barbus* (292 species) includes some species growing to 90 cm long, important food and sport fish (see Banister, 1983), and numerous small species, very similar in appearance and hard to identify, often endemic to a particular river system. Fishes of the genus *Labeo* (revised by Reid, 1978; 81 species in Daget *et al.*, 1984), suctorial-mouth detritus feeders, include some growing to 80 cm long. Several *Labeo* species have supported important fisheries in rivers and lakes, but overfishing them on their upriver spawning migrations has led to their decline. *Vari-*

corhinus (23 species) also includes some valued food fishes. Among 20 other cyprinid genera over a dozen include only one or two species. Among the bariliine cyprinids revised by Howes (1980), African species formerly included in *Barilius* are now assigned to *Raiamas* (16 species, with others in India and Southeast Asia), *Leptocypris* (4 species) and *Opsaridium* (9 species). The large *O. microlepis* and *O. microcephalus* are fished as they migrate up affluent rivers from Lake Malawi. Among the small lacustrine zooplankton-feeding cyprinids, *Engraulicypris* is now considered to be monotypic, *E. sardella* endemic to Lake Malawi. This species and the comparable *Rastineobola argentea*, endemic to Lake Victoria, are increasingly important food fishes in their respective lakes.

African characiformes fall into three groups (Vari, 1979), but relationships between these groups and with the Neotropical characoids are not yet determined. The monospecific Hepsetidae with *Hepsetus odoe*, a primitive characiform, was thought by Fink & Fink (1981) to be close to the South American genera *Hoplias* and *Ctenolucius*. The Citharinidae includes three genera, the monospecific *Citharidium*, *Citharinops* (2 species) and *Citharinus* (6 species; Daget *et al.*, 1984). They are deep-bodied, mud-sucking fishes, groups of three sympatric species share habitats in West Africa and another three in Zaire (see Daget, 1962). The related Distichodontidae (90 species in 17 genera; Daget *et al.*, 1984) in addition to the macrophyte-feeding *Distichodus* (22 species) and some small related forms, now includes genera formerly assigned to the Ichthyboridae; these are long slender fishes, found mainly in Zaire, specialized to feed on the fins of other fishes (Matthes, 1961). The characid assemblage of some 109 species in 18 genera (Daget *et al.*, 1984) includes large piscivorous *Hydrocynus* (6 species); *H. vittatus* in the Zambezi system and *H. brevis* and *H. forskalii* in West Africa have been much studied as these piscivores greatly affect the biology of other fishes (see Jackson, 1961; Balon, 1974; Lauzanne, 1975; Lewis, 1974 b; Bell-Cross, 1976). The omnivorous *Alestes*, which often change their main diets in wet and dry seasons, include the large species *A. baremose* and *A. dentex*, widely distributed across West Africa to the Nile, important food fishes which migrate up rivers to spawn (see Durand, 1978, Paugy, 1978). There are also numerous smaller characid species (ca 50 species in 14 genera, see Poll, 1967; Daget *et al.*, 1984).

The eight families of siluriform catfishes include three also present in Asian freshwaters (Bagridae, Clariidae, Schilbeidae), two occurring in the sea (Ariidae, Plotosidae) and three endemic ones (Mochokidae, Amphiliidae, Malapteruridae). *Arius gigas*, which grows to 1 m and over 50 kg over muddy bottoms in the Niger, is the only true freshwater arid in Africa. The Bagridae (ca. 16 genera and 100 + species; Poll, 1957, 1973) includes very large *Chrysichthys* species in the rivers of West Africa and Zaire, and a flock of six *Chrysichthys* species has evolved in Lake Tanganyika (Poll, 1953). *Bagrus* is one of the main predators over a wide area and supports important fisheries in the Great Lakes, *B. docmac* in Lake Victoria and *B. meridionalis* in Lake Malawi, as well as in rivers. *Auchenoglanis* species are particularly abundant in equatorial West Africa, but the omnivorous *A. occidentalis* has a very wide distribution. In the Zaire River small species of endemic bagrids live over sandy bottoms in swift water (Poll, 1957, 1959). The Schilbeidae (8 genera and 42 species) includes small almost transparent, laterally-compressed openwater-living species in West Africa and Zaire, several of which have become very abundant in the pelagic zone of the new man-made lakes (Reynolds, 1970; Lewis, 1974a; Mok, 1975); the more robust *Schilbe mystus* and *Eutropius* species are very widely distributed.

The family Clariidae (14 genera, see Poll, 1977, with 100+ spp. in Africa), elongated catfishes with long dorsal and anal fins and no dorsal fin spines, includes two widely distributed genera *Clarias* and *Heterobranchus*. Africa has over 50 nominal species of *Clarias*, compared with but 12 in Asia; their surprising absence from the Arabian Peninsula is discussed by Banister & Clarke (1977). Most *Clarias* live over muddy bottoms where they are omnivorous feeders (see Bruton 1979 a, b). An arborescent respiratory organ in a cavity above the gills enables *Clarias* to live in very deoxygenated water and to wriggle through damp grass, which helps to explain their wide distribution. Clariids living in the open waters of the Great Lakes, (*Xenoclaris* endemic to Lake Victoria and *Dinotopterus* in Lakes Tanganyika and Malawi) or in turbulent well-oxygenated rivers (*Gymnallabes* in the Lower Zaire) have lost these accessory respiratory devices. A number of anguilliform genera are adapted for burrowing. A monotypic albino clariid

(*Uegitoglanis*), which lacks eyes, lives in subterranean waters in Somalia. The large *Dinotopterus*, of which there is a species flock in Lake Malawi, belongs to the *Heterobranchus* group. There are about nine species of *Heterobranchus* in Africa, of which the large *H. longifilis* (growing to over 170 cm long) is a widely distributed food fish; *Heterobranchus fossilis* occurs in Lower Pleistocene deposits in India.

The endemic family Mochokidae (9 genera, 155 species) includes 108 species of *Synodontis* (see Poll, 1971), catfishes with heads protected by bony armour and with formidable dorsal and pectoral spines. Most are bottom dwellers, exploring soft deposits with the ventral mouth surrounded by barbels, but a few species live inverted, taking food or oxygen (Roberts, 1975) from the water surface; these species have reversed countershading. *Synodontis* species are often distinctively spotted or coloured, the young marked differently from the adults. In the Niger river at Kainji, eighteen species of *Synodontis* were taken from between two coffer-dams (Motwani & Kanwai, 1970). This family also includes another eight genera mainly of smaller species living in streams; the multispecific *Chiloglanis* is widely distributed, but the other genera are mostly restricted to the Zaire basin and have relatively few species.

The Amphiliidae (8 genera, ca. 50 species) is an endemic family of stream catfishes, many armoured, with elongate slender bodies, living over hard bottoms in torrential streams. The electric catfish *Malapterurus electricus* is widely distributed in rivers and common in Lakes Tanganyika and Kariba; the dermal electric organ can give a formidable shock.

Of the endemic families, the Mormyridae has the most numerous genera (18) and species (about 200, Taverne, 1972; Daget *et al.*, 1984), these are especially abundant in Zaire and West Africa. Nocturnal fishes, they retreat under banks by day. Mormyroids all have electrogenic and electroreceptor organs, and they appear to use the electric signals to sense their way around their habitats and for communication. The mormyroid *Gymnarchus niloticus*, an electric fish growing to over one metre long, moves by undulations of the long dorsal fin; this species makes a floating nest in swamps. Another endemic osteoglossomorph, *Pantodon*, is a short compressed species well-known to aquarists. Found from Zaire to the Lower Niger, *Pantodon* lives close to the water surface feeding on insects; it makes a floating nest for its large eggs.

The Kneriidae (3 or 4 genera, ca 24 species; see Poll, 1965, 1973) and Phractolaemidae (monotypic) are endemic families of small species, the latter probably derived from the former. Like the cyprinids these produce 'alarm substances', pheromones which warn other members of the school to take avoiding action if one is damaged. Greenwood (1975) considered these to be primitive ostariophysan fishes (Anotophysii), as distinguished from the Otophysi which comprise the previously accepted Ostariophysii; they share various unique osteological and anatomical features with the old Ostariophysii, but do not have Weberian ossicles, the chain of small bones (derived from vertebral elements) which link the swimbladder to the inner ear, and which assist underwater hearing. The many *Kneria* species live in swift mountain streams in Angola, Cameroon and West Africa, feeding mainly on aufwuchs (algae with contained organisms). The microphagous *Phractolaemus* lives in swampy regions of the Lower Niger and Zaire; it has an accessory respiratory organ. The monotypic Cromeriidae (*Cromeria nilotica*) and monotypic Grasseichthyidae (*Grasseichthys gabonensis*) were included in the family Kneriidae by Greenwood (1975).

The endemic Polypteridae (the monospecific *Calamoichthys*, an elongate form in West Africa, and *Polypterus*, with about nine species in Zaire and West Africa), one eastwards to the Nile, are archaic fishes with brachypterous paired fins and shiny ganoid scales. The adults respire partly by a swim-bladder lung; the young have external gills (see Poll & Deswattines, 1967). Voracious carnivores, they do not aestivate.

Of the non-endemic families, the Osteoglossidae includes one African species *Heterotis niloticus*, a microphagous fish which grows rapidly in fish ponds. From West Africa to the Nile, *H. niloticus* lives in a swampy places, where the parents make a nest among aquatic plants in the wet season and there guard the young. Other archaic fishes include the dipnoan lungfish *Protopterus* (four species, for distribution see Poll, 1961), well known for their ability to breathe air and to aestivate in a mucous cocoon in the dry season. Carnivorous fishes with strong crushing jaws, their diet includes molluscs. They nest in swamps; the tadpole-like young have four pairs of external gills. The small percomorph family Nandidae also occurs in the three tropical areas;

most numerous in Asia, where they go into brackish water, Africa and South America, each have two endemic genera of small species (*Polycentropsis* in many West African rivers).

Of families present both in Africa and Asia, the Anabantidae, a very important family of food fishes in Asia, is represented in Africa by a few (ca. 29) small species of *Ctenopoma* and *Sandelia*. These have a labyrinthine accessory respiratory organ in a suprabranchial cavity which enables them to live in deoxygenated water. *Ctenopoma* eggs are laid in a bubble nest at the water surface. The family Notopteridae includes elongate, laterally flattened fishes propelled by undulations of the long anal fin; Africa has but two species, *Papyrocranus afer* (which resembles the Asian *Notopterus*, Greenwood, 1963) and *Xenomystus nigri*, both found mainly in West Africa and Zaire, where they live on the bottom amongst plants, feeding nocturnally on insects and small fishes; they have an epibranchial respiratory organ. The Channidae, (= Ophiocephalidae) (one genus, 3 species), long cylindrical predatory fishes with accessory respiratory organs, are common in Asia; of the three species in Africa, *Parachanna obscura* is widely distributed in marshy places. Mastacembelids which also occur in Asia are anguilliform; most live among rocks. The African subfamily has two major lineages: *Caecomastacembelus*, a species flock of 22 species endemic to the Lower Zaire rapids (some with reduced eyes, Roberts & Stewart, 1976), and *Afromastacembelus* of 16 + species including 7 species endemic to Lake Tanganyika which may not be a monophyletic group (Travers, 1984).

It is notable that so many of the species of fish present in both Africa and Asia have accessory respiratory organs; this suggests the value of such organs for wide distribution and that the fishes have had to cross swampy, or otherwise deoxygenated, waters in their passage from one continent to the other, or to survive deoxygenated conditions at some time in their life history (as discussed by Roberts, 1975; Roberts & Stewart, 1976).

Of the peripheral families of marine origin, the Clupeidae (taken to include the Congothrisidae and Dussumieridae by Greenwood *et al.*, 1966) are represented by 20 genera with 38 species (See Poll, 1974; Daget *et al.*, 1984). These are mostly small species living in rivers, but they have colonized and multiplied in the new man-made lakes Volta and Kainji, exploiting the zooplankton-feeding niche (Reynolds, 1970; Otobo, 1974). Lake Tanganyika has two monospecific endemic genera which support one of the main fisheries in the lake; one of these (*Limnothrissa miodon*) has been stocked in Lake Kariba where it now supports an important fishery. Lake Mweru has three clupeid species. The Synbranchidae, long eel-like fishes, are represented by *Opisternon afrom* in West Africa (Rosen & Greenwood, 1976). True eels include six species of *Anguilla*, of which four species migrate up the rivers of eastern Africa from the sea (Frost, 1955), and at least one species occurs in Lake Kariba (Balon, 1974) and Lake Malawi. About six tetraodont pufferfish species live in the Zaire basin. An endemic freshwater flatfish (*Dagetichthys*) and an endemic stingray (*Dasyatis garouaensis*) both occur in the Benue River far from the sea; once thought to be relics of seas here in ancient times, they are probably more recent immigrants (see Reid & Sydenham, 1979).

2 - RIVERINE AND LACUSTRINE FISH FAUNAS.

Figure 2 also shows clear basic differences in composition between faunas of the main river systems of Africa (Niger, Zaire, Zambezi) and those of the East African Great Lakes (Victoria, Tanganyika, Malawi), which have cichlid-dominated faunas. Of these three river systems, the Zaire has the richest fauna; Poll (1973) reported 669 known species of which 548 (80%) in «42 genera» are endemic to the Zaire basin (excluding Lake Tanganyika). Each expedition produces new species. Geographical distributions within Africa are considered by Roberts (1975) and Greenwood (1983). In addition to the Ostariophysi which dominate the Zaire fauna (23% siluriforms, 16% cypriniforms, 15% characiforms), this basin has a spectacular number of mormyrids (75 species, 18% of the fauna). The catfishes include 36 mochokid species, 27 bagrids and 23 clariids, many belonging to endemic genera. The Cichlidae (32 species) also includes endemic genera. The polypterids are here represented by seven species, *Protopterus* by two species. The numerous endemic genera include the mormyrid *Genyatremus*, the characid *Clupeopetersius*, the distichodontids *Mesoborus*, *Phagoborus*, *Belonophago* and *Eugnatichthys*, the cypri-

mid *Leptocypris*, the bagrid *Gnathobagrus*, the clariid *Channallabes*, and cichlids *Teleogramma*, *Heterochromis* and *Steatocranus*. The very complex fish communities and the ecology of Zaire fishes are well described by Poll (1959), Gosse (1963) and Matthes (1964), with Roberts & Stewart (1976) reporting on the rapids in the Lower Zaire.

The Niger fauna has many species in common with the Nile (some of them subspecifically distinct). This subtropical «sudanian» region, which includes the savanna rivers south of the Sahara from Senegal on the Atlantic coast across the Chad basin to the Nile, has a much richer and more diverse fauna than has the Zambezi savanna system south of the equatorial zone. This sudanian fauna has recently been reviewed by Daget & Durand (1981). Both Niger and Nile have the osteoglossid *Heterotis niloticus*, the mormyroid *Gymnarchus niloticus*, *Cromeria nilotica*, and share species of the mormyrid genus *Hyperopisus*, and the catfishes *Siluranodon*, *Clarotes* and *Mochokus*. However, West Africa has a much richer fauna than the Nile River; 74 of the 115 species in the Nile also occur in the Niger, and 22 of these are found in the Zaire too (Greenwood, 1976b, 1983). Poll (1957) considered the differentiation between Niger and Nile faunas to be almost as great as between Niger and Zaire. Fish common to Zaire and Niger but not found in the Nile include species of *Phractolaemus*, *Pantodon*, the characoids *Hepsetus* and *Bryconaethiops*, the cyprinid *Garra* and certain *Polypterus*. Although the sudanian region has far fewer fish species than the Zaire, it still has a very diverse fauna, made up primarily of Ostariophysi. In addition to families found in Zaire, West Africa has an osteoglossid, a nandid and denticipid, and also *Calamoichthys*, a second polypterid genus. This sudanian fauna is probably a very ancient one, formerly even more widely distributed than at present, a suggestion supported by the presence in Tanzania of a fossil denticipid (Greenwood, 1960) and a fossil osteoglossid (Greenwood & Patterson, 1967), both families now restricted to West Africa and the Nile. Relict status also seems to explain the five Nile species (*Protopterus aethiopicus*, *Polypterus bichir*, *P. senegalus*, *Ichthyoborus besse* and *Oreochromis niloticus*) occurring in the upper Lualaba tributary of the Zaire system (Greenwood, 1976b), which Poll (1975) had interpreted as indicating a former connection between the Nile and Upper Zaire.

Many of these sudanian savanna species, which often grow larger than their ecological counterparts in forested streams (the «guinean» fauna, considered below), migrate long distances upriver and out onto the vast floodplains annually, so it is not surprising that these species have become widely distributed.

In West Africa the sudanian fishes living in the waters of the extensive savanna-covered plain, and guinean species in forested streams, have been distinguished by Daget & Iltis (1965) and Daget & Durand (1981). Ecological replacement species are well marked in some genera (for example among clariids, anabantids and cyprinodonts). The frequent river captures and variations in climate over long geological periods have resulted in guinean and sudanian species occurring within the same river system, separated neither by watersheds nor waterfall barriers. Ecological conditions, particularly presence or absence of forest, would appear to account for their continued coexistence within one river system; it may also be difficult for a species to extend its range when the river already holds a related species. Guinean species are found in the upper reaches of the Niger tributaries and in the higher more dissected country in Guinea, but in the Ivory Coast the situation is reversed as they occur in the lower reaches of the river which are here forested, while the open country to the north carries sudanian species. This suggests that the overriding factor is shade or food from the forest. The Dahomey Gap, where a belt of savanna comes right to the coast, breaks the guinean forest zone into western and eastern sectors, affecting the distribution of certain guinean fishes.

Though the ichthyofauna of the Nile drainage basin is the second largest in Africa, this is due to the highly endemic and diversified faunas of the four lakes: Victoria, Kyoga, George and Edward; the Nile River itself has but 115 species, of which 26 (ca. 23%) are endemic. There are interesting differences in the Nile fauna from those of Zaire and West Africa) the Nile lacks clupeids and has fewer osteoglossids and notoapterids (*Heterotis*, *Xenomystus* and *Cromeria* occur in the Nile, but neither *Pantodon* nor *Papyrocranus*); the Nile *Barbus* also appear to be of a different phyletic lineage from those in West Africa and Zaire (Greenwood, 1976b). The less rich and diversified fauna of the Nile compared with the Zaire probably reflects the different histo-

ries of the basins, but also the less varied habitats and the greater seasonality of conditions in the Nile compared with the Zaire.

The Nile has, however, a somewhat more diversified fauna than the Zambezi (115 vs ca. 101 species), though less diverse than the Angola Province (ca. 270 species). Only six Nile River species occur in the Zambezi River, and these same six are also in the Zaire (*Hydrocynus vittatus*, *Micralestes acutidens*, *Schilbe mystus*, *Heterobranchus longifilis*, *Malapterurus electricus*, *Aplocheilichthys hutereaui*) (Greenwood, 1976b). Banister & Bailey (1979) discussed Poll's (1957, 1963) suggestion that the fauna of the Upper Lualaba had some nilotic affinities, but could find no support for this theory.

The Zambezi fauna is much less rich in families well represented in West Africa and Zaire; it lacks polypterids, and has but seven kinds of mormyrids and eleven of characoids, though the number of cyprinid species (ca. 22) is high. The fauna of the Lower Zambezi appears to have more in common with the Zaire fauna than has that of the Upper Zambezi and Kafue which share the watershed with the Zaire headwaters; this is discussed by Bowmaker, Jackson & Jubb (1978). The peripheral marine families Carcharinidae, Pristidae, Elopidae and Megalopidae are represented in the Lower Zambezi, together with four *Anguilla* species.

As Figure 2 shows clearly, the lacustrine faunas are dominated by cichlids, with the exceptions of Lakes Albert and Turkana (Rudolf) which have retained nilotic riverine faunas. Most of the cichlid species are endemic to a particular lake. The explosive speciation of these cichlids within a lake has enabled them to exploit (or resulted from the exploitation of - the order in which speciation and adaptive radiations occur is still under discussion) the many environmental opportunities offered by lakes compared with rivers. The non-cichlid faunas of these Great Lakes reflect those of the drainage system within which the lake lies: Victoria draining to the Nile, Tanganyika to the Zaire and Malawi to the Zambezi. Of Victoria's 38 non-cichlid species, 16 (42%) are endemic; of Tanganyika's 67 non-cichlid species, 47 (70%) are endemic; of Malawi's 42 species, 26 (62%) are endemic. In Lake Albert and Lake Turkana, endemism among the non-cichlids is much lower (only 3/36 species, 8%, in Lake Albert, and 2/32 species, 5%, in Lake Turkana). The higher endemism in Lakes Tanganyika and Malawi has been thought to reflect the depths and probably greater ages of these lakes, though the greater diversity of Tanganyika's fauna must be related in part to the rich Zairean stocks which have contributed to it. Roberts & Stewart (1976) pointed out that 7 of the 10 families which contribute endemics to the Lake Tanganyika fauna are also represented by endemics in the rapids of the Lower Zaire River (viz Characidae, Cyprinidae, Bagridae, Clariidae, Mochokidae, Cichlidae and Mastacembelidae). The only family with endemics in the rapids but missing from the lake is the Mormyridae, while the lake has endemic clupeids, cyprinodonts and centropomids missing from the rapids. Robert & Stewart (1976) suggested that evolution in the rocky habitats of the Zaire basin has played a major role in preadapting such families as Cichlidae, Mastacembelidae, Mochokidae, Clariidae, Bagridae and Cyprinidae to the rocky littoral of Lake Tanganyika, especially in the case of the endemic Zairean cichlid genus *Lamprologus*. Riverine fishes that become established as lacustrine species often spawn on rocky wave-washed shores.

3 - RESPONSES TO ENVIRONMENTAL CONDITIONS.

3.1 - Water level changes - seasonality. The ecology and behaviour of tropical riverine fishes is geared primarily to changes in water level. Such changes occur with the rains and the position of the waterbody in the drainage system. In equatorial regions rain falls throughout the year, with slight equinoxial peaks. With increasing latitude rainfall becomes more seasonal, both north and south of the equator (a mirror image effect particularly well shown in Africa). Rains follow the overhead sun, so floods generally come at the warmest time of year. The equatorial rainfall regime supports rainforest, that at higher latitudes grassland, where vast floodplains are inundated seasonally. Some rivers have two peak levels a year. In equatorial rivers these may be caused by the equinoxial rainfall peaks (as in the Nzoia River flowing into northern Lake Victoria), but in the huge Zaire system mainly by tributaries reaching far to the north and south

of the equator flooding at «opposite» times of year. The Niger in Nigeria also has two floods a year, in this case a «white flood» due to local rains and a «black flood» from rainfall in the Upper Niger which takes time to travel downriver.

The majority of riverine fishes spawn at the start of the flood season (see Welcomme, 1979). The floods cause an explosive growth of food organisms. The young fish are thus produced at a time of maximum food production and when luxuriant vegetation provides cover from the numerous predators. Growth is extremely rapid in the highwater season, and fat stores are laid down which tide the fish over the dry season, when they have to retreat to the river beds or are stranded in savanna pools with little to eat. Thus reproduction, feeding and growth are all geared to the flood cycle. The annual breeding and cessation of growth in the dry season make it very much easier to determine ages and growth rates of these fishes than for those living in equatorial lakes, which may spawn at any time of year and grow continuously throughout the year. The higher the latitude, the more seasonal the environment, affecting all aspects of the fish's life history (as discussed by Lowe-McConnell, 1975, 1979).

3.2 - Main sources of food. Collating data from many studies reveals a general sequence of main food sources for the fishes (Lowe-McConnell, 1975). In forested headwater streams allochthonous forest products (vegetable debris, insects and spiders etc) form the basis of the food webs. As rivers widen and deepen, benthic invertebrates assume greater importance as fish food. Floodplains provide rich and varied food of both plant and animal origin seasonally : epiphytic algae are important in waters open to the sun. Fish populations are geared to exploit these seasonal increases in food production. Where rivers are dammed forming lakes, plankton (phyto- and zooplankton) becomes a main food, and soft bottom deposits with their infaunas of worms and insect larvae, molluscs etc, provide rich feeding for fishes adapted to extract these. Temperature stratification in still waters will, however, lead to the bottom waters being deoxygenated, cutting the fishes off from the benthic invertebrate foods that they used in rivers. In estuarine reaches, crustaceans are often increasingly important ; as the heavier more saline water underlies the lighter freshwater, benthic organisms are able to penetrate further upriver than are surface dwelling ones.

3.3 - Man-made lake studies. Lakes form when rivers are dammed, either naturally or by man. Recent ecological studies in the new man-made lakes have illuminated ways in which riverine fish communities become converted to lacustrine ones. Some riverine fishes drop out of the new lake faunas in a regular sequence, generally because they cannot adapt to changed feeding conditions, for example by being cut off from benthic foods by deoxygenated bottom water, or to changed breeding conditions, when no longer able to migrate up streams to spawn. Lakes challenge species to exploit new sources of foods (such as the Ephemeroptera nymphs, *Povilla*, abundant in the wood of drowned trees), and new breeding conditions. Once the lake is stabilized, species new to the area may appear and become abundant. These presumably originate from strays which only become established when they find suitable ecological conditions. In Lake Kariba, for example, the immigrant *Alestes lateralis*, which spawns on the roots of the abundant floating water plants, replaced the shore-spawning *Alestes imberi* (Balon, 1974).

3.4 - Deoxygenation. Deoxygenation provides a special challenge to fishes living in warm waters, and some form of aerial respiration has evolved in many families. The small cyprinodontiform fishes use the well-oxygenated water below the surface film. Accessory respiratory organs are found in thirteen other families in Africa : Osteoglossidae and Synbranchidae (shared with South America and Asia), Notopteridae, Cobitidae, Clariidae, Channidae, Anabantidae, Mastacembelidae (all shared with Asia), and in five endemic families, Protopteridae, Polyp- teridae and the monotypic Pantodontidae, Gymnarchidae, Phractolaemidae. This suggests the survival value of aerial respiration, as almost all the archaic families still extant practice this. Aerial respiration in so many families shared with Asia suggests that the passage between Asia and Africa may have selected forms with aerial respiration.

Many of these archaic families are represented by few species. The largest air-breathing families in Africa are the Clariidae and Anabantidae. The Clariidae appear to be the only air-breathing

Ostariophysans in Africa (though air-breathing characoids as well as various catfishes occur in South America). None of the African cyprinids or cichlids appear to air-breathe. Roberts (1975) stressed the vital role that parental care has for the survival of young in oxygen-poor habitats (over and above its anti-predation value); the primary division fish which care for their young are all air-breathers.

3.5 - Interactions between types of fishes. As mentioned above, primary and secondary division fishes tend to exclude peripheral fishes from faunas. Also, in West Africa, sudanian and guinean faunas seem to be more or less mutually exclusive. Roberts (1975) described a «taxon cycle», i.e. the succession of taxa that inhabit a waterbody as it becomes available for colonisation and gradually acquires a richer fauna, then loses taxa as conditions become unfavourable again. Climatic fluctuations and the evolution of habitats lead to changes in the fish communities living in them. Genera which appear in places that can only support a few species (ecologically simple waters, often with a highly irregular food supply) include *Barbus*, *Clarias*, anguillid eels, cyprinodontiforms (of which *Nothobranchius* species are well-adapted to temporary habitats by their resistant resting eggs), tilapias and other cichlids. As conditions change, communities gradually become more complex; certain families only appear when five or more other families are already represented. Stenotopic species will probably displace eurytopic ones. The whole forms a complex of interacting species, the dynamically changing environmental conditions affecting the relative numbers of the component species. Studies of such interactions are in their infancy, but Matthes (1964) gave a good picture of the ecological conditions permitting so many fish species to coexist in the very complex fish communities in the central Zaire basin.

Roberts (1975), commenting on the success of the Mormyridae and Ostariophysi (which together contain 90% of the primary division fishes of Africa), attributed their success to the key adaptations involving (1) non-visual sense organs (electric organs in the Mormyridae, Weberian ossicles, pheromones and barbels in the Ostariophysi), and (2) diversification of feeding habits. Bowmaker *et al.* (1978) considered the essential characteristic of riverine fishes, as opposed to lacustrine ones, to be their generalization; also that most of them swim upstream to spawn and have a high potential fecundity compared with cichlids in lakes. Poll (1980) when comparing the ostariophysan-dominated riverine faunas with cichlid-dominated lacustrine ones, drew attention to environmental factors favouring one or other group :

(1) that ionic concentrations are higher in lakes than in rivers, which favours the euryhaline cichlids rather than the stenohaline ostariophysans;

(2) that rivers become deoxygenated locally whereas lakes stratify giving them a good depth of water above a more stable deoxygenated layer; the physostome Ostariophysi are better able to surface rapidly when need arises, whereas the physoclist cichlids can live at depths without having to surface;

(3) rivers are generally more turbid than lakes; the senses of the ostariophysans are well suited to life in turbid waters, whereas cichlids are sight-orientated and those living deep in lakes have well developed lateral line organs. Clearly many selection pressures have resulted in the cichlids and ostariophysans dominating lacustrine and riverine environments respectively.

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RÉSUMÉ

Les 2000 espèces connues de poissons d'eau douce africains appartiennent à différentes familles (tableau 1) qui comprennent :

- (1) des vestiges de groupes archaïques à très vaste répartition ;
- (2) un grand nombre de familles endémiques (14) représentées surtout par des poissons assez primitifs et qui ont, de toute évidence, évolué sur le continent africain lui-même ;
- (3) des éléments communs avec la région néotropicale dont l'origine remonte probablement au Gondwana, avant la séparation de l'Afrique et de l'Amérique du Sud au Crétacé supérieur ;
- (4) des éléments communs avec la région orientale ; bien que certains puissent provenir également du Gondwana, l'existence de 8 genres communs à l'Afrique et à l'Asie est le signe d'échanges faunistiques plus récents ;
- (5) des espèces « périphériques » de familles à affinités marines dont certaines sont à l'origine d'espèces d'eau douce en Afrique, et d'autres comprennent des espèces qui pénètrent en eau douce.

La composition des faunes en Afrique, Asie et Amérique du Sud ainsi que dans les lacs et rivières d'Afrique est comparée dans la fig. 2. En Afrique comme ailleurs, l'ichtyofaune des rivières est composée principalement d'ostariophysiens, mais les rivières et marais africains possèdent également des groupes endémiques isolés sur le plan phylogénétique. Les faunes lacustres sont connues pour leur spéciation spectaculaire, notamment chez les Cichlidés ; les poissons à affinités marines (Clupeidae et Centropomidae) prospèrent également dans certains lacs. Beaucoup de familles communes à l'Afrique et à l'Asie possèdent une forme de respiration aérienne, ce qui laisse supposer l'importance de celle-ci pour leur survie et leur répartition.

Les différentes familles de poissons sont très inégalement représentées en Afrique : les Cichlidae, avec plus de 700 espèces, et les Cyprinidae, avec 475, sont les plus diversifiées, suivies par la famille endémique des Mormyridae (198 espèces) et celle des Mochokidae (environ 155 espèces), alors que beaucoup d'autres familles, y compris des familles endémiques, ne sont représentées que par 1 ou 2 espèces.

Quelques réponses aux variations des conditions de milieu ont été rapidement passées en revue, telles que :

- (1) les changements saisonniers du niveau de l'eau ;
- (2) les sources de nourriture principales dans différentes parties du système fluvial ;
- (3) les nouvelles conditions offertes par les réservoirs ;
- (4) la désoxygénation des eaux.

Le matériel allochtone est la source de nourriture principale dans le cours supérieur des rivières, les invertébrés benthiques devenant progressivement importants dans l'alimentation des poissons lorsque la rivière s'élargit et devient plus profonde.

Durant la mise en eau saisonnière des plaines d'inondation, un nombre plus important de niches est disponible, comme c'est le cas dans les lacs où le plancton et le benthos constituent une nourriture abondante et où la stabilité plus grande au cours de l'année permet une plus grande spécialisation trophique. Dans les lacs de barrage, les nouvelles conditions de nutrition et de reproduction offrent d'autres possibilités mais aussi certaines difficultés aux espèces lotiques qui doivent s'adapter aux conditions lacustres.

Les interactions entre différents types de poissons sont passées en revue rapidement ainsi que les raisons possibles de succès des ostariophysiens dans les rivières et des Cichlidae dans les lacs.

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