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CHAPTER 7
FRESHWATER FISHES OF THE ZAMBEZI BASIN

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7.1 INTRODUCTION

The Zambezi is the largest African river flowing into the Indian Ocean, draining a basin of around 1.2 to 1.5 million km^2 (estimates vary; Davies 1986). The modern river basin is the result of various geological processes that occurred during the Quaternary, which include a dramatic series of river captures, the deposition of wind-blown sands in the western part of the basin, the formation of the Rift Valley, and the rejuvenation of the erosion cycle in the eastern part. These forces have influenced its fish fauna and contributed to its present diversity (about 160 species) in the river system proper plus several hundred endemic cichlids in Lake Malawi (Bell-Cross 1972, Jackson 1986, Skelton 1994).

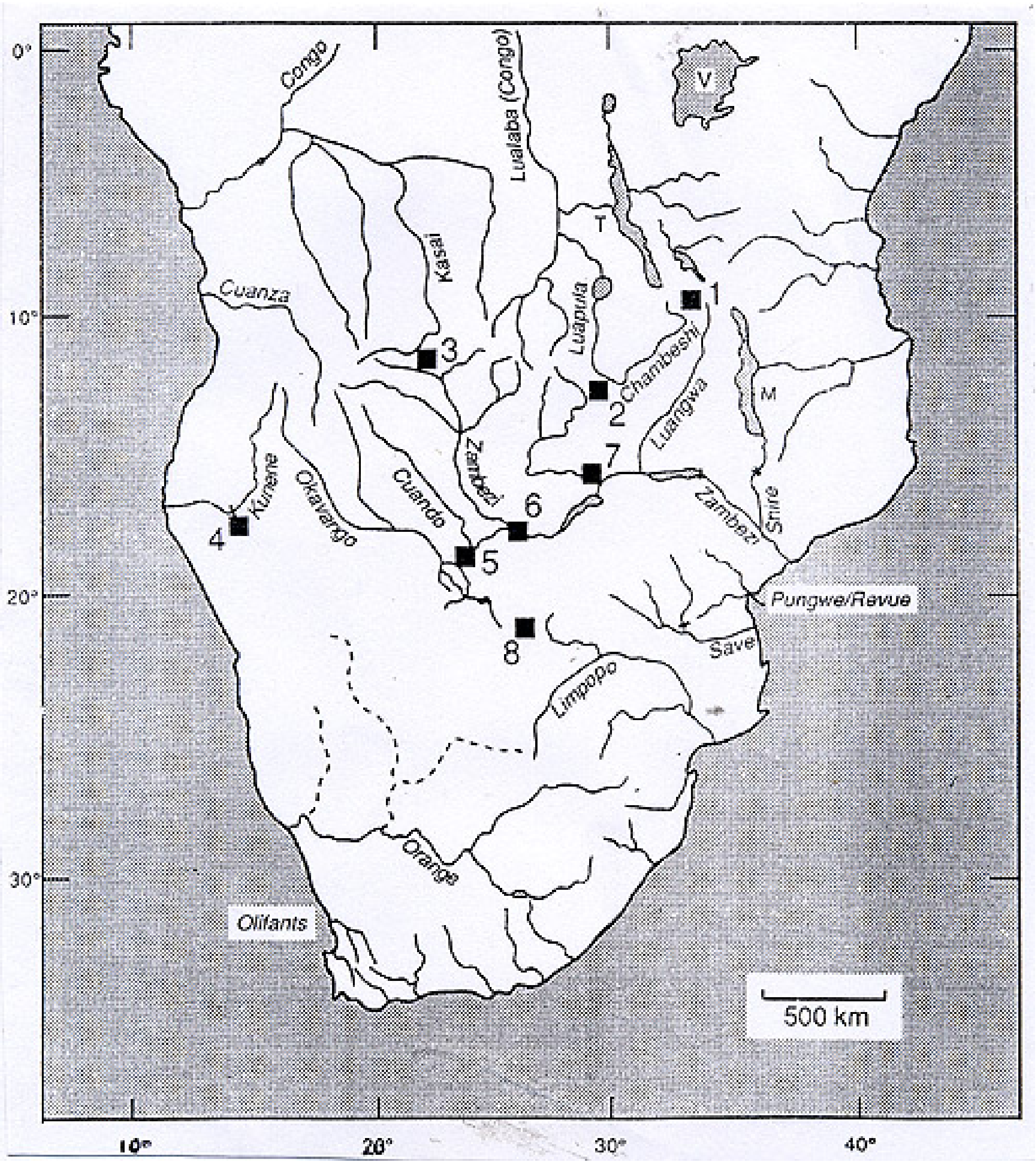
The Zambezi-Congo watershed forms a natural zoogeographical boundary that marks the northern limit of the Zambezian ichthyological province (Roberts 1975). This includes areas that were once part of the Zambezi system, such as the Cunene and Okavango basins, or the Limpopo system. Fish in the east coast rivers from the mouth of the Zambezi south to the Phongola, in northern Kwazulu-Natal, are also a part of the Zambezian system since they have been connected in various ways with the Zambezi itself. The fish populations of these rivers also include elements of the east coast fauna and they are a major component of the fauna of the Middle and Lower Zambezi as well. Some understanding of the evolution of the system and the zoogeography of the fish is essential in understanding its biodiversity and this issue is addressed in the following section.

7.2 THE ORIGIN AND ZOOGEOGRAPHY OF ZAMBEZIAN FISHES

A fundamental question in biology is why are there so many species of living things? In searching for the answer biologists need to know what determines the distribution of these species and why they occur in some areas and not others. The discipline of biogeography deals with these matters using evidence from many disciplines, including biology, geology, palaeontology and geography. This paper gives an introduction to the zoogeography of the fishes of the Zambezi Basin and it draws heavily on Skelton (1993, 1994), which should be referred to for further information.

The land surfaces of today represent the end of an immensely long period of geological activity. In the last 100 million years southern Africa has been subjected to major geological processes like the formation of the Rift Valley and associated fault systems that caused the Zambezi and Luangwa valleys. The western parts of the basin have been relatively stable over a long period of time, but the eastern parts have been subjected to considerable change, including uplifting that initiated a series of erosion cycles. In parts of Zimbabwe, for example, uplifting led to six cycles of erosion (Lister 1979) in which the eastern highlands were uplifted several times while the western Kalahari basin remained relatively static. These cycles allowed westward erosion by east coast rivers like the Limpopo and Zambezi, which captured several formerly southward-draining rivers. River capture is one of the most important geological influences on fish distribution and several major river captures in southern Africa (Figure 7.1) have influenced the distribution of fish.

Figure 7.1 The major river systems of southern Africa. The principal river captures, which are indicated by the symbol ■, are as follows: 1, the ancient link between the Upper Congo and Luangwa/pre-Lake Malawi systems, possibly via Lake Rukwa; 2, the Chambeshi-Kafue link severed by the Luapula; 3, an Upper Zambezi tributary captured by the Kasai; 4, the southward flow of the Cunene disrupted after capture by a west-flowing stream; 5, the Kwando-Okavango connection severed by tectonic movements that divert the Kwando into the Zambezi; 6, the Upper Zambezi captured by the Middle Zambezi following rejuvenation of the erosion cycle; 7, the Kafue captured by the Middle Zambezi; 8, the former link between the Upper Zambezi and Limpopo systems broken by the diversion of the former and the infilling of the Kalahari Basin. T = Lake Tanganyika, V = Lake Victoria and M = Lake Malawi.



Fish cannot move overland or live out of water for any length of time and this restricts the ways in which they can move from one river system to another. Changes in the direction of river flow, either because of earth movements or by river capture, are among the most important. Falling sea levels are also important since the courses of rivers that currently discharge separately into the sea often join at a lower sea level. For example, the Pungwe, Buzi and Zambezi rivers were probably connected when the sea level fell during the last Ice Age. The Zambezi and Pungwe are still connected by low-lying wetlands and these coastal connections must have been more extensive when the climate was wetter than it is today. Furthermore, a wetter climate may also have allowed fish to cross from one watershed to another, provided suitable marshy areas existed. Fish have been seen to move across the Congo-Zambezi watershed in this way (Bell-Cross 1965).

7.2.1 **The major fish groups**

Fish are the oldest true vertebrates and jawless fish (Agnatha) first appeared in the Silurian era (320 million years BP). They flourished for about 40 million years but most of them had disappeared by the end of the Devonian. About 60 or so species of these fish still survive today but none of them occur in Africa. The Devonian era (300 million years BP) is often called "the age of fish" since four distinct forms of jawed fish originated during this period. Only two of them have survived and flourished to the present day. The cartilaginous fish (Elasmobranchs), which include the sharks and rays, are a marine group and are found in all the oceans. A few species penetrate freshwater and one of them, the Sawfish, *Pristis microdon*, has been collected in the Lower Zambezi and the Zambezi Delta (Bell-Cross 1972). A second species, the Bull Shark, *Carcharhinus leucas*, has been taken in the Zambezi at Tete and some of its tributaries, like the Ruenya River just before the Zimbabwean border. It is said to have been taken at Chirundu (Bell-Cross & Minshull 1988), but this record is not listed in earlier books (Jubb 1960, 1967, Jackson 1961a) and it may never, in fact, have penetrated the Zambezi beyond the Cabora Bassa Gorge.

In the early Devonian, the bony fish (Osteichthyes) produced two quite distinct and possibly unrelated lineages. The first of them, the lobe-finned fish (Crossopterygii) are the ancestors of the terrestrial vertebrates. They were abundant in the Devonian but their numbers decreased after that and today they are represented only by the coelacanth and the lungfishes. The coelacanth *Coelacanthus granulatus* from the Karoo sediments of Zimbabwe, is one of the few named fossil fishes from the basin and, unusually, it was found in sediments deposited in freshwater, while all other coelacanths, including the only living species, lived in the sea (Bond 1973). The lungfish were once distributed on all continents but now have a relict distribution in Australia (1 species), South America (1 species) and Africa (4 species). One of the African species, *Protopterus annectens*, occurs in the Middle and Lower Zambezi valley while another, *P. amphibius*, is found in the floodplains of the Lower Zambezi.

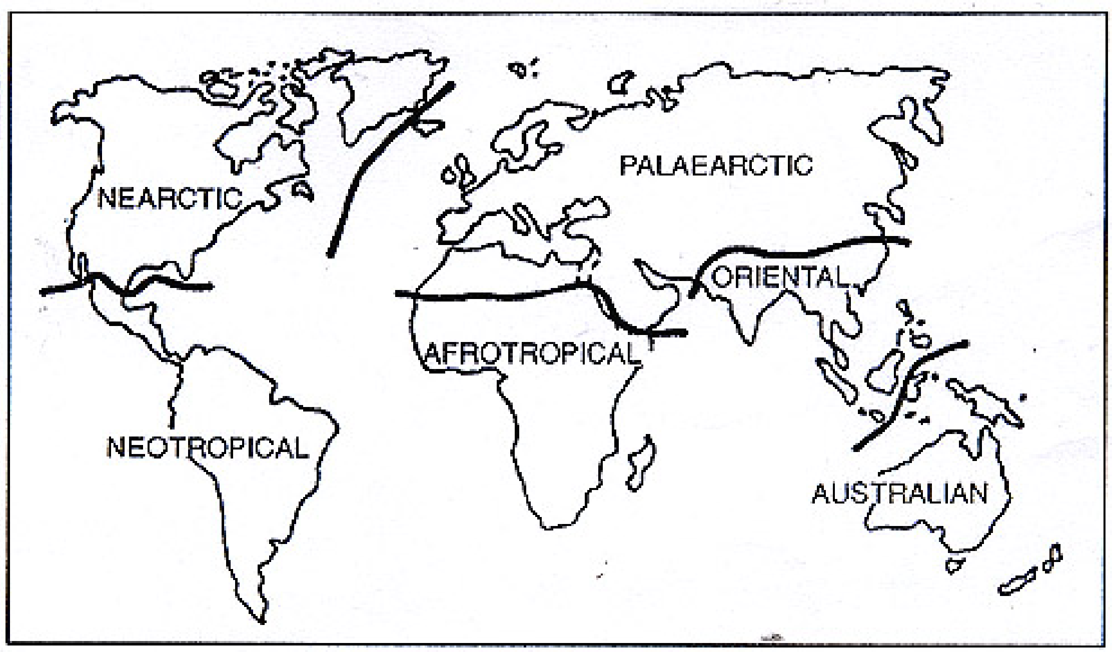
The largest and most diverse vertebrate group, with some 20,000 species, is the ray-finned fish (Actinopterygii). They come in an astonishing variety of body forms and are found in almost any water that can support fish. These range from the furthest depths of the ocean to high mountain lakes, and include inhospitable environments like hot springs and temporary pools. One of the other named fossil species found in the basin, *Namaichthys molyneuxi*, which lived in Zimbabwe about 250 million years ago (Bond 1973), is a representative of one of the most ancient bony fish groups, the Palaeoniscoidea. Primitive forms like the palaeoniscids were progressively replaced by more advanced ones during the 200 million years between the Devonian and the mid-Cretaceous. Only a few archaic bony fish have survived to the present time and none occur in the Zambezi system.

The most advanced group, the Teleostei, first appeared in the fossil record in the mid-Jurassic (130 million years BP) and by the mid-Cretaceous (90 million years BP) they had become the most abundant and successful group of bony fish. The radiation of the teleosts coincided with a period of rapid continental drift and their distribution and evolution was greatly influenced by this activity.

7.2.2 The influence of continental drift

In 1876 Alfred Russell Wallace divided the world into six major zoogeographical regions on the basis of their distinctive fauna that included a number of families unique to each (Figure 7.2). Although he could not have known it at the time, Wallace's regions reflect the way in which the continents moved during the last 150 million years. The linkages between the families of freshwater fishes of Africa and those in other continents clearly reflect the impact of continental drift.

Figure 7. 2 The principal zoogeographic regions of the world, after Alfred Russell Wallace. The River Nile has enabled African fish to penetrate Egypt and the Levant, and these areas could be treated as extensions of the Afrotropical.



About 150 million years ago the single supercontinent of Pangea began to break into Laurasia (North America and Eurasia) and Gondwanaland. This early split is reflected by the fact that only two Zambezian families of fish are also found in the Palaearctic and Nearctic regions (Table 7.1). One of them, the Cyprinidae, is the largest family of freshwater fish with more than 1600 species occurring throughout North America, Eurasia and Africa.

The break-up of Gondwanaland began about 70 million years ago. Australia was the first to be isolated from the rest and only one family, the Galaxiidae, occurs in both the Afrotropical and Australian regions. The sole African galaxiid species is restricted to the southern Cape and does not occur anywhere else on the continent. South America seems to have broken away next and only two families of Zambezian fish also occur in the Neotropical. The Characidae, which include well-known species like the African tigerfishes and the South American piranhas, are most diverse in the Neotropics and may have prevented the cyprinids from invading South America. The Cichlidae,

Table 7.1 The families of fish found in the Zambezi Basin and their wider distribution. N = number of species in family in the basin, FW = freshwater, M = marine.

		Afrotropical	Oriental	Neotropical	Palaearctic	Nearctic	Australian	N	Origin
Protopteridae	Lungfish	■						2	FW
Mormyridae	Snoutfish	■						9	FW
Kneriidae	Knerias	■						4	FW
Cyprinidae	Carp, barbs	■	■		■	■		46	FW
Distichodontidae	Citharinids	■						5	FW
Characidae	Characins	■		■				6	FW
Hepsteidae	African pike	■						1	FW
Claroteidae	Claroteid catfish	■						1	FW
Amphiliidae	Amphiliid catfish	■						4	FW
Schilbeidae	Butter catfish	■	■					2	FW
Clariidae	Air-breathing catfish	■	■					7	FW
Malapteruridae	Electric catfish	■						1	FW
Mochokidae	Squeakers	■						13	FW
Aplocheilidae	Killifish	■	■					4	FW
Cyprinodontidae	Topminnows	■	■		■	■		4	FW
Cichlidae	Tilapias, bream	■	■	■				31	FW
Anabantidae	Climbing perch	■	■					2	FW
Mastacembalidae	Spiny eels	■	■					3	FW
Anguillidae	Eels	■	■	■	■	■	■	4	secondary FW
Gobiidae	Gobies	■	■	■	■	■	■	2	secondary FW
Megalopidae	Tarpons	■	■	■	■	■	■	1	M
Eleotridae	Sleepers	■	■	■	■	■	■	2	M
Ambassidae	Glassies	■	■	■	■	■	■	2	M
Mugilidae	Mullets	■	■	■	■	■	■	2	M
Syngnathidae	Pipefish	■	■	■	■	■	■	2	M
Monodactylidae	Moonies	■	■	■	■	■	■	2	M
Sparidae	Sea bream	■	■	■	■	■	■	1	M
Carcharhinidae	Sharks	■	■	■	■	■	■	1	M
Pristidae	Sawfish	■	■	■	■	■	■	1	M

which include the tilapias and their allies, are most diverse in Africa and also extend into Asia with a few species in the Middle East and India.

Cichlids are one of eight families that occur in southern Asia as well as in Africa. The link between the Afrotropical and Oriental regions seems, therefore, to be rather stronger than the link between the Afrotropics and the Neotropics. Other families that occur in both regions include the air-breathing catfishes (Clariidae), many of which are similar to the well-known African catfish, *Clarias gariepinus*, the climbing perch (Anabantidae) and the spiny eels (Mastacembalidae).

Most of the evolution of African fish over the last 60 million years or so took place within the continent. Consequently, half of the fish families found in the Zambezi Basin are of African origin and are found nowhere else. Madagascar evidently broke away from Africa before this radiation took place and only three Zambezian families also occur on that island.

Finally, another eight families are of marine origin and have a global distribution in all oceans. Two goby species (Gobiidae) are found in the Zambezi and breed in fresh water. Four species of eels (Anguillidae) occur in the system but they breed at sea after spending up to 15 years in rivers and streams. The remaining six families represent estuarine species (including the shark) that occasionally penetrate fresh water and all have been collected in the lower reaches of the Zambezi.

7.2.3 **Post-Gondwana dispersion**

The freshwater fish fauna of the Zambezi Basin is made up of two major elements, the Zambezian and the East Coast. These elements evolved during the early Tertiary (about 50-60 million years BP) when the drainage patterns of southern Africa were quite different from those of the present (Figure 7.3a). The Zambezian fish fauna arose and evolved in the area of Upper Zambezi as it was then. This includes the present-day Cunene, as well as the Upper Kasai and the Chambeshi that were formerly part of the system but were later isolated through river capture. The Blotched Catfish, *Clarias stappersii*, is an example of a species whose distribution reflects its Zambezian origin (Figure 7.3b). The East Coast fauna lived in the then relatively short rivers that drained into the Indian Ocean. A few species, like the East Coast Barb, *Barbus toppini*, still retain this distribution (Figure 7.3b). Most others have been greatly modified, principally by penetrating inland along the Zambezi and Limpopo rivers.

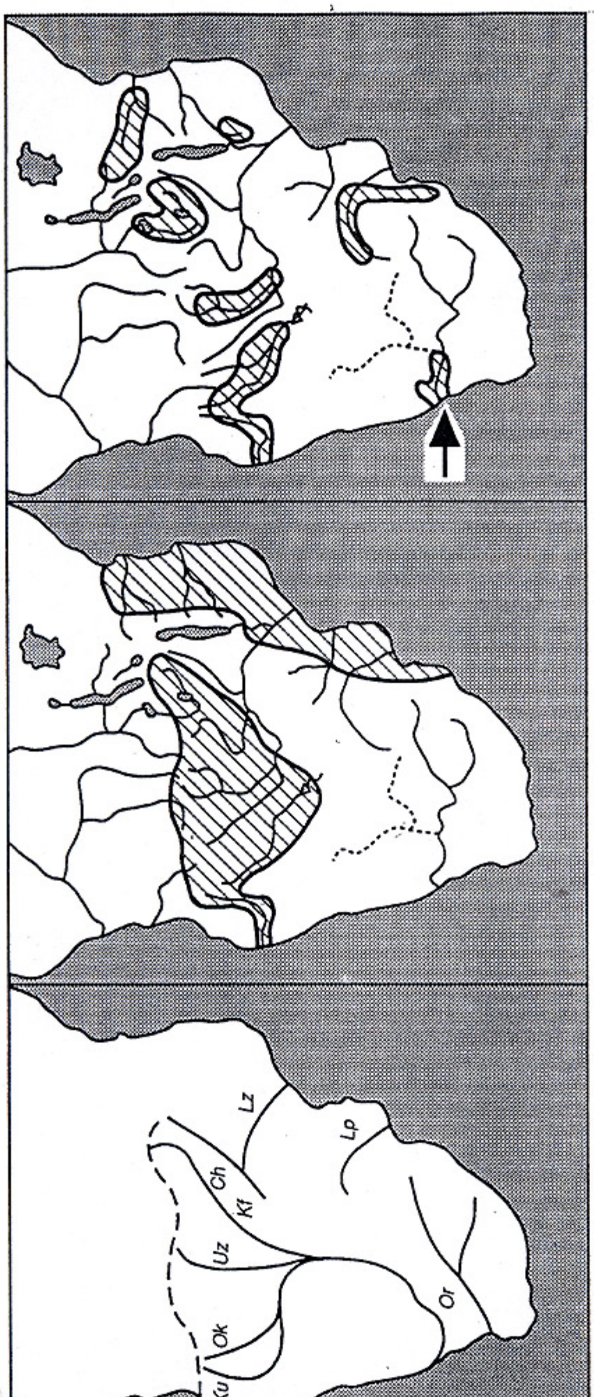
During this time, the Zambezi evidently drained into the Atlantic Ocean somewhere near the present-day mouth of the Orange River. Supporting evidence for this is provided by some species with a universal distribution in southern Africa or others like the River Sardine, *Mesobola brevianalis*, which has a fragmented but widespread distribution. It includes an isolated population in the Lower Orange (Figure 7.3c) which probably dates from the time the Zambezi discharged in this area.

Drainage patterns changed dramatically during the mid-Tertiary (about 20-30 million years BP). The course of the Upper Zambezi was diverted from the south to the southeast, i.e. from the Orange to the Limpopo. This event seems to have coincided with the infilling of the Kalahari basin (Figure 7.4a). The link between the Kafue and Chambeshi rivers was severed when the Chambeshi was captured by the Luapula to become part of the Congo drainage. The connection between the Kafue and the Upper Zambezi was severed when the former was captured by the Middle Zambezi. Evidence that the Zambezi once flowed to the Indian Ocean via the Limpopo is provided by the distribution of some Upper Zambezi fish in the Limpopo, such as the River Sardine (Figure 7.3c)

Figure 7.3 (a) Drainage patterns in southern Africa during the early Tertiary. Ku = Cunene, Ok = Okavango, Uz = Upper Zambezi, Kf = Kafue, Ch = Chambeshi, Lz = Lower Zambezi, Lp = Limpopo, Or = Orange.

(b) The typically Zambezian distribution of the Blotched Catfish, *Clarias stappersii* (left), which includes the Cunene, the upper Kasai and the Lake Bangweulu/Chambeshi system, and the typical east coast distribution of the East Coast Barb, *Barbus toppini* (right).

(c) The distribution of the River Sardine, *Mesobola brevianalis*; the isolated population in the Lower Orange (arrow) suggests an ancestral link with the Zambezi via the Kalahari.



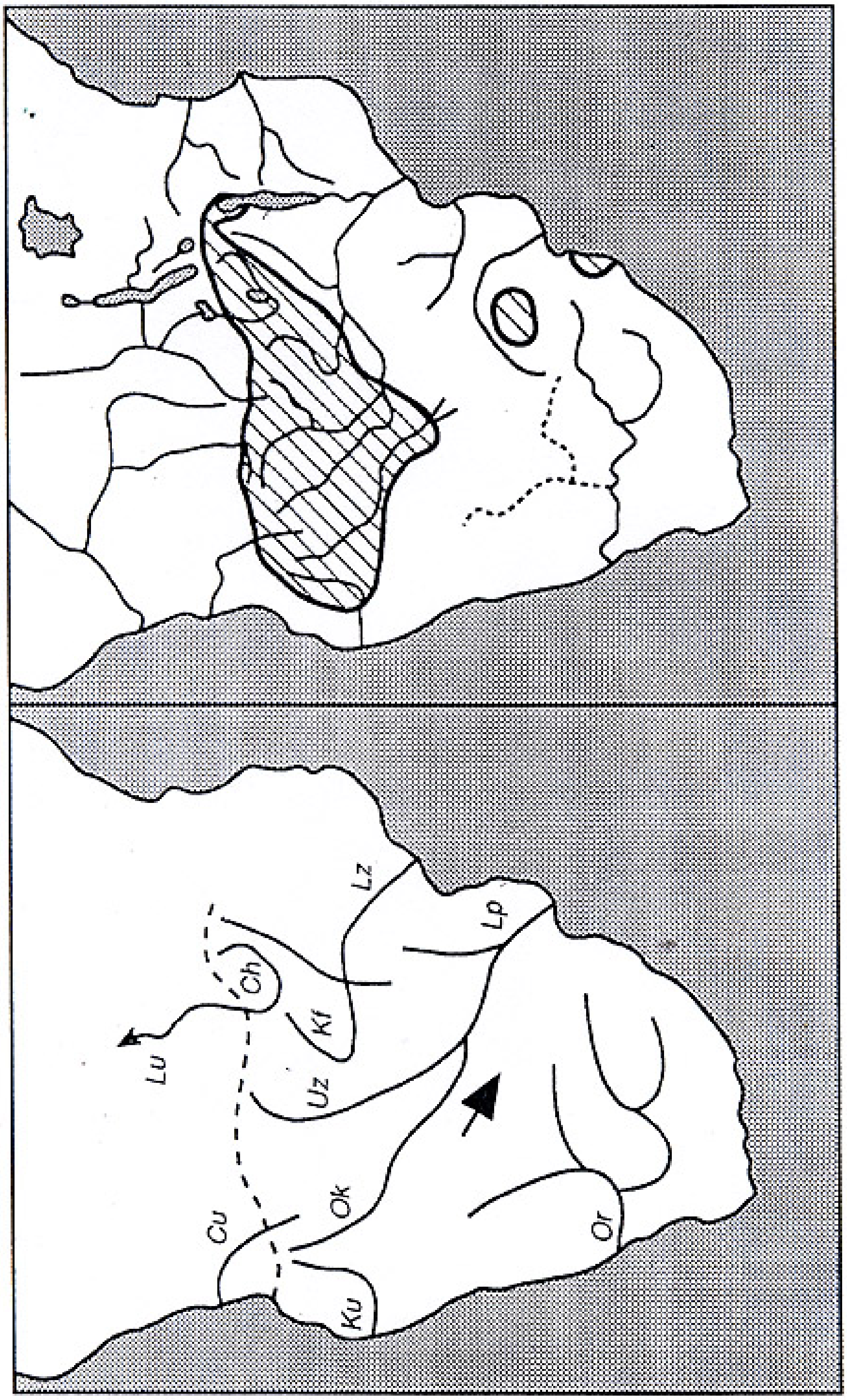
7.3(c)

7.3(b)

7.3(a)

Figure 7.4 (a) Drainage patterns in southern Africa during the mid-Tertiary. Abbreviations as in Fig. 7.3, plus Cu = Cuanza, Lu = Luapula.

(b) The distribution of the Hyphen barb, *Barbus bifrenatus*, showing its presence in rivers now isolated from the Zambezi, a relic of the former Zambezi-Limpopo connection.



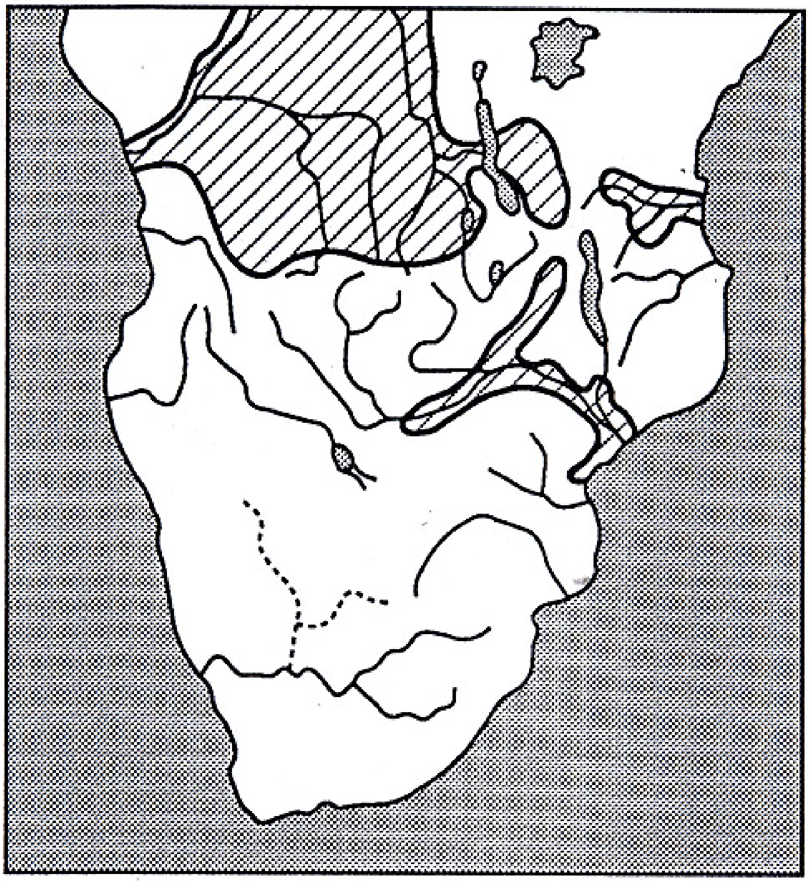
7.4(b)

7.4(a)

and the Hyphen Barb, *Barbus bifrenatus*. The latter are widespread in the Upper Zambezi and occur in the Cunene, Cuanza, Kafue and Chambeshi rivers, all streams isolated from the Zambezi by river capture. In the south an isolated population in the high-altitude tributaries of the Limpopo reflects the former connection between the two systems (Figure 7.4b).

The Hyphen Barb also occurs in the upper reaches of Lake Malawi and there was evidently a connection between the Chambeshi, the Congo and the Lower Zambezi systems in this region. The exact nature of this connection is unclear since the tectonic movements that formed the Rift Valley have obscured the evidence. Nevertheless several Upper Zambezi and Congo fish species have reached the Lake Malawi system by this route, while others have reached the Middle and Lower Zambezi, possibly via the Luangwa. They include well-known species like the Manyame labeo, *Labeo altivelis*, and the Vundu, *Heterobranchus longifilis* (Figure 7.5).

Figure 7.5 The distribution of the Vundu, *Heterobranchus longifilis*, a Congo species that was able to colonize the Middle and Lower Zambezi from the north.



The connection between the Zambezi and the Limpopo was severed in the late Tertiary when uplift during the Pliocene (about 5 million years BP) rejuvenated the erosion cycle, enabling the Middle Zambezi to capture the Upper Zambezi, creating the Victoria Falls and the Batoka Gorge (Figure 7.6a). This enabled a number of Upper Zambezi fish to colonise the Middle and Lower sections of the river. The Sickle-fin Barb, *Barbus haasianus*, found in the Upper Zambezi and the Chambeshi as well as the Lower Zambezi, Lower Shire and Pungwe rivers, is an example (Figure 7.6b).

Figure 7.6 (a) Evolution of the modern drainage pattern in southern Africa during the late Tertiary, with the capture of the Upper Zambezi by the Middle Zambezi. Abbreviations as in Figs. 3 and 4, plus Lm = Lake Malawi. The broken line indicates the ancestral Zambezi-Congo watershed.

(b) The distribution of the Sickle-fin barb, *Barbus haasianus*, an Upper Zambezi species that was able to reach the floodplains of the Lower Zambezi.

(c) The southern distribution of the Tigerfish, *Hydrocynus vittatus*, another invader of the Middle Zambezi. It was unable to reach the Kafue or Lake Malawi because of physical barriers to its upstream movement.

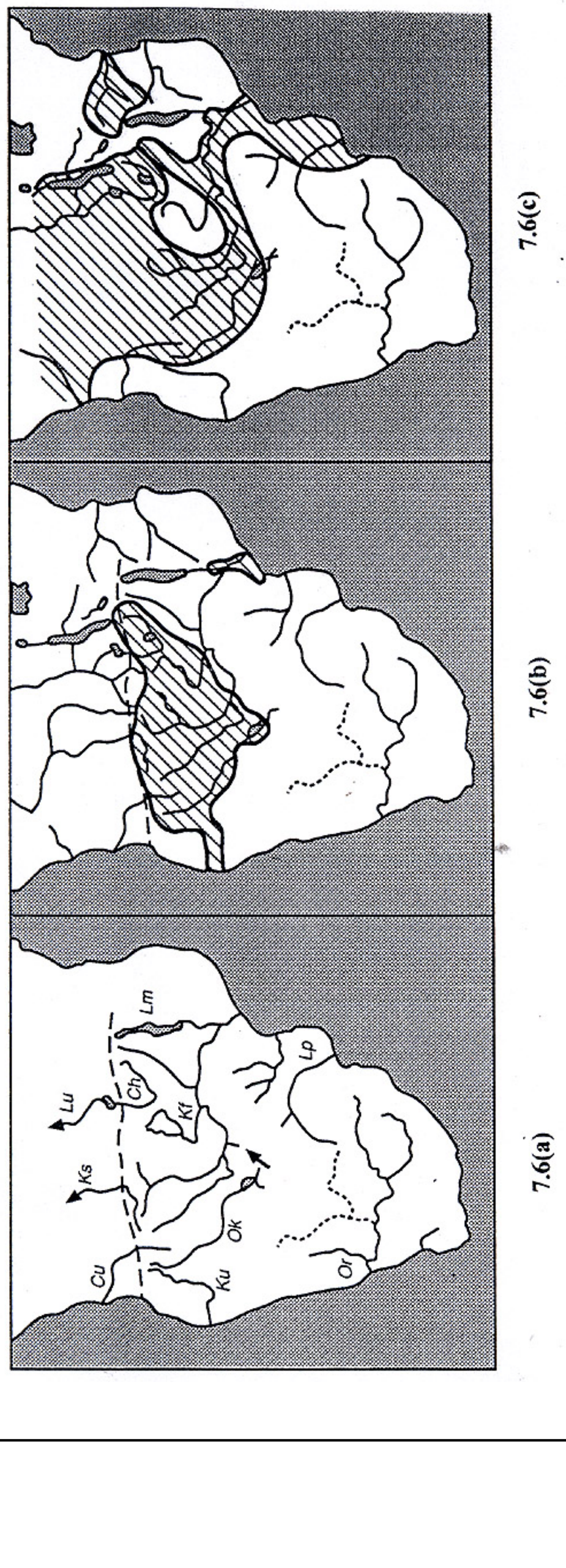
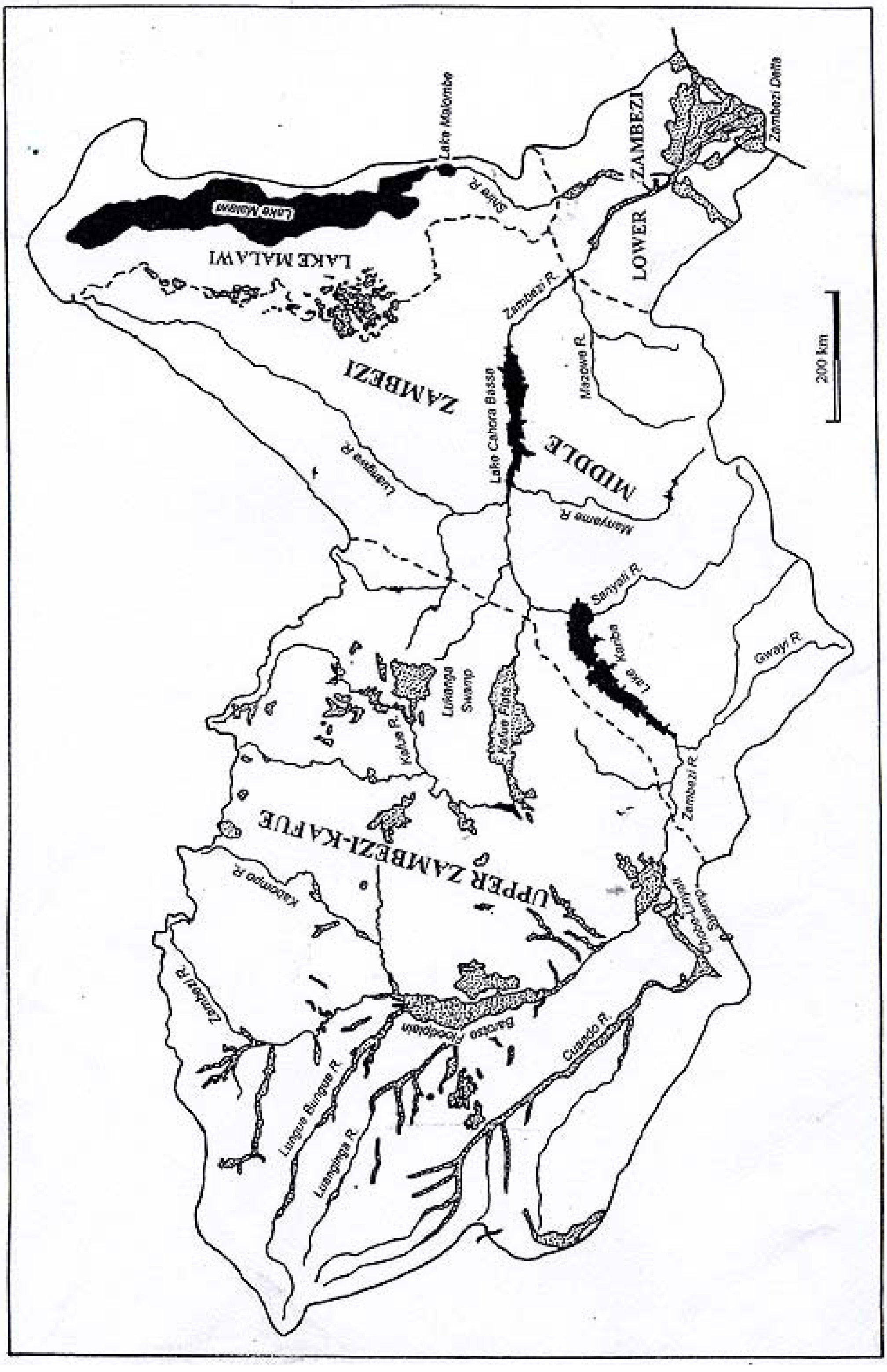


Figure 7.7 The Zambezi Basin and its four major ichthyological divisions. The principal floodplains and wetlands are indicated by stippling, while the larger lakes and reservoirs are indicated by black shading. Based on a map drawn from data in Hughes & Hughes (1992). Note that the Okavango system is excluded, but it resembles the Upper Zambezi-Kafue by having extensive wetlands and floodplains.



The interrupted distribution of the Sickle-fin Barb came about because of its habitat preferences. It is a species that inhabits swamps and floodplains. These are widespread in the Upper Zambezi but absent in the lower river except along the coast and along the Lower Shire. Here the Sickle-fin Barb has been able to establish itself. One reason why the Middle Zambezi was so inhospitable to many Upper Zambezi species was a lack of vegetation growing in the water. This made them vulnerable to predation by the Tigerfish, *Hydrocynus vittatus*, itself an invader (Figure 7.6c). After the capture of the Upper Zambezi, it colonized the river downstream and its major tributary, the Luangwa and spread southwards into rivers of the east coast. The tigerfish could not invade the Kafue or go up the Shire into Lake Malawi because waterfalls on these rivers prevented them from moving upstream.

7.3 ICHTHYOLOGICAL REGIONS OF THE ZAMBEZI

The hydrological basin of the Zambezi can be divided into four principal ichthyological regions, each with its own distinctive fish species and families (Figure 7.7). The fish fauna in some other areas is still dominated by fish of Zambezian origin even though they are no longer linked hydrologically to the Zambezi system. The nature of these regions, and the evolution of their fish fauna, has been described in detail elsewhere (e.g. Bell-Cross 1972, Bowmaker, Jackson & Jubb 1978, Jackson 1986, Skelton 1994).

7.3.1 **The Upper Zambezi-Kafue system**

The Zambezi Basin can be divided into two distinct regions by a line extending from the Victoria Falls north-eastwards along the northern escarpment of the mid-Zambezi valley in Zambia to the northern watershed of the Luangwa. To the north and west of this line lie the drainage basins of the Upper Zambezi and Kafue rivers, the first of its four ichthyological regions. These rivers drain one of the most ancient African land surfaces that has been subjected to rather gentle pressures over millennia, leading to gradual uplift and subsidence and resulting in a landscape of "swells and depressions" and low relief (Handlos 1982). The gradients of the main rivers are gentle; the Zambezi falls by only 500 m over a distance of 1080 km from its source to the Victoria Falls (Davies 1986), while the Kafue falls by 380 m in the 1500 km between its source and the Kafue Gorge (Handlos 1982).

This topography, combined with relatively high rainfall, has produced extensive swamps and floodplains that regulate the flow of the rivers so that they seldom exhibit large variations in height. The floodplains have water on them for long periods, while the low water flows are of relatively short duration. Marginal vegetation is abundant and provides cover for small fish species, and juveniles of larger ones. These rivers have been termed "reservoir" rivers (Jackson 1986) and favour the evolution of fish species. Consequently, there are more fish species in the Upper Zambezi than in any other part of the system, except for Lake Malawi, and many of them are adapted to living in marshes.

Special features of the fish fauna include a radiation of serranochromine cichlids in the genera *Serranochromis* (6 species) and *Sargochromis* (5 species) and of mochokid catfishes in the genus *Synodontis* (7 species), while there is a larger number of small cyprinids and characids compared to the rest of the river. Other distinctive fish in this basin include the African Pike, *Hepsetus odoe*, two anabantids (*Ctenopoma multispine* and *C. intermedium*) and two mastacembelids (*Aethiomastacembelus frenatus* and *A. vanderwaali*).

In this region, the Zambezi River and its tributaries support the most species, 89 in total, of which 29.2% are cyprinids, 21.3% are cichlids and 10.1% mochokids (Table 7.2 - see end of review). The fish fauna of the Okavango is virtually the same as that of the Upper Zambezi and reflects the fact that the two systems are still intermittently connected via the Selinda spillway, which joins the Okavango and the Chobe-Linyati at periods of very high flood. Also, some of the Upper Zambezi species are only known from single specimens, e.g. *Paramormyrops jacksoni*, or a few from isolated localities, e.g. *Barbus mattozi, Schilbe yangambianus*. There are essentially no significant differences between the two systems, which is not the case as far as the Kafue system is concerned.

The Kafue was thought to have been isolated from the Upper Zambezi in the mid-Tertiary and it has fewer species than the latter (Table 7.2). It was also isolated from what is now the Zambian Congo drainage when the Chambeshi River was captured by the Luapula at about the same time. Consequently, it was not colonized by Congo species that invaded the Upper Zambezi, e.g. *Hippoptamyrus discorhynchus* and *Hydrocynus vittatus*, or the Middle Zambezi via the Chambeshi/Lake Rukwa/Luangwa River connection, e.g. *Labeo altivelis*, *Brycinus imberi* and *Heterobranchus longifilis*. The radiation of serranochromine cichlids in the Kafue is very similar to that of the Upper Zambezi, with nine species in the former compared to eleven species in the latter (*Serranochromis altus* and *S.longimanus* are absent from the Kafue). But the mochokid catfishes differ markedly, as there are only two species in the Kafue compared to eleven in the Upper Zambezi. Despite its relatively long isolation from the Zambezi, there is only one endemic species in the Kafue system, the killifish *Nothobranchius kafuensis* (although it may extend to the East Caprivi strip, in which case it loses this status).

The Cunene was isolated from the Zambezi at about the same time as the Kafue but its fish fauna is considerably different from both of those systems. Like the Kafue, it only has 66 fish species, but 9 of them (13.6%) do not occur anywhere else in the Zambezi system, and there are many more endemics. Six species, including four cichlids, are endemic to the Cunene system, namely *Kneria maydelli*, *Barbus breviceps*, *Orthochromis machadoi*, *Thoracochromis albolabrus*, *T. buysi* and *Sargochromis coulteri*. Two of the remainder have relict distributions that reflect the ancient connection between the Upper Zambezi and the Limpopo; *Labeo ruddi* occurs also in the Limpopo and Incomati systems, and there is a localised population of *Barbus argenteus* in the northern Drakensberg escarpment of South Africa. Finally, *Labeo ansorgii*, occurs in the Kwanza system in Angola as well as the Cunene.

The Chambeshi River, which once flowed into the Zambezi via the Kafue, was isolated some time in the early Tertiary when it was captured by the Luapula to become part of the Congo system. The Chambeshi and Lake Bangweulu were cut off from the Lower Luapula by the Johnston and Mumbatuta Falls and therefore have fewer species than the Lake Mweru/Luapula system (Table 7.3). Some typical Congo forms like the clupeids (sardines) failed to reach the Bangweulu system but others, like the tigerfish, *H. vittatus* and the Vundu, *H. longifilis*, did so. Nevertheless, the Chambeshi may have been a route for some of these Congo species to invade the Middle and Lower Zambezi.

7.3.2 **The Upper/Middle Zambezi boundary: waterfalls as barriers**

The transition from the Upper to the Middle Zambezi is abrupt and sharply demarcated. At the Victoria Falls the Zambezi drops by about 100 m while the Kafue falls by about 600 m in the 30 km stretch of the Kafue Gorge. Smaller tributaries of the Zambezi and the Luangwa which rise on the western plateau, such as the Kalomo, Mulungushi and Lunsemfwa, also drop steeply over the

Table 7.3 The number of species in each family in the Mweru/Luapula and Bangweulu/ Chambeshi systems of the Zambian Congo. Based on Jackson (1961a), updated as far as possible from CLOFFA (Daget *et al*. 1984, 1986, 1991). The list is probably incomplete.

	Mweru/ Luapula	Bangweulu/ Chambeshi
Protopteridae	1	
Mormyridae	15	8
Clupeidae	3	
Kneriidae	2	
Cyprinidae	25	20
Distichodontidae	2	1
Characidae	11	8
Hepsetidae	1	
Claroteidae	1	1
Amphiliidae	3	2
Schilbeidae	3	3
Clariidae	8	6
Mochokidae	8	5
Aplocheilidae	2	1
Cyprinodontidae	4	3
Cichlidae	15	10
Anabantidae	2	2
Mastacembelidae	2	1
Total number of species	103	67

escarpment. These rivers have Upper Zambezi or Kafue species in their plateau sections, but Middle Zambezi species below (Bell-Cross 1972, Balon 1974a), and the waterfalls that separate the two systems have always been regarded as major barriers.

The appearance in Lake Kariba during the late 1960s of several fish species typically found in the Upper Zambezi opened a debate on the nature of the Victoria Falls as a zoogeographical boundary. Balon (1974a, 1974b, 1978) asserted that the falls were not a major barrier to fish movements, as previous workers had thought, because fish had always been able to survive the drop over them but could not live in the harsh conditions of the river below. He postulated that the creation of Lake Kariba had changed this situation by providing a favourable habitat and, consequently, these fish were in the process of invading the system. Southern African workers challenged this view. They argued that (a) many of the alleged invaders were species that were widespread elsewhere in the Middle Zambezi, and (b) the few true Upper Zambezi invaders were more likely to have by-passed the falls through the turbines at the hydroelectric power station (Jubb 1976, Bowmaker *et al*. 1978, Marshall 1979, Kenmuir 1984). The importance of this debate, of course, lies in the general view that human activities, in the form of hydroelectric power stations, were breaking down major zoogeographical barriers in the system, which would change the species composition downstream of them.

Now, two decades later, these ideas can be examined again and there has clearly been little movement of fish across the barrier of the Victoria Falls. Twelve Upper Zambezi species have now been recorded from the Batoka Gorge below the Victoria Falls and from Lake Kariba (Table 7.4). But only two of them, the characid *Brycinus lateralis*, which may already have been in the river, and the cichlid *Serranochromis macrocephalus*, have successfully established themselves in the lake and invaded the river below the Kariba dam (Balon 1971, Marshall 1998). They almost certainly did this by passing through the hydroelectric turbines; the only other species to have done so was the introduced sardine *Limnothrissa miodon* (Junor & Begg 1971). Movement in the reverse direction, i.e. upstream, is obviously more difficult but may not be impossible since the only eel, *Anguilla bengalensis*, to have been collected from the Upper Zambezi was collected in the header dam at the Victoria Falls power station (Bell-Cross 1974).

The fact that only a few species have been able to invade the Middle Zambezi via hydroelectric turbines calls into question the importance of these structures as a means of breaking down zoogeographical barriers. Furthermore, there are no records of fish species invading the Middle Zambezi through other hydropower schemes, like that on the Kafue Gorge. Other explanations for the presence of Upper Zambezi species below the Victoria Falls should therefore be considered and the distribution of one of them, the Dash-tailed Barb, *Barbus poechii*, may provide one.

This fish is widely distributed in the Upper Zambezi and Upper Kafue drainage basins but it has also been taken from a number of places in the Zambezi system below the Victoria Falls (Figure 7.8). It occurs in the Kalomo River above the Siengwazi Falls (which has a typically Upper Zambezi fauna; Balon 1974b), in the Batoka Gorge, and again in the headwaters of the Matetsi and Deka Rivers. This distribution pattern suggests that the Batoka Gorge may be a transitional zone between the Upper and Middle Zambezi systems. It may also reflect the drainage system in the mid-Tertiary when the Zambezi flowed southwest into what is now the Kalahari Basin (another remnant of which is visible in the Ngwezi River that flows southwest to join the Zambezi west of the Victoria Falls). This drainage pattern was severed when the Middle Zambezi captured the Upper Zambezi to create the Victoria Falls, and the existing populations of *B. poechii* may therefore be relicts from this time. The same could apply to the other Upper Zambezi species and their appearance in Lake Kariba in 1968-69 may reflect the existence of some relict populations below the Batoka Gorge. Balon (1974a, 1974b, 1978) suggested that the survival of Upper Zambezi species would be assured by the new and more favourable environment of the lake, but this does not seem to have been the case. Those species collected only in the Batoka Gorge have not moved into the lake, while those collected from the lake itself seem to have disappeared or, if present, occur in very small numbers. Evidently, the lake has not offered an especially favourable environment for them and they may have failed to compete with the more numerous native species. This behaviour is more consistent with that of relict species, rather than that of strongly invasive ones.

Table 7.4 Records of Upper Zambezi fish species from the Zambezi River below Victoria Falls (Batoka Gorge) and Lake Kariba. From data in Balon (1974a, 1974b), Kenmuir (1983), Sanyanga & Feresu (1994), Anon. (1995a), Sanyanga *et al*. (1995) and Marshall (1998), as well as unpublished records from the Natural History Museum of Zimbabwe, Bulawayo (NMZB).

Species	Batoka Gorge	Lake Kariba	Remarks (number of specimens in brackets)
Mormyrus lacerda	●		Specimen in NMZB
Brycinus lateralis	●	●	Abundant throughout middle Zambezi
Hepsetus odoe		●	Deka R. (2) and Lake Kariba (1).
Barbus poechii	●	●	Lake Kariba, 1968-69 (9); no further records. Batoka specimen in NMZB
Barbus afrovernayi	●		Specimen in NMZB
Labeo lunatus		●	Lake Kariba, 1968-69 (1); possibly misidentified as specimen weighed only 14 g, no further records.
Hemichromis elongatus	●		Specimen in NMZB
Serranochromis robustus		●	Lake Kariba, 1968-69 (2); no further records
Serranochromis macrocephalus		●	Lake Kariba, 1966; now widespread and has reached Zambezi R. downstream
Sargochromis giardi		●	Lake Kariba, 1968-69 (127) and 1997 (1)
Sargochromis carlottae		●	Lake Kariba, 1968-69 (24); no further records
Oreochromis andersonii		●	Lake Kariba, 1968-69 (15); no further records
Aethiomastecembalus vanderwaali	●		Specimen in NMZB

The Churchill, *Petrocephalus catostoma*, is another species with a possibly relict distribution in the Middle Zambezi. It is widespread in the Upper Zambezi and is said to occur throughout the Middle Zambezi (Skelton 1993). But in Zambia it occurs only on the plateau sections of Zambezi tributaries (Jackson 1961a) and there are no records from the Zambezi itself or Lake Kariba (Jackson 1961b, Kenmuir 1983), or any of the Zimbabwean tributaries of the Zambezi (unpublished records, Natural History Museum, Bulawayo). Finally, Bell-Cross (1972) noted the presence of a catfish, which he referred to as *Clarias submarginatus*, in Lake Lusiwashi, a small waterbody on a tributary of the Luangwa. This species is not, in fact, *C. submarginatus* but probably *C. stappersii*, which occurs in the Chambeshi but not the Middle Zambezi. This probably represents a relict distribution from a time when the upper reaches of some Luangwa tributaries drained into the Chambeshi.

7.3.3 **The Middle Zambezi system**

Conditions to the east and south of the line that divides the Upper Zambezi and Kafue dividing line are very different from each other. The Middle Zambezi flows through a part of the continent that has been broken into deep troughs by the processes associated with the evolution of the African Rift Valley. The Middle Zambezi trough extends from the Victoria Falls to the Cabora Bassa Gorge, with a north-eastern extension up the Luangwa Valley. Its floor is much lower than the upper Zambezi-Kafue plateau and both rivers drop precipitously into it. The Middle Zambezi flows through several deep gorges, two of which (Kariba and Cabora Bassa) have been dammed to create huge artificial lakes.

Figure 7.8 Records of the Dash-tailed Barb, *Barbus poechii*, in the Zambezi system below the Victoria Falls. The circles denote records from the Natural History Museum, Bulawayo (NMZB) and the squares are records from Balon (1974). The open circle and square on the Sebungwe and Lusito rivers, respectively, are records for which the exact locality is not known. The shaded area is that part of the basin draining into the Upper Zambezi and Upper Kafue, where *B. poechii* is widespread.