The distribution of freshwater fish in Namibia

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This paper reviews current perspectives on the biogeography of freshwater fish in Namibia. It further discusses the distribution of the fish fauna in the Zambezian and Southern Provinces as well as in the interior of Namibia. A similarity index (SI) is presented to indicate the close historical linkage between the rivers in the north. The distribution of the fish fauna is discussed at species level and presented in a tabulated form. The presence of one undescribed clariid from the Kunene River is recorded. Several new distributions are also mentioned.

INTRODUCTION

The distribution of freshwater fish in Namibia has been outlined in the past by several authors. This has taken the form of either a checklist of species (*vide* Bethune & Roberts 1991), or as species lists for the various river systems (Barnard 1948; Cambray 1984; Hay 1991; Hay in press (a); Hay *et al.* 1996; van der Waal 1991; van der Waal & Skelton 1984). The biogeography of Southern Africa freshwater fishes has also been outlined by Bell-Cross (1966, 1982); Farquharson (1962); Gabie (1965); Gaigher (1969); Gaigher & Pott (1973); Jubb (1964); Jubb & Farquharson (1965); Ladiges (1964); Roberts (1975) and Skelton (1986a, 1994).

Recent surveys by the Ministry of Fisheries and Marine Resources in Namibia resulted in new distributions, as well as the collection of an undescribed catfish species. The translocation of several species within Namibia has also been recorded. Although not important in a biogeographical sense, a knowledge of the distribution of especially alien species is necessary for effective management of our natural resources. A paper recording the distribution and biogeography of freshwater fish in Namibia is, therefore, long overdue.

The total number of fish species decreases dramatically from central to Southern Africa, and several species reach their southern limit in the Kunene, Okavango and Zambezi River Systems. Being an arid country, Namibia has isolated freshwater fish populations in the interior. Only the Kunene, Okavango, Upper Zambezi, Chobe, Kwando and Lower Orange Rivers bordering Namibia are perennial rivers that have a relatively high degree of species diversity. Table 1 and Appendix 1 list the distribution of freshwater fish in Namibian waters. The Kwando and Chobe Rivers are included separately, but do form part of the Upper Zambezi System.

Roberts (1975) separated the freshwater ichthyofauna into three separate divisions, the first being the Peripheral Division which includes species which are able to tolerate both fresh and sea water and are able to freely disperse *via* the sea. This division includes the families Gobiidae, Megalopidae and Salmonidae. The Secondary Division includes species which are present in freshwater, but are able to tolerate seawater to such a degree as to enable them to disperse *via* the sea. The families Anabantidae, Cichlidae, Clariidae and Cyprinodontidae are included in this Division. The Primary Division includes those fish species which are unable to

Table 1. Freshwater fish species from major dams in Namibia (HDP = Hardap; NT= Naute; OMK = Omatako; OTJ = Otjivero; SWAK = Swakoppoort; VBACH = Von Bach; X = species present; X* = species introduced).

SPECIES	MAJOR DAMS IN NAMIBIA					
	HDP	NT	OMK	OTJ	SWAK	VBACH
Barbus cf. *kimberleyensis*	X					
Barbus paludinosus	X	X			X	X
Cyprinus carpio	X*			X*	X*	X*
Labeo capensis	X	X				
Labeo umbratus	X					
Clarias gariepinus	X	X	X*	X	X	X
Micropterus salmoides						X*
Oreochromis macrochir					X*	
Oreochromis mossambicus	X*	X*	X*	X*	X*	X*
Tilapia rendalli					X*	
Tilapia sparrmanii					X	

utilise the sea for dispersal, the sea hereby acting as an ecological barrier for dispersal. Continental drainage factors here play an important rôle in the dispersal of these species. This Division includes the families Bagridae, Characidae, Cyprinidae, Hepsetidae, Kneriidae, Mochokidae, Mormyridae, Mastacembelidae and Schilbeidae.

Several authors accept that central tropical Africa is the source of origin of freshwater fish species of central and Southern Africa, with numerous proposed invasion routes (Bell-Cross 1966, 1982; Farquharson 1962; Gabie 1965 and Jubb & Farquharson 1965). These dispersal routes show several anomalies and unaccountable phenomena. Skelton (1994), however, suggested that there is no evidence of a north to south movement of freshwater fish. He further suggests that the evolution of freshwater fish took place *in situ* and that modern distributions are the result of drainage evolution within a region. Skelton (1986a) divided the fish fauna of Southern Africa into tropical and temperate species with the Orange River as the southern limit for the tropical species. Skelton (1986b) does not consider the Orange River a 'stepping stone' for the freshwater fish from central Africa, but sees it as an evolutionary arena for the temperate fauna.

The drainage systems within Namibia fall into two Ichthyofaunal Provinces, the Zambezi and Southern Provinces, with the former divided into a western and an eastern sector (Skelton, 1994). The perennial rivers in the north (the Kunene, Okavango and Upper Zambezi Rivers) are included in the western sector as well as the Kafue River. The eastern sector includes the Middle and Lower Zambezi, the Buzi, the Save, Limpopo, Incomati and the Pongola Rivers. Skelton (1994) points out that the southern tributaries of the Limpopo, the Orange River and the Fish River in Namibia, is the northern limit of the Southern Province.

The authors and dates of publication for each recorded species are listed in Appendix 1.

DRAINAGE BASINS

Bell-Cross (1966, 1982) suggested two internal drainage basins in central Africa during the Tertiary Period. The Kunene, Okavango, Upper Zambezi, Kafue and Chambeshi River Systems formed part of the Western End Tertiary Drainage System with Zairean affinities, and the Eastern End Tertiary Drainage System comprising the Middle and Lower Zambezi, Luangwa and Shire River Systems with Nilotic affinities. Each drainage basin had its own characteristic freshwater fish fauna.

According to Burke (1996), Trans-Tswana and Karoo Systems dominated the early Tertiary drainage of the southern continent. McCarthy (1983) and Moon & Dardis (1988) also suggested a large southerly drainage, the Trans-Tswana, to the sea via the Proto-Lower Orange River. The development of the Kalahari Basin during the Oligocene at about 30 Ma disrupted the Trans-Tswana drainage and separated the southern Kalahari and Karoo systems from the central African drainage systems. At about 15 Ma a proto-drainage pattern consisting of west flowing (Kunene and Orange-Vaal-Koa), east flowing (Zambezi-Shire and Limpopo), and internal (Okavango) systems were established (Burke 1996). The subsequent development of these systems, and further disruption of internal drainage basins, were due to river capture and diversion (Partridge & Maud 1987). The Kunene River was captured by a coastal tributary, the Chambeshi was diverted to the Lualaba System and the Kafue to the Middle Zambezi. The Okavango and Upper Zambezi formed part of the Zambezi River as the situation is at present. Skelton (1994), however, pointed out that the fact that only six Zambezian fish species are present in the Orange River, weakening this hypothesis. Furthermore, the presence of fossil records of clariid fin spines from the Orange

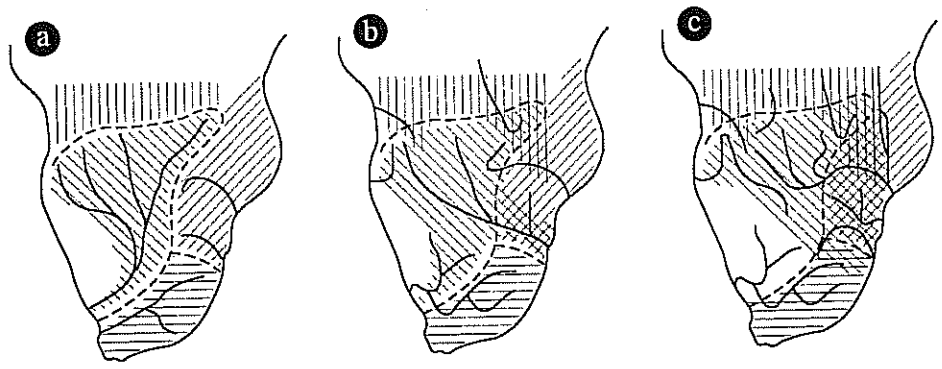

Figure 1. Outlines of Southern Africa. Biogeographic model for the dispersal of Zambezian freshwater fishes (after Skelton 1994) (a) Early Tertiary; (b) Mid-Tertiary; (c) Late-Tertiary. (a) In the Early-Tertiary the freshwater fish fauna of Southern Africa was established in four evolutionary arenas (1) the southern (horizontal hatching), (2) western arena (left slanting hatching), (3) eastern arena (right slanting hatching), (4) Zairean arena (vertical hatching). (b) By the later-Tertiary there was a second infusion of western fauna into the eastern arena and further infusion of Zairean fauna into the western arena. Minor faunal infusions occur along contact zones of the faunal arenas e.g. western/eastern elements into the Southern Arena.

River mouth may strengthen biological support for the geomorphological evidence.

Skelton (1994) proposed an alternative model of Zambezian biogeography that incorporates some of the ideas presented by Bell-Cross (1966, 1982). He proposed three phases as outlined in Figure 1. Stage 1 (Figure 1a) involved the establishment of western and eastern faunas, as well as a southern fauna. During stage 2 (Figure 1b) the western fauna became fragmented. This extended towards the southeast via the Okavango/Upper Zambezi/Limpopo drainage systems. With stage 3 (Figure 1c), the south-eastern extension of the western fauna ended with a north-east extension establishing itself through the Middle and Lower Zambezi. Major waterfalls also played an important rôle during these stages. Skelton (1994) further suggested that the boundaries of the western fauna as indicated by Bell-Cross (1966, 1982) may already have been a diminished set of the original arena.

The Fish River within Namibia forms part of the Orange River Drainage Basin. Gabie (1965), Gaigher & Pott (1973), Farquharson (1962), and Jubb & Farquharson (1965) postulated that the Orange System and also Southern Africa received its fish fauna from the northern drainage basins. Jubb & Farquharson (1965) indicated two possible routes into the Orange Drainage Basin. The first was during the Mid-Pliocene with a direct link between the Okavango and Orange Rivers. The second proposed invasion was during the Mid-Pleistocene with catchment exchange that took place between the Epukiro and Nossob Rivers to the Orange River. Dispersal also took place *via* the Lower Zambezi and Limpopo Rivers during this invasion. Gaigher & Pott (1973) did not agree with the suggested second invasion and submitted an alternative route. They indicated a possible Orange/Limpopo headwater exchange. Farquharson (1962) also proposed two invasions for the cyprinids in Southern Africa during the Pleistocene. An earlier invasion resulted in the presence of endemic species in the south-western Cape and Orange River. Farquharson considers the rise and fall of the coastline and the exchange of river catchments to be the main factors for dispersal. Gabie (1965) suggested a link between the Okavango and Orange Rivers via the Fish and Nossob Rivers. Skelton (1986a) approached it differently, dividing the temperate fauna into the Cape and Karroid ichthyofauna that developed in isolation from the tropical fauna.

DISTRIBUTION PATTERNS

THE ZAMBEZI PROVINCE

Skelton (1994) grouped the distribution patterns of the Zambezi Province into several categories. These are: 1) the non-endemic species with a wide distribution within the Province, 2) endemic species confined to western sector drainages, 3) non-endemic species confined to the western sector drainages, 4) endemic species confined to the eastern sector drainages, 5) non-endemic species confined to the eastern sector drainages and 6) western sector species with sporadic eastern sector presence that could be in either the northern or the southern rivers. Examples of these species assemblages are listed in Appendix 2.

Table 2 summarizes the species diversity of Namibia's perennial rivers and also presents the similarity indexes (SI) of these rivers. The SI is the highest for the Okavango/Upper Zambezi comparison. This was followed by the Kunene/Okavango and Kunene/Upper Zambezi comparisons. The SI for these northern rivers are all more than 0.48 which provides support for historical links between these rivers in the western sector (Skelton, 1994). The upper reaches of the Kunene and Okavango Rivers have not been well sampled and further studies may reveal new distributions. This may even lead to higher SI values.

Table 2: Summary of the Similarity Indexes (SI) of the different river systems in Namibia. FAM = number of families; GEN = number of genera; SPEC = number of species.

System	FAM	GEN	SPEC	Compared	Combined	Number Shared	SI
Kunene	12	27	65	Kunene/Okavango	100	51	0.51
Okavango	15	38	87	Okavango/Upper Zambezi	95	82	0.86
Upper Zambezi	16	40	90	Kunene/Upper Zambezi	104	50	0.48
Lower Orange	4	7	12	Kunene/Lower Orange	72	5	0.07
				Lower Orange / Upper Zambezi	97	5	0.05
				Lower Orange/Okavango	94	5	0.05

Only five species are found in the Okavango, which are not listed for the Upper Zambezi, namely: *Parakneria fortuita, Barbus breviceps, Chiloglanis fasciatus, Sargochromis gracilis* and *Aplocheilichthys moeruensis.* Twelve *Parakneria* species are known, of which two occur in Southern Africa (Skelton 1993). The remaining species are recorded from Zaire and northern Cameroon (Penrith 1973). *Parakneria fortuita* is believed to be limited to the type locality at the bridge between Chitembo and Chimbangombe (Angola) in the Cutato River, a tributary of the Okavango River (Penrith 1973). Penrith (1973) suggested a lack of preferred habitats, such as rocky areas, to be the main factor limiting its distribution.

Very little is known about *Barbus breviceps.* Skelton (1993) indicates that it appears to be similar to the chubbyhead group, which is confined to the southern fauna, preferring cooler conditions. This species is, however, strictly confined to the Zambezi Province and was first sampled from a brook 100 km south-east of Quibala, Angola, in the Longa River System (Trewavas 1936). *Barbus breviceps* prefers fountain habitats. This was emphasized during a survey to the Kunene River when this species was sampled from similar habitats (Hay pers. obs.).

Chiloglanis fasciatus, although not listed for the Upper Zambezi, was identified from the Kwando River that forms part of the Upper Zambezi System. *Sargochromis gracilis* was recorded from the Cutato River, a tributary of the Okavango River in Angola, and recently also from the Kunene River (Greenwood 1984; Skelton 1993). The taxonomy of this species, is currently under review and the genus is likely to change (Skelton 1993). *Aplocheilichthys moeruensis* was identified from the Okavango River (Hay *et al.* 1996), but the taxonomy of this group is in need of revision (Skelton pers. comm.)

Eight species are recorded in the Upper Zambezi which are absent from the Okavango River, namely: *Barbus afrohamiltoni, B. bellcrossi, Paramormyrops jacksoni, Schilbe yangambianus, Chiloglanis neumanni, Nothobranchius* sp., *Hypsopanchax jubbi* and *Sargochromis mortimeri.* The *Nothobranchius* sp. is endemic to the Caprivi and inhabits temporary rainpools. *Barbus bellcrossi* is listed from the upper reaches only. *Chiloglanis neumanni* is replaced by *C. fasciatus* from the Okavango River. The latter has been recorded from the Kwando River. Very little is known about *Paramormyrops jacksoni* and *Hypsopanchax jubbi* except that they are present in the upper reaches of the Upper Zambezi.

There is a remarkable difference in species diversity between the Kunene River and the Okavango River (49 species not shared) and the Kunene River and the Upper Zambezi River (54 species not shared). This emphasizes the fact that the Kunene River was diverted at an earlier period from the western sector. Five of these species are endemic to the Kunene River, namely: *Kneria maydelli, Schwetzochromis machadoi, Sargochromis coulteri, Thoracochromis albolabris* and *T. buysi*. The status of a further two species is not known. One is *Chetia welwitschi*, which is known only from a small number of museum specimens, and the other is an undescribed *Clariallabes* sp. (Skelton pers. comm.).

SOUTHERN PROVINCE

The Lower Orange River, which forms part of the Southern Province, shares only six species with the rivers of the north (Appendix 2). These are *Barbus paludinosus, Tilapia sparrmanii, Mesobola brevianalis, Clarias gariepinus* (in all perennial rivers of Namibia), *B. trimaculatus* (in the Kunene River) and *Pseudocrenilabrus philander* (in the Okavango and Upper Zambezi Rivers). The comparisons between the rivers in the north and the Lower Orange River yielded low SI values (Table 2).

The Lower Orange River has a low species diversity as compared to the northern perennial rivers in Namibia. Several invasion routes have been postulated in the past, when considering the cyprinids, which is the dominant family in the Lower Orange River. Gaigher & Pott (1973) grouped *Labeo umbratus* and *L. ruddi* together, with the latter present in the Kunene and Limpopo Rivers. They postulated an Orange/Okavango River linkage for the presence of *L. umbratus* in the Lower Orange River System. The absence of *L. ruddi* from the Okavango and Upper Zambezi Rivers, shifts the possible route to a Limpopo/Orange River linkage. Another Limpopo/Orange River linkage through the Molopo River is indicated by the presence of *Mesobola brevianalis* in the Lower Orange River. Forty-two percent of the total number of species occurring naturally in the Lower Orange River are endemic to that system.

INTERIOR OF NAMIBIA

A total of 15 species within five families are present in Namibia's interior, excluding the perennial rivers and the Fish River. Figures 2-5 illustrate the distribution of these fish species in the interior of Namibia. The species which are unknown, the yellowfish, fish from Lake Otjikoto and the Cichlidae as indicated on these figures are from local farmers' reports. Six species are aliens, these being: *Carassius auratus, Cyprinus carpio, Micropterus salmoides, Oreochromis mossambicus, Poecilia reticulata*, and *Xiphophorus helleri*. Five species namely: *Clarias gariepinus, Pseudocrenilabrus philander, Tilapia guinasana, T. rendalli* and *T. sparrmanii* have been translocated. *Clarias cavernicola* and *Tilapia guinasana* are endemic to the Aigamas cave and Lake Guinas respectively. *Barbus paludinosus* and *Clarias gariepinus* have a much wider distribution throughout Namibia. *Barbus anoplus* was identified from the Gaub River (Dixon & Blom 1974), a tributary of the Kuiseb River, but is in need of confirmation (Skelton pers. comm.).

Poecilia reticulata and *Xiphophorus helleri*, present in Lake Otjikoto, and *Carassius auratus* with isolated populations do not currently pose a threat to indigenous species.

Oreochromis mossambicus has a wide distribution in Namibia and poses a serious threat of genetic pollution in the Kunene and Okavango Rivers, as it has been recorded as interbreeding with *O. andersonii* (Jackson 1961). *Oreochromis mossambicus* is present in the Nossob/Olifants System, west flowing rivers, Lower Orange River, Omuramba Omatako and Owamboland. The high fertility of *O. mossambicus*, declared as an

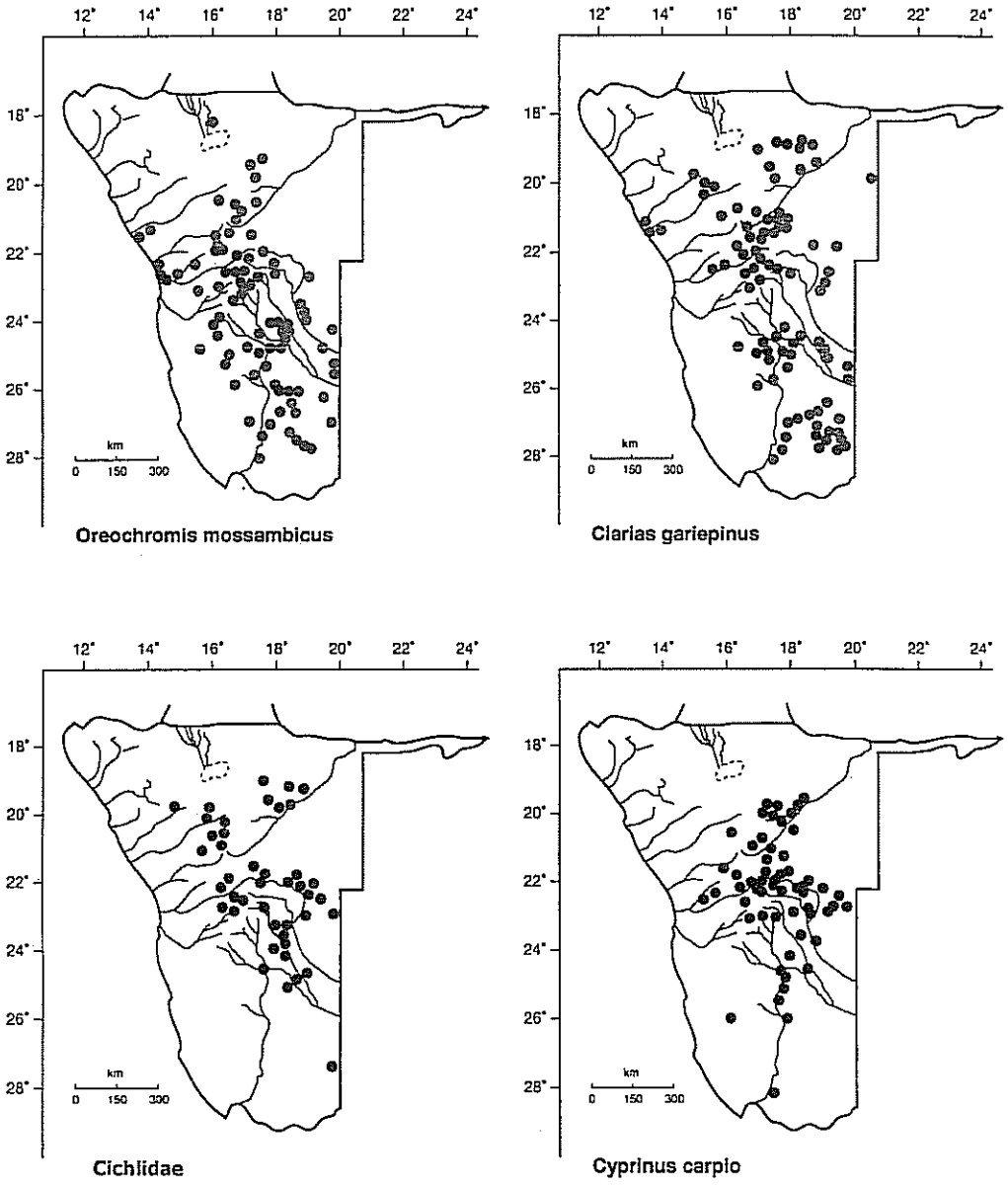

Figure 2. Distribution of *Oreochromis mossambicus*, *Clarias gariepinus*, Cichlidae and *Cyprinus carpio* in the interior of Namibia.

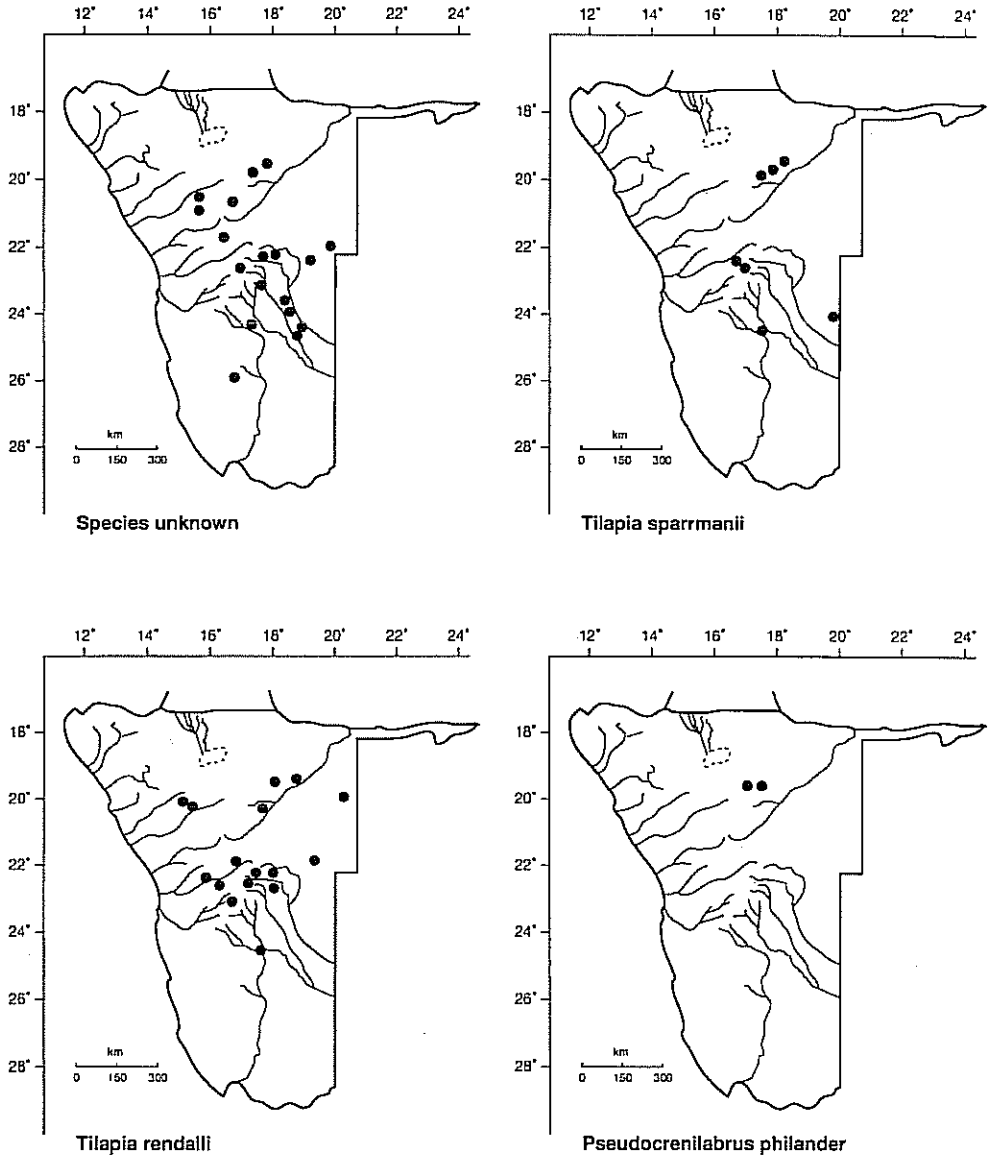

Figure 3. Distribution of unknown species, *Tilapia sparrmanii*, *T. rendalli* and *Pseudocrenilabrus philander* in the interior of Namibia.

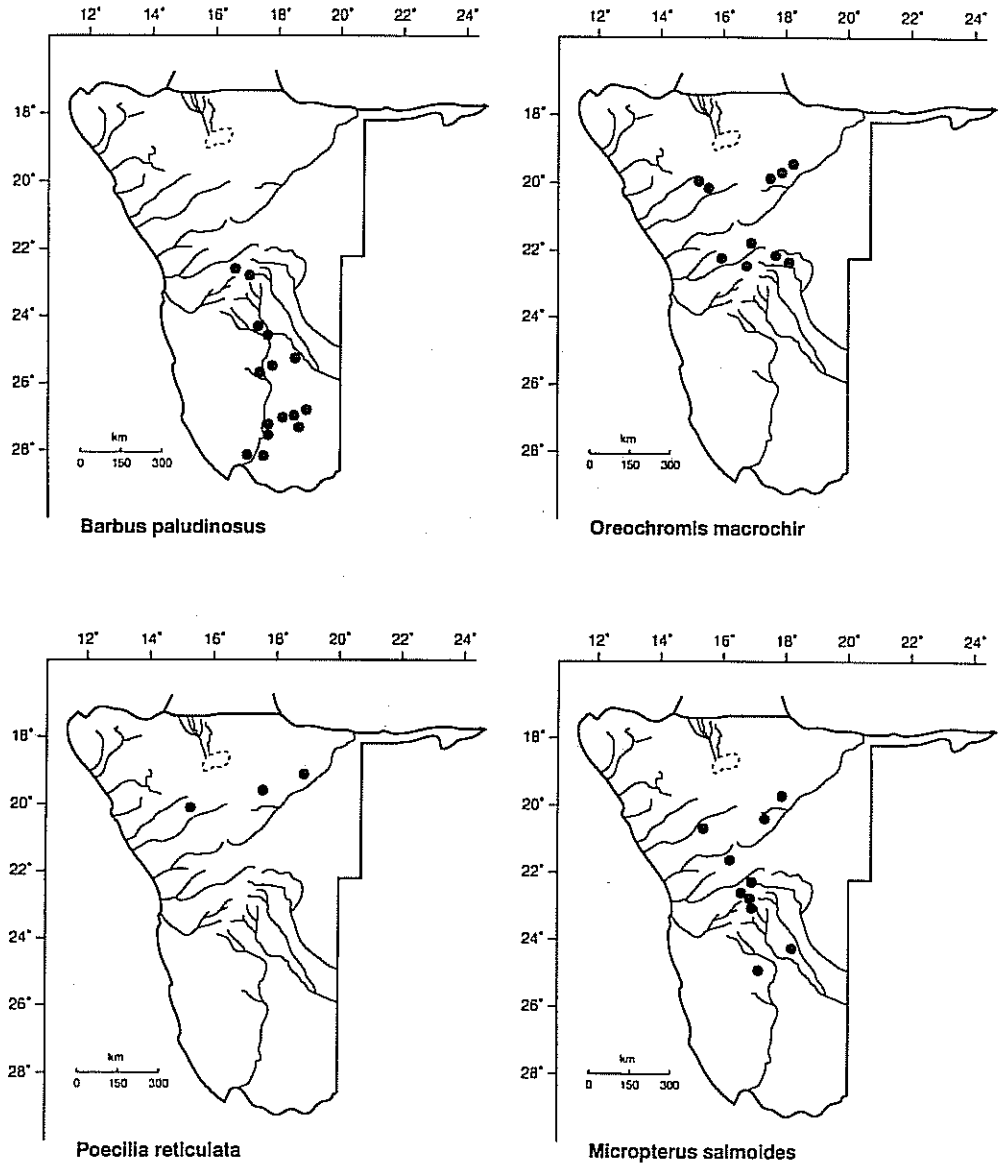

Figure 4. Distribution of *Barbus paludinosus, Oreochromis macrochir, Poecilia reticulata* and *Micropterus salmoides* in the interior of Namibia.

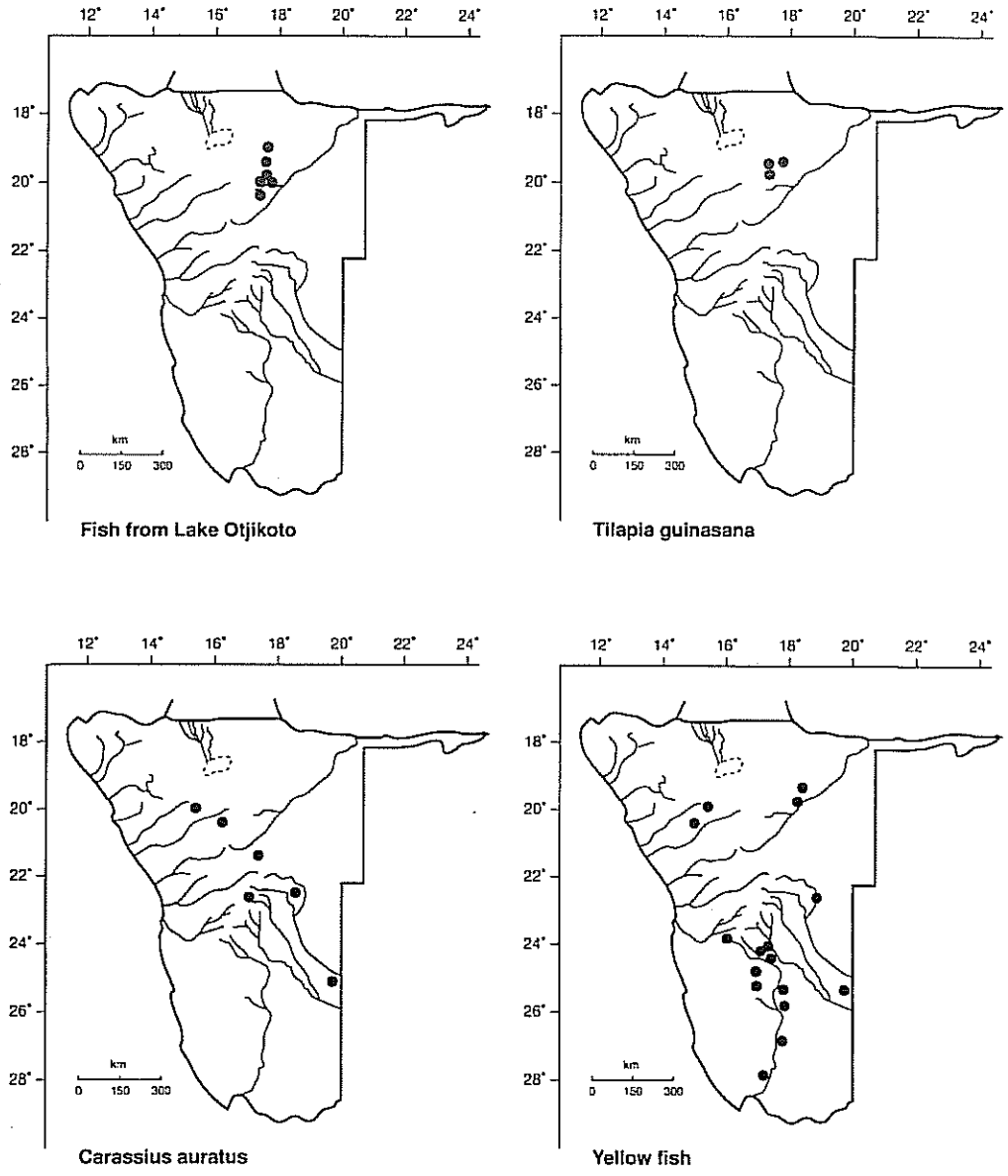

Figure 5. Distribution of freshwater fish from Lake Otjikoto (species unknown), *Tilapia guinasana*, *Carassius auratus* and yellowfish (species unknown) in the interior of Namibia.

international pest (Bruton & Van As 1986), increases the danger of invasion.

Cyprinus carpio is present in all ephemeral rivers in Namibia as well as in the Lower Orange River. It may well have been introduced into Namibia by early settlers (Gaigher 1975). Although serious, this invasion is not as critical as that posed by *O. mossambicus*, as the species does not appear to overpopulate a system (Hay 1991). *Cyprinus carpio* being a substrate feeder, may increase the turbidity of a system which in turn will affect the predatory species which rely on vision for the capture of their prey. *Micropterus salmoides* is mainly present in central Namibia, where the high turbidity appears to be a limiting factor in the distribution of this species.

Translocation has also played a major role in Lake Otjikoto where five of the six species are alien to the lake with *Pseudocrenilabrus philander* being the only indigenous species (Trewavas 1936).

SPECIES DISTRIBUTION WITHIN NAMIBIA

The family Mormyridae includes 18 genera and 200 species in Africa, of which seven species occur in the Zambezi Province. This family is widespread throughout the Zambezi Province. Both *Marcusenius macrolepidotus* and *Petrocephalus catostoma* are well distributed throughout the western and eastern sectors of the Zambezi Province. *Paramormyrops jacksoni* is known only from the type specimen from the Longa River in the Upper Zambezi River.

The Kneriidae forms part of the gonorynchiformes which also includes marine fishes. Members of the family Kneriidae are found in the upper reaches of the Okavango, Upper Zambezi and Kunene River Systems. Only one member of this family, *Kneria maydelli*, has been recorded within the boundaries of Namibia. According to Skelton (1994) the phylogenetic interrelationships and distribution of these species are uncertain making any biogeographical conclusions difficult.

The characin families include the Characidae, Hepsetidae and Distichodontidae in Southern Africa. More than 200 species are present in Africa with 12 in Southern Africa. *Hydrocynus vittatus* and *Micralestes acutidens* (Characidae) are both widespread in the Zambezi Province. The former, however, is absent from the Kunene and Kafue Rivers. *Rabdalestes maunensis* is restricted to the western sector, whereas *Hemigrammopeterius barnardi* is recorded from the Lower Zambezi, Pungwe and Buzi Rivers.

Hepsetus odoe is the only species of the family Hepsetidae known to occur in Africa. It is part of the Primary Division (Roberts 1975), which has a low invasion potential. Despite this handicap it is well distributed throughout Africa, but notably absent from the eastern sector. According to Skelton (1993), it is closely related to the Ctenoluciidae from South America.

Speciation occurred within the family Distichodontidae with *Hemigrammocharax multifasciatus, H. machadoi* and *Nannocharax macropterus* listed exclusively from the western sector and *Distichodus mossambicus* and *D. shenga* from the eastern sector. *Nannocharax macropterus* is not present in the Kunene River, but being a habitat specialist, further surveys in the upper reaches of this system may reveal its presence.

The Cyprinidae is a very large family occurring in Africa, Europe, North America and Asia. They are grouped as primary fishes by Roberts (1975), where continental drainage factors played a major rôle in the dispersal of these fishes. The Cyprinidae is the second largest family in Africa, with the highest species diversity in Namibian waters. Three cyprinid species, *Barbus paludinosus, B. radiatus* and *Labeo cylindricus* are widespread and are included in the east coast fauna. The first mentioned also being present

in the southern fauna. Speciation occurred in the western sector with the presence of *Barbus afrovernayi, B. barnardi, B. barotseensis, B. bellcrossi, B. breviceps, B. brevidorsalis, B. codringtonii, B. dorsolineatus, B. poechii, B. thamalakanensis, Coptostomabarbus wittei, Labeo ansorgii* and *L. lunatus* being restricted to this sector. Several *Labeo* spp. are endemic to the Zambezian Province namely: *Labeo molybdinus, L. ansorgii, L. ruddi, L. rosae* and *L. lunatus. Labeo cylindricus* has a wide distribution in the western and eastern sectors, but is absent from the Kunene River. *Labeo ruddi* is present in the Kunene River, Limpopo, Incomati and Pongola Systems, but absent from the Okavango and Upper Zambezi Rivers. *Labeo ansorgii* is restricted to Angola in the Quanza and Kunene Rivers. Two alien cyprinids have been identified as occurring in Namibia. These are *Cyprinus carpio* and *Carassius auratus* with the former being present in several impoundments, ephemeral rivers, Lower Orange River, Omatako Omuramba and farm dams. *Carassius auratus* is present chiefly in ponds in several Namibian towns.

The Siluriformes (catfishes) are one of the largest groups of fishes in the world. Six families are present in Namibia *viz.* Clariidae, Schilbeidae, Amphiliidae, Claroteidae, Austroglanididae and Mochokidae. Several species have a wide distribution within the eastern and western sectors e.g. *Schilbe intermedius, Amphilius uranoscopus, Clarias gariepinus, C. ngamensis* and *C. theodorae.* The Mochokidae, however, exhibit a high degree of endemism in the western sector. *Synodontis nigromaculatus, S. woosnami, S. macrostigma, S. macrostoma, S. leopardinus, S. thamalakanensis* and *S. vanderwaali* are all restricted to the western sector. Of these, *S. nigromaculatus* and *S. thamalakanensis* are absent from the Kunene and Kafue Rivers. *Schilbe yangambianus* is known only from one locality in the upper reaches of the Upper Zambezi River. It is also present in the Zaire System which relates to a drainage capture between the Zambezi and Zaire Rivers (Skelton, 1994). *Clariallabes platyprosopos* is endemic to the Upper Zambezi and Okavango Rivers with a new distribution of an undescribed *Clariallabes* sp. from the Kunene River (Skelton, pers. comm.). No *Clariallabes* spp. are listed from either the eastern sector of the Zambezi Province or the east coast fauna. *Clarias cavernicola* is endemic to the Aigamas cave near Otavi with its nearest relative, *C. theodorae*, present in the Kunene, Okavango and Upper Zambezi Rivers. One species (only three known species, all in Southern Africa) from the family Austroglanididae are listed in Namibia, namely *Austroglanis sclateri.* It is present only in the Orange River.

Micropterus salmoides, is the only species of the Centrarchidae known to occur in Namibia. It is an alien species with its first introduction recorded in 1932 (Schrader, 1985). It is widely distributed within Namibia in habitats such as impoundments, Omatako Omuramba and farm dams.

The order Cyprinodontiformes includes the families Aplocheilidae, Cyprinodontidae and Poeciliidae. These are favourite aquarium fishes and are also use as biological control agents for mosquitoes (Skelton 1993). Six species of Cyprinodontidae are listed as occurring in Namibia, of which *Aplocheilichthys johnstoni* and *A. katangae* have wide distributions within the western and eastern sectors. The former is also present in the east coast fauna. Several anomalies occur within this group. *Hypsopanchax jubbi* is restricted to the Upper Zambezi, *A. macrurus* to the Kunene River and *A. moeruensis* to the Okavango River. The taxonomic status of the last two named species is still unclear (Skelton pers. comm.). The group is currently under investigation.

Two species of the family Poeciliidae have been recorded from Lake Otjikoto. Both *Poecilia reticulata* and *Xiphophorus helleri* are alien species and are favoured aquarium species.

The Aplocheilidae is more diversified in the eastern sector with only two species listed from the western sector. *Nothobranchius* sp. is endemic to the Caprivi and inhabits temporary rainpools.

The perciformes is the largest order of fishes worldwide and includes the Cichlidae and the Anabantidae. The order consists of over 7800 species. The Cichlidae is the largest family in Africa, but second to the cyprinids in Namibia. Some degree of speciation occurred within this family especially within the genera *Sargochromis* and *Serranochromis*. Only one (*Serranochromis meridianus*) of the seven *Serranochromis* spp. is listed from the eastern sector, with the exception of *S. robustus*, which has been translocated (Skelton, 1993). Species with a wide distribution are *Pseudocrenilabrus philander, Tilapia rendalli* and *T. sparrmanii*. The presence of *P. philander* in the Kunene River is doubtful (Hay & Skelton pers. obs.). It appears that this species is replaced by *Schwetzochromis machadoi*. Further studies will clarify the situation. *Schwetzochromis machadoi, Sargochromis coulteri, Thoracochromis alholabris* and *T. buysi* are all endemic cichlids present in the Kunene River. *Tilapia guinasana* is again endemic to Lake Guinas, but has been translocated to Lake Otjikoto and several farm dams in northern Namibia. The only alien cichlid in Namibia is *Oreochromis mossambicus* present in several impoundments and in the Omuramba Omatako. It has also been identified in the Cuvelai System (Hay in press (b)). This species was first introduced from the Cape in 1947 (Schrader, 1985). The natural distribution is from the Lower Zambezi River along the east coast to the Bushmans River in the Eastern Cape (Skelton, 1993).

The Anabantidae is present in the Zambezian Province, the East Coast fauna and in the southern fauna. No anabantids are present in the Kunene River. Three species of the family Mastacembelidae are present in the Zambezi Province, two from the western sector and one from the eastern sector. This family is also absent from the Kunene River.

CONCLUSIONS

The distribution of freshwater fish in Namibia may be divided into the Zambezi Province, the western sector which includes the Kunene and Okavango Rivers and the Cuvelai and Caprivi Systems and in the Southern Province which includes the Lower Orange River with its northern tributary, the Fish River. The SI of the northern perennial rivers are all more than 0.48 which indicates definite historical links. The high SI values between the Okavango and Upper Zambezi Rivers indicates an even closer link between these two rivers. The Kunene River fish fauna suggests an earlier capture by a coastal tributary that resulted in several endemic species within this system. The apparent absence of *Pseudocrenilabrus philander* from the Kunene River is an enigma as this species is widely distributed within Southern Africa. The Kunene River is also less diversified regarding families, genera and species when compared to the Okavango and Upper Zambezi River Systems.

The species composition of the Cuvelai System is closer in comparison with the Kunene River than with any other river system. This is emphasized by the presence of *Labeo ansorgii, L. ruddi, Thoracochromis alholabris, T. buysi* and *Sargochromis coulteri*. The artificial linkage between these two systems may, however, have contributed to this (Hay in press (b)).

The species composition difference between the Okavango and Upper Zambezi Systems is mostly due to rare species or habitat specialists present in the upper reaches of these rivers. More detailed future surveys in these regions may yet yield higher SI values.

Only six species overlap between the Zambezi Province and the Lower Orange River indicating

that the fish in the Lower Orange River probably developed in isolation from the fish fauna in the north. The Lower Orange River is also less diversified regarding species diversity when compared to the Zambezi Province.

Freshwater fish fauna of Namibia is dominated by species from the western sector of the Zambezi Province. *Barbus paludinosus, B. trimaculatus, Mesobola brevianalis, Clarias cavernicola, C. gariepinus, Pseudocrenilabrus philander, Oreochromis macrochir, O. mossambicus, Tilapia guinasana, T. rendalli* and *T. sparrmanii* are all present south of the northern perennial rivers in Namibia. Distribution in the ephemeral rivers in Namibia is sporadic and depends on very good rains. The species composition of these rivers is limited to *Barbus paludinosus, Clarias gariepinus, Oreochromis mossambicus* and *Cyprinus carpio.* When these rivers recede to pool habitats, the conditions for the survival of fish deteriorate and it is only the most tolerant species which are able to survive.

A more detailed study of Angolan rivers is necessary in order to obtain a clearer picture of fish distribution in that part of Southern Africa.

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Appendix 1. Distribution of freshwater fish species in Namibia (A = Alien species; E = Endemic species; H = Hybrids; R = Red data species; M = Marine species).

SPECIES	OKAVANGO	UPPER ZAMBEZI	KWANDO	CHOBE	LOWER ORANGE	INTERIOR	KUNENE	CUVELAI
MORMYRIDAE								
Hippopotamyrus ansorgii (Boulenger, 1905)	X	X					X	X
H. discorhynchus (Peters, 1852)	X	X	X				X	
Marcusenius macrolepidotus (Peters, 1852)	X	X	X	X			X	X
Mormyrus lacerda Castelnau, 1861	X	X	X	X			X	X
Pollimyrus castelnaui (Boulenger, 1911)	X	X		X			X	X
Paramormyrops jacksoni (Poll, 1967)		X						
Petrocephalus catostoma (Günther, 1866)	X	X	X	X			X	X
KNERIIDAE								
Kneria maydelli Ladiges & Voelker, 1961							E	
K. polli Trewavas, 1936	X	X					X	
Parakneria fortuita Penrith, 1973	E							
CHARACIDAE								
Brycinus lateralis (Boulenger, 1900)	X	X	X	X			X	X
Hydrocynus vittatus Castelnau, 1861	X	X	X	X				
Micralestes acutidens (Peters, 1852)	X	X	X	X			X	X
Rabdalestes maunensis (Fowler, 1935)	X	X	X	X			X	X
HEPSETIDAE								
Hepsetus odoe (Bloch, 1794)	X	X	X	X			X	X
DISTICHODONTIDAE								
Hemigrammocharax machadoi Poll, 1967	X	X	X	X			X	X
H. multifasciatus Boulenger, 1923	X	X	X	X			X	
Nannocharax macropterus Pellegrin, 1925	X	X						
CYPRINIDAE								
Barbus aeneus (Burchell, 1822)					X			
B. afrohamiltoni Crass, 1960		X						
B. afrovernayi Nichols & Boulton, 1927	X	X		X			X	
B. anoplus Weber, 1897						X		
B. barnardi Jubb, 1965	X	X	X	X			X	X
B. barotseensis Pellegrin, 1920	X	X		X			X	
B. bellcrossi Jubb, 1964		X						
B. bifrenatus Fowler, 1935	X	X	X	X			X	X
B. breviceps Trewavas, 1936	X						X	
B. cf. eutaenia	X	X						
B. codringtonii Boulenger, 1908	X	X						

Appendix 1. cont. Distribution of freshwater fish species in Namibia (A = Alien species; E = Endemic species; H = Hybrids; R = Red data species; M = Marine species).

SPECIES	OKAVANGO	UPPER ZAMBEZI	KWANDO	CHOBE	LOWER ORANGE	INTERIOR	KUNENE	CUVELAI
Barbus dorsolineatus Trewavas, 1936							X	
B. eutaenia Boulenger, 1904	X	X					X	
B. fasciolatus Günther,1868	X	X	X	X			X	
B. haasianus David, 1936	X	X		X				
B. hospes Barnard, 1938					E,R			
B. kimberleyensis Gilchrist & Thompson, 1913					X			
B. cf. kimberleyensis					H			
B. lineomaculatus Boulenger, 1903	X	X		X			X	
B. mattozi Guimaraes, 1884			X				X	X
B. mielepis Boulenger, 1902	X	X						
B. multilineatus Worthington, 1933	X	X	X	X			X	
B. paludinosus Peters, 1852	X	X	X	X	X	X	X	X
B. brevidorsalis Boulenger, 1915	X	X						
B. radiatus Peters, 1853	X	X	X	X			X	X
B. kerstenii Peters, 1868	X	X		X			X	X
B. paechii Steindachner, 1911	X	X	X	X				X
B. thamalakanensis Fowler, 1935	X	X	X	X				
B. trimaculatus Peters, 1952					X		X	
B. unitaeniatus Günther, 1866	X	X	X	X			X	X
Coptostomabarbus wittei David & Poll, 1937	X	X	X	X				X
Cyprinus carpio Linnaeus, 1758					A	A		
Carassius auratus (Linnaeus, 1758)						A		
Labeo ansorgii Boulenger, 1907							X	X
L. capensis (A. Smith, 1841)					X			
L. capensis x umbratus					H			
L. cylindricus Peters, 1852	X	X		X				
L. lunatus Jubb, 1963	X	X	X	X				
L. ruddi Boulenger, 1907							X	X
L. umbratus (A. Smith, 1841)					X			
Mesobola brevianalis (Boulenger, 1908)	X	X			X		X	X
Opsaridium zambezense (Peters, 1852)	X	X	X					
CLAROTEIDAE								
Parauchenoglanis ngamensis (Boulenger, 1911)	X	X	X	X				
AMPHILIIDAE								
Leptoglanis cf. dorae (non Poll, 1967)	X	X	X					

Appendix 1. cont. Distribution of freshwater fish species in Namibia (A = Alien species; E = Endemic species; H = Hybrids; R = Red data species; M = Marine species).

SPECIES	OKAVANGO	UPPER ZAMBEZI	KWANDO	CHOBE	LOWER ORANGE	INTERIOR	KUNENE	CUVELAI
Leptoglanis rotundiceps (Hilgendorf, 1905)	X	X					X	
Amphilius uranoscopus (Pfeffer, 1889)	X	X						
AUSTROGLANIDIDAE								
Austroglanis sclateri (Boulenger, 1901)					R			
SCHILBEIDAE								
Schilbe intermedius Rüppel, 1832	X	X	X	X			X	X
S. yangambianus (Poll, 1954)		X						
CLARIIDAE								
Clariallabes platyprosopus Iubb, 1964	R	R						
Clarias cavernicola Trewavas, 1936						E,R		
C. gariepinus (Burchell, 1822)	X	X	X	X	X	X	X	X
C. liocephalus Boulenger, 1898	X	X	X	X			X	
C. ngamensis Castelnau,1861	X	X	X	X			X	X
C. stappersii Boulenger, 1915	X	X					X	
C. theodorae Weber, 1897	X	X	X	X			X	
Clariallabes sp.							X	
CENTRARCHIDAE								
Micropterus salmoides (Lacepède, 1802)						A		
MOCHOKIDAE								
Chiloglanis fasciatus Pellegrin, 1936	X		X					
C. neumanni Boulenger, 1911		X					X	
Synodontis leopardinus Pellegrin, 1914	X	X	X	X			X	X
S. macrostigma Boulenger, 1911	X	X	X	X			X	X
S. macrostoma Skelton & White, 1990	X	X					X	
S. nigromaculatus Boulenger, 1905	X	X	X	X				
S. thamalakanensis Fowler, 1935	X	X						
S. vanderwaali Skelton & White, 1990	X	X					X	
S. woosnami Boulenger, 1911	X	X	X	X			X	X
CYPRINODONTIDAE								
Aplocheilichthys hutereaui (Boulenger, 1913)	X	X	X	X				
A. johnstoni Günther, 1893	X	X	X	X			X	X
A. katangae (Boulenger, 1912)	X	X	X	X			X	
A. macrurus (Boulenger, 1904)							X	
A. maeruensis (Boulenger, 1914)	X							

Appendix 1. cont. Distribution of freshwater fish species in Namibia (A = Alien species; E = Endemic species; H = Hybrids; R = Red data species; M = Marine species).

SPECIES	OKAVANGO	UPPER ZAMBEZI	KWANDO	CHOBE	LOWER ORANGE	INTERIOR	KUNENE	CUVELAI
Hypsopanchax jubbi Poll & Lambert, 1965		X						
POECILIIDAE								
Poecilia reticulata Peters, 1859						A		
Xiphophorus helleri Heckel, 1848						A		
APLOCHEILIDAE								
Nothobranchius sp.		E,R						
CICHLIDAE								
Chetia welwitschi (Boulenger, 1898)							X	
Hemichromis elongatus (Guichenot, 1859)	X	X	X					
Pharyngochromis acuticeps (Steindachner, 1866)	X	X	X	X				
Pseudocrenilabrus philander (Weber, 1897)	X	X	X	X	X	X		
Schwetzochromis machadoi (Poll, 1967)							E	E
Oreochromis macrochir (Boulenger, 1912)	X	X	X	X		X	X	X
O. mossambicus (Peters, 1852)					A	A		A
O. andersonii (Castelnau, 1861)	X	X	X	X			X	X
Serranochromis altus Winemiller & Kelso-Winemiller, 1990	X	X					X	
S. angusticeps (Boulenger, 1907)	X	X	X	X			X	X
S. longimanus (Boulenger, 1911)	X	X	X					
S. macrocephalus (Boulenger, 1899)	X	X	X	X			X	X
S. robustus (Günther, 1864)	X	X	X	X				
S. thumbergi (Castelnau, 1861)	X	X	X				X	X
Sargochromis carlottae (Boulenger, 1905)	X	X	X	X				
S. codringtonii Boulenger, 1908)	X	X	X	X				
S. coulteri (Bell-Cross, 1975)							E	E
S. giardi (Pellegrin, 1903)	X	X	X	X			X	X
S. greenwoodi (Bell-Cross, 1975)	X	X	X					
S. gracilis Greenwood, 1984	X						X	
S. mortimeri (Bell-Cross, 1975)		X						
Tilapia guinasana Trewavas, 1936						E,R		
T. rendalli (Boulenger, 1896)	X	X	X	X	A	A	X	X
T. ruweti (Poll & Thys van den Audenaerde, 1965)	X	X	X	X				
T. sparrmanii A. Smith, 1840	X	X	X	X	X	X	X	X
Thoracochromis albolabris (Trewavas & Thys van den Audenaerde, 1969)							E	E

Appendix 1. cont. Distribution of freshwater fish species in Namibia (A = Alien species; E = Endemic species; H = Hybrids; R = Red data species; M = Marine species).

SPECIES	OKAVANGO	UPPER ZAMBEZI	KWANDO	CHOBE	LOWER ORANGE	INTERIOR	KUNENE	CUVELAI
Tilapia-buysi (Penrith, 1970)							E	E
ANABANTIDAE								
Microctenopoma intermedium (Pellegrin, 1920)	R	R	R	R				
Ctenopoma multispine Peters, 1844	X	X	X	X				
MASTACEMBELIDAE								
Aethiomastacembelus frenatus (Boulenger, 1901)	X	X	X	X				
A. vanderwaali (Skelton, 1976)	R	R						
GOBIIDAE								
Chonophorus guineensis (Peters, 1876)							M	
Ctenogobius lepturus Pfaff, 1933							M	
Nematogobius ansorgei Boulenger, 1910							M	
ELEOTRIDAE								
Batanga lebretonis (Steindachner, 1870)							M	
Eleotris vittata Duméril, 1858							M	
EXOCETIDAE								
Cheilopogon milleri (Gibbs & Staiger, 1970)							M	
CARANGIDAE								
Lichia amia (Linnaeus, 1758)					X		M	
POMADASYSIDAE								
Pomadasys jubilini (Cuvier, 1830)							M	
SCIAENIDAE								
Argyrosomus coronus Griffiths & Heemstra, 1995							M	
MUGILIDAE								
L. falcipinnis (Valenciennes, 1836)							M	
L. richardsoni (Smith, 1846)					M			
Mugil cephalus Linnaeus, 1758					M		M	
POLYNEMIDAE								
Galeiodes decadactylus (Bloch, 1795)							M	
ARIIDAE								
Arius latiscutatus Günther, 1864							M	

Appendix 2. Categories of distribution patterns of the Zambezi Province (after Skelton 1994).

Species	Non-endemic species with a wide distribution in the Province	Endemic species confined to the western sector drainages	Non-endemic species confined to the western sector drainages	Endemic species confined to the eastern sector drainages	Non-endemic species confined to the eastern sector drainages	Western sector species with sporadic eastern sector presence in the northern* or southern** rivers
Marcusenius macrolepidotus	X					
Petrocephalus catostoma	X					
Barbus paludinosus	X					
B. trimaculatus	X					
B. radiatus	X					
B. unitaeniatus	X					
Labeo cylindricus	X					
Hydrocynus vittatus	X					
Micralestes acutidens	X					
Amphilius uranoscopus	X					
Schilbe intermedius	X					
Clarias gariepinus	X					
Aplocheilichthys johnstoni	X					
Pseudocrenilabrus philander	X					
Tilapia rendalli	X					
T. sparrmanii	X					
Kneria maydelli		X				
Parakneria fortuita		X				
Barbus barnardi		X				
B. bellcrossi		X				
B. codringtonii		X				
B. thamalakanensis		X				
Labeo lunatus		X				
L. ansorgii		X				
Hemigrammocharax machadoi		X				
Parauchenoglanis ngamensis		X				
Clariallabes platyprosopos		X				
Chiloglanis fasciatus		X				
Synodontis leopardinus		X				
S. macrostigma		X				
S. macrostoma		X				
S. thamalakanensis		X				

Appendix 2. cont. Categories of distribution patterns of the Zambezi Province (after Skelton 1994).

Species	Non-endemic species with a wide distribution in the Province	Endemic species confined to the western sector drainages	Non-endemic species confined to the western sector drainages	Endemic species confined to the eastern sector drainages	Non-endemic species confined to the eastern sector drainages	Western sector species with sporadic eastern sector presence in the northern* or southern** rivers
Synodontis vanderwaali		X				
S. woosnami		X				
Nothobranchius sp.		X				
Aethiomastacembelus vanderwaali		X				
Sargochromis carlottae		X				
S. coulteri		X				
S. giardi		X				
S. greenwoodi		X				
S. mortimeri		X				
Serranochromis altus		X				
S. angusticeps		X				
S. longimanus		X				
S. thumbergi		X				
Schwetzochromis machadoi		X				
Thoracochromis buysi		X				
T. albolabris		X				
Marmyrus lacerda			X			
Pollimyrus castelnaui			X			
Kneria polli			X			
B.afrovernayi			X			
B. barotseensis			X			
B. dorsolineatus			X			
B. fasciolatus			X			
B. haasianus			X			X*
B. multilineatus			X			
Coptostomabarbus wittei			X			
Hemigrammocharax multifasciatus			X			
Nannocharax macropterus			X			
Synodontis nigromaculatus			X			
Aethiomastacembelus frenatus			X			
Oreochromis macrochir			X			
Tilapia ruweti				X		

Appendix 2. cont. Categories of distribution patterns of the Zambezi Province (after Skelton 1994).

Species	Non-endemic species with a wide distribution in the Province	Endemic species confined to the western sector drainages	Non-endemic species confined to the western sector drainages	Endemic species confined to the eastern sector drainages	Non-endemic species confined to the eastern sector drainages	Western sector species with sporadic eastern sector presence in the northern* or southern** rivers
Parakneria mossambica				X		
Barbus afrohamiltoni				X		
B. brevipinnis				X		
B. marequensis				X		
B. viviparus				X		
Chetia brevis				X		
Protopterus annectens					X	
Mormyrus longirostris					X	
Barbus macrotaenia					X	
B. toppini					X	
Labeo altivelis					X	
Brycinus imberi					X	
Synodontis zambezensis					X	
Oreochromis mossambicus					X	
Hippopotamyrus ansorgii						X*
H. discorhynchus						X*
Barbus kerstenii						X*
Aplocheilichthys hutereaui						X*
Pharyngochromis acuticeps						X*
Barbus bifrenatus						X**
B. mattozi						X**
Labeo ruddi						X**
Mesobola brevianalis						X**
Barbus lineomaculatus						X**
Brycinus lateralis						X**
Clarias theodorae						X**
Ctenopoma multicpine						X**