

Monograph on
**Endemism in the
Highlands and Escarpments
of Angola and Namibia**



Angola Cave-Chat *Xenocopsychus ansorgei*
Photo: M Mills

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Fishes of the highlands and escarpments of Angola and Namibia

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ABSTRACT

The fishes of the highlands and escarpments of Angola and Namibia (HEAN) are described broadly and a brief biogeographical explanation sketched. The fishes of this region are poorly documented in the literature and few records are available. Species of the families Kneriidae, Mormyridae, Cyprinidae, Danionidae, Amphiliidae, Clariidae, Mochokidae, Cichlidae and Mastacembelidae are highlighted and noted. An extraordinary radiation of *Labeobarbus* in the Cuanza River is a distinct feature. Two river systems in western Angola and Namibia, the Cuanza and the Cunene, extend from the interior down the escarpment to the coast and their fish faunas are considerably enriched. Affinities of the various taxa are pointed out including signature links with the southern Congo River basin, and East Africa. West African connections via the coast or the Congo Basin are sparse. West Zambebian faunal links are strongest but generally restricted to elements that favour rocky environments. The fishes of typical Kalahari sand systems, such as floodplains and swamps, are absent. Isolated and fragmented distributions of certain elements attest to relict situations indicative of early, more favourable, widespread distributions.

Keywords: Angola, escarpment, fishes, highlands, Namibia

INTRODUCTION

Some of the first descriptions of freshwater fishes of Angola are from the rivers originating in the highlands and escarpments of Angola and Namibia (HEAN) as these were accessible from the Atlantic ports used by early explorers. The lack of precise localities in these early descriptions hampers the understanding of the link between fish presence and elevation and it was not until several expeditions in the 1920s and 1930s from European and western countries (Nichols & Boulton 1927, Fowler 1930, 1935, Pellegrin 1936, Trewavas 1936) that more precision was introduced. There were two subsequent sources of records for freshwater fishes from the highlands, firstly, pioneering ecologically orientated studies conducted by scientists from Hamburg, Germany (Ladiges & Voelker 1961) and, secondly, collections made by individuals associated with the Dundo Museum and described by Poll (1967). More recently, surveys made in both Namibia and Angola by a post-independence generation of individuals and institutions have added to the available data.

Skelton (2019) provided a checklist of freshwater fishes from the Angolan coastal drainages. These drainages generally extend from a divide that includes the western highlands, or beyond in a few instances, to the Atlantic and consequently not all the species occur exclusively in the highland reaches. Other specific accounts that contribute data include Hay *et al.* (1997) for the Cunene and a few unpublished surveys such as Tate and Kindler (2019) for Longonjo in Huambo Province. In this account I

have compiled a list of fish species (Table 1) expected to occur in the highland reaches of Atlantic coastal rivers south of the Cuanza, based on personal experience in the highlands and the Kalahari sands regions to the east.

FISHES

The fishes of the HEAN are, in general, not well known. The rivers of the highlands have not been comprehensively surveyed and the list in Table 1 is preliminary, based on current knowledge. However, there is clear evidence of an endemic HEAN fauna; in many cases species are restricted to a narrow range or even just a single river system. Figures 1a and 1b illustrate some representative fish from the HEAN. Brief summaries of the families follow.

Kneriidae

The kneriids are small specialised stream fishes, placed in two genera, *Kneria* and *Parakneria*. They belong to an ancient clade of gonorhynchiform fishes estimated by Lavoué (2019) to have been present in Africa since the Cretaceous (145–66 mya). They favour rocky habitats and are primarily distributed around the elevated rim of the Congo Basin with an extension into West Africa and outliers in East and southeastern Africa. At least five species have been recorded from the HEAN including three *Kneria* and two *Parakneria* species. *Parakneria fortuita* is known from the Cubango–Upper Zambezi systems and *P. marmorata* from the Cuanza (Table 1). *Kneria* species include *K. maydelli* which is known from streams in the mountains along the southern edge of

Table 1: A selection of fishes associated with the highlands and escarpments in Angola and Namibia (HEAN).

Family and species	Species author and original record reference	HEAN river system	Comments
Kneriidae			
<i>Kneria ansorgii</i>	(Boulenger, 1910)	Cuanza	
<i>Kneria maydelli</i>	Ladiges & Voelker, 1961	Cunene	
<i>Kneria polli</i>	Trewavas, 1936	Queve, Cubal–Catumbela	
<i>Parakneria fortuita</i>	Penrith, 1973	Cubango–Okavango	Upland western tributaries of the Cunene and Okavango are considered here as part of the highlands
<i>Parakneria marmorata</i>	(Norman, 1923)	Cuanza	
Mormyridae			
<i>Cyphomyrus cubangoensis</i>	(Pellegrin, 1936)	Cubango–Okavango	
<i>Heteromormyrus ansorgii</i>	(Boulenger, 1905)	Cuanza	
<i>Heteromormyrus longilateralis</i>	Kramer & Swartz, 2010	Cunene	
<i>Heteromormyrus pappenheimi</i>	(Boulenger, 1910)	Cuanza	
<i>Heteromormyrus pauciradiatus</i>	(Steindachner, 1866)	Cuanza	
<i>Marcusenius multisquamatus</i>	Kramer & Wink, 2013	Cunene	
<i>Petrocephalus cunganus</i>	Boulenger, 1910	Cuanza	
Danionidae			
<i>Engraulicypris howesi</i>	Ridden <i>et al.</i> , 2016	Cunene	
<i>Raiamas ansorgii</i>	Boulenger, 1910	Cuanza	
Cyprinidae			
<i>Enteromius argenteus</i>	(Gunther, 1868)	Cuanza	
<i>Enteromius breviceps</i>	(Trewavas, 1936)	Cunene, Cubango–Okavango	
<i>Enteromius dorsolineatus</i>	(Trewavas, 1936)	Queve	
<i>Enteromius eutaenia</i>	(Boulenger, 1904)	Cunene	Related species in Limpopo and SE Africa coastal rivers
<i>Enteromius evansi</i>	(Fowler, 1930)	Cuanza, Cubango–Okavango	
<i>Enteromius greenwoodi</i>	(Poll, 1967)	Cuanza	
<i>Enteromius kessleri</i>	(Steindachner, 1866)	Cuanza	
<i>Enteromius lineomaculatus</i>	(Boulenger, 1903)	Cunene, Upper Zambezi	
<i>Enteromius mattozi</i>	(Guimaraes, 1884)	Cunene, Cuanza, Upper Zambezi	Extended clade species in Inkisi, Upper Congo, Ruvuvu, Lake Malawi, Limpopo
<i>Enteromius mocoensis</i>	(Trewavas, 1936)	Queve, Cubango–Okavango	
<i>Enteromius paludinosus</i>	(Peters, 1852)	Cunene, Cubango–Okavango, Upper Zambezi, Lower Zambezi, Lower Orange	Related species complex in East Africa, Ethiopia, and Lower Zambezi south to KwaZulu-Natal in South Africa
<i>Enteromius trimaculatus</i>	(Peters, 1852)	Cunene, Cubango–Okavango, Lower Orange, Lower Zambezi south to KwaZulu-Natal in South Africa	Related species <i>E. poechii</i> in Okavango–Upper Zambezi–Kafue; <i>E. jacksoni</i> in East Africa
<i>Enteromius wellmani</i>	(Boulenger, 1911)	Queve	
<i>Labeo ansorgii</i>	Boulenger, 1907	Cunene	
<i>Labeo rocadasi</i>	Boulenger, 1907	Cuanza	
<i>Labeobarbus ansorgii</i>	(Boulenger, 1906)	Cuanza	
<i>Labeobarbus boulengeri</i>	Vreven, Musschoot, Snoeks & Schliewen, 2016	Cuanza, Inkisi, Lower Congo	
<i>Labeobarbus codringtonii</i>	(Boulenger, 1908)	Cubango–Okavango, Upper Zambezi, Kafue	Rocky habitats preferred
<i>Labeobarbus ensifer</i>	(Boulenger, 1910)	Cuanza	
<i>Labeobarbus ensis</i>	(Boulenger, 1910)	Cuanza	
<i>Labeobarbus girardi</i>	(Boulenger, 1910)	Cuanza	
<i>Labeobarbus gulielmi</i>	(Boulenger, 1910)	Cuanza	

Family and species	Species author and original record reference	HEAN river system	Comments
<i>Labeobarbus lucius</i>	(Boulenger, 1910)	Cuanza	
<i>Labeobarbus rhinophorus</i>	(Boulenger, 1910)	Cuanza	
<i>Labeobarbus rocadasi</i>	(Boulenger, 1910)	Cuanza	
<i>Labeobarbus rosae</i>	(Boulenger, 1910)	Cuanza	
<i>Labeobarbus steindachneri</i>	(Boulenger, 1910)	Cuanza	
<i>Labeobarbus stenostomata</i>	(Boulenger, 1910)	Cuanza	
<i>Labeobarbus varicostoma</i>	(Boulenger, 1910)	Cuanza	
Amphiliidae			
<i>Amphilius cubangoensis</i>	Pellegrin, 1936	Okavango	
<i>Amphilius lentiginosus</i>	Trewavas, 1936	Queve	
<i>Amphilius pagei</i>	Thomson & Swartz, 2018	Cuanza	
<i>Doumea angolensis</i>	Boulenger, 1906	Cuanza	
<i>Doumea</i> sp.		Cuanza	SAIAB records
<i>Zaireichthys kunenensis</i>	Eccles, Tweddle & Skelton, 2011	Cunene	
Clariidae			
<i>Clarias cavernicola</i>	Trewavas, 1936	Aigamas Cave	A karstveld outlier to the highlands
<i>Clarias dumerilii</i>	Steindachner, 1866	Queve	As identified by Trewavas (1936)
<i>Clarias liocephalus</i>	Boulenger, 1898	Cunene, Cubango–Okavango	
<i>Clariallabes</i> sp.		Cunene	SAIAB records; possible links with Queve (<i>C. dumerilii</i>); Cuanza and Okavango–Upper Zambezi (<i>Clariallabes</i> sp.)
<i>Platyclarias machadoi</i>	Poll, 1977	Cuanza	SAIAB records; <i>Platyclarias machadoi</i> in Cuango; Bernt <i>et al.</i> (2023)
Mochokidae			
<i>Chiloglanis angolensis</i>	Poll, 1967	Cunene	
<i>Chiloglanis fasciatus</i>	Pellegrin, 1936	Cubango, Zambezi	
<i>Chiloglanis sardinhai</i>	Ladiges & Voelker, 1961	Longa	
Cichlidae			
<i>Chetia gracilis</i>	(Greenwood, 1984)	Cutato Nganguela (Cubango–Okavango)	
<i>Chetia welwitschi</i>	(Boulenger, 1898)	Cunene, Longa	<i>Chetia welwitschi</i> in Longa, see Tate & Kindler (2019)
<i>Orthochromis machadoi</i>	(Poll, 1967)	Cunene	
<i>Thoracochromis albolabris</i>	(Trewavas & Thys van den Audenaerde, 1969)	Cunene	
<i>Thoracochromis buysi</i>	(Penrith, 1970)	Cunene	
<i>Thoracochromis lucullae</i>	(Boulenger, 1913)	Cuanza	
<i>Tilapia guinasana</i>	Trewavas, 1936	Guinas lake	A karstveld species of the highlands
Mastacembelidae			
<i>Mastacembelus ansorgii</i>	Boulenger, 1905	Cuanza, Queve	Queve records SAIAB
<i>Mastacembelus frenatus</i>	(Boulenger, 1901)	Cubango–Okavango	

the Cunene River gorge below Ruacana. This is the southernmost distribution of *Kneria* in the HEAN.

Mormyridae

The family Mormyridae is also an ancient lineage in Africa dating from Cretaceous times. These fishes are essentially nocturnal and have electrogenic and electroreceptive properties. Various species are

present in the rivers of the HEAN, especially the middle-order and main streams in both rocky and floodplain environs. There is a fair degree of catchment endemism in the family with at least two endemic *Heteromormyrus* species in the Cunene and at least four endemic species generally associated with highland streams in the Cuanza. The genus *Heteromormyrus* was recently reviewed by Sullivan



Figure 1a: Representative fish from the highlands and escarpments of Angola and Namibia (HEAN). Top to bottom: *Heteromormyrus longilateralis*, Cunene River (photo: R Bills); *Parakneria marmorata*, Cuanza River (photo: E Swartz); *Enteromius breviceps*, Queve River (photo: P Skelton); *Enteromius evansi*, Queve River (photo: P Skelton); *Enteromius eutaenia*, Cunene River (photo: R Bills); *Labeo ansorgii*, Cuanza River (photo: E Swartz); *Labeobarbus* sp., Cuanza River (photo: E Swartz); *Labeobarbus* sp., Cuanza River (photo: E Swartz); *Labeobarbus* sp., Cuanza River (photo: E Swartz).



Figure 1b: Representative fish from the highlands and escarpments of Angola and Namibia (HEAN). Top to bottom: *Micralestes argyrotaenia*, Queve River (photo: P Skelton); *Clarias* sp. (cf. *Iiocephalus*), Queve River (photo: P Skelton); *Platyclarias machadoi*, Cuanza River (photo: E Swartz); *Amphilius pagei*, Cuanza River (photo: E Swartz); *Doumea angolensis*, Cuanza River (photo: E Swartz); *Chiloglanis* sp., Queve River (photo: P Skelton); *Mastacembelus* sp. (cf. *frenatus*), Queve River (photo: P Skelton); *Chetia* sp., Queve River (photo: P Skelton); *Pharyngochromis* sp., Queve River (photo: P Skelton); *Austrotilapiine* cichlid, Cuanza River (photo: R Bills).

et al. (2022) and recognised as the valid genus for the cluster of ‘slender stonebashers’ from southern Africa, which were previously classified within the genus *Hippopotamyrus*. Species of *Cyphomyrus*, *Heteromormyrus*, *Marcusenius* and *Petrocephalus* make for a diverse representation of the family, especially in the larger river systems like the Cunene and the Cuanza.

Danionidae

The presence of the Family Danionidae, (subfamily Chedrinae) genus *Engraulicypris* (*E. howesi* in the Cunene, *E. brevianalis* in the Limpopo) (Ridden *et al.* 2016) is notable. The chedrins in the highlands are also represented by *Raiamas ansorgii* from the Cuanza, and *Opsaridium zambezense* in the headwaters of the Okavango (the Cubango River). The latter species is widespread in the Zambezi.

Cyprinidae

The Cyprinidae (*sensu stricto*, after Tan & Armbruster 2018) is, by far, the largest fish family occurring in the HEAN rivers. In Africa south of the Sahara the family includes the subfamilies Labeinae (labeos), Torinae (hexaploid yellowfishes) and the Smiliogastrinae (minnows). Although the systematic status of many species is not yet settled and distributions are not fully mapped in the highlands, endemism is clearly indicated for some species or species groups. An outstanding feature is the high number of species ($n = 14$, Skelton 2019) of large hexaploid yellowfish in the genus *Labeobarbus* found in the Cuanza River system. Recent collections in the Longa River to the south of the Cuanza include a possible conspecific *Labeobarbus* that might indicate drainage linkage between these systems (Tate & Kindler 2019). Another species of uncertain identity has been recorded in the Queve (pers. obs.), the headwaters of which share the divide with the upper reaches of the Cuanza. A single species, *Labeobarbus codringtonii*, occurs in the headwaters of the Cubango-Okavango and Zambezi. However, this widespread Afrotropical genus has not been recorded from the Cunene. There are several minnow species (Smiliogastrini) that also connect across the drainages in the highlands such as *Enteromius mattozi*, *E. argenteus* and *E. evansi* in the Cunene-Cuanza; and *E. breviceps*, *E. evansi*, *E. mocoensis*, *E. paludinosus* and *E. trimaculatus* in the Cunene-Okavango-Upper Zambezi. Few *Labeo* species have been recorded from the HEAN. Tate and Kindler (2019) found an extremely slender *Labeo* in the Catumbela that may be an undescribed species or an eco-phenotype of *L. ansorgii*. It is possible that *L. ansorgii* (with *L. rocadasi*) reflects a Cunene-Cuanza linkage. The trans-Kalahari Cunene-Limpopo presence of *L. ruddi* is echoed by *Enteromius eutaenia* in both systems and the distribution of a related pair of minnows, *Enteromius mattozi* (Cunene) and *E. rapax* (Limpopo).

Amphiliidae

Amphiliid catfishes are significant markers of many African highland systems but they are few and relatively restricted in the HEAN. Three genera are recorded, two in the Cuanza – *Doumea* and *Amphilius*. *Doumea* is largely a Congo and Central West African genus. There are two species in the Cuanza including *Doumea angolensis* and a second, possibly undescribed, species. *Amphilius* is an Afrotropical genus with two sublineages, an east and southeastern lineage (High Africa) with 9+10 primary caudal fin rays, and a Low Africa (Congo-West Africa) lineage with a reduced number of caudal fin rays (6+7). Three species of *Amphilius* are found in the HEAN, two related species from the Low-African lineage in the Cuanza and the Queve as well as the Cuango-Congo (*A. lentiginosus*, *A. pagei*), and a representative of the ‘High Africa’ clade, *A. cubangoensis*, from the Cubango-Okavango-Upper Zambezi (Trewavas 1936, Thomson & Swartz 2018, Skelton 2019). In the Cunene the family is represented by the diminutive sand-dwelling *Zaireichthys cunenensis*, indicating a Cunene-Okavango linkage.

Clariidae

Clariid airbreathing catfishes are common and widespread in Afrotropical rivers and lakes. Characteristic of swamps and lakes they are not typically ‘highland’ fishes and it is a measure of the relatively low elevation from the interior of the HEAN that several clariid species do occur in low-order tributaries of the rivers. Few species with broad depressed heads and reduced post-orbital bones characteristic of the genera *Clariallabes* and *Platyclarias* occur in rocky reaches of certain rivers in the HEAN. *Platyclarias* is presently only known from the Cuango-Congo (Poll 1977) but a species (*P. machadoi*) from the Cuanza is attributed to this genus (Bernt *et al.* 2023). *Clariallabes* is present in rocky habitats of the Upper Zambezi-Okavango and the Cuanza and an unidentified broad-headed rock-dwelling species in the Cunene is possibly of this genus. *Clarias dumerilii* collected by Karl Jordan from the Queve (Serra do Môco) in the 1930s and identified by Trewavas (1936) is an unconfirmed, broad-headed species. These observations indicate that rivers in the HEAN host several rock-dwelling clariids that require further investigation before their significance is realised. A unique cave-dwelling clariid (*Clarias cavernicola*) inhabits a karst cave-lake system (Aigamas, Namibia) on the southern rim of the highlands (Trewavas 1936, Jacobs *et al.* 2021). This troglobitic species appears to be of the *Clarias* (*Anguilloclarias*) lineage, which are small, slender-headed clariids that inhabit floodplains, swamps and bogs. It is therefore probably a stranded relict from a former pluvial period and is not typical of other highland clariid species.

Mochokidae

Mochokid catfishes of the genus *Synodontis* are uncommon and not characteristic of the HEAN. The genus is known from the Cuanza (Skelton 2019) and the Cunene (Hay *et al.* 1997), where five recorded species occur and all are also reported from the Cubango–Okavango (Skelton 2001). Several suckermouth catlets (*Chiloglanis*) are distinctly associated with the highlands. *Chiloglanis angolensis* was described from the Cubal system in the Catumbela at 1,500 masl where it was collected together with *Kneria polli*. This species is likely to occur in the Cunene that shares a watershed with the Cubal. *Chiloglanis sardinhai* has been recorded from the Longa, south of the Cuanza (Ladiges & Voelker 1961). *Chiloglanis fasciatus* from the Cubango–Okavango is possibly also in the Catumbela system (Tate & Kindler 2019).

Cichlidae

Several species of cichlid fishes are associated with the HEAN. In particular the haplotilapiine cichlid fishes of the Cunene (Greenwood 1984) and those of the Cuanza (Schwarzer *et al.* 2012) are singled out for

their endemicity and interest. The Cunene River has four endemic cichlids – *Thoracochromis albolabris*, *T. buysi*, *Orthochromis machadoi* and the downstream species *Sargochromis coulteri*. *Thoracochromis lucullae*, and downstream species *Serranochromis cuanza* and *S. swartzi* are endemic to the Cuanza and there are several species detected by the molecular analysis of Schwarzer *et al.* (2012) that have not yet been dealt with taxonomically. The precise type locality for *Chetia welwitschi*, given by Boulenger (1898) as ‘Fluilla, Angola’, is uncertain (Greenwood 1984) and the species is poorly known from the Angolan coastal systems. A specimen photographed by R Tate from the Longa River in 2018 (Tate & Kindler pers. comm.) appears to be of this species. Specimens from the upper reaches of the Cunene have also been tentatively identified (pers. obs.). *Chetia gracilis* described by Greenwood (1984) from the upper reaches of the Cutato Nanguela in the Cubango–Okavango system is a second species of the genus that might be characteristic of the HEAN. *Orthochromis machadoi* from the Cunene below Ruacana is another HEAN endemic. *Tilapia sparrmanii* and *Coptodon rendalli* are present



Figure 2: Major rivers of the highlands and escarpments of Angola and Namibia (HEAN, orange outline).

in the Cuanza and the Cunene but are not characteristic of the highland streams. Likewise *Oreochromis angolensis* is present in the coastal reaches of the Angolan coastal rivers but is not characteristic of the scarp or highland streams. *Tilapia guinasana*, closely related to *T. sparrmanii*, is an aberrant polychromatic species narrowly endemic to the Guinas sinkhole lake in the southern karst belt (Namibia). As with the cave catfish, the presence of this species is likely a relict of former pluvial conditions that prevailed from time to time over the region and is not characteristically a ‘highland’ species. The general conclusion is that the cichlids of the HEAN are poorly known and, based on work such as Schedel *et al.* (2019) and Schwarzer *et al.* (2009, 2012), could represent early radiations of the ‘Haplotilapiines’ in Africa.

Mastacembelidae

Spiny-eels (Mastacembelidae) are uncommon and known from only three rivers along the HEAN – the Cuanza (*Mastacembelus ansorgii*), the Okavango (*M. frenatus*) and the Queve (*M. sp.*). This distribution

reinforces the observation of interconnection between these systems that was noted previously. Furthermore, the shared presence of the genus in both the Congo and the Upper Zambezi–Okavango indicates connection eastward into the Kalahari Basin. The rarity of such records also highlights the need for further, more comprehensive surveys of the streams and rivers in the HEAN.

Order Characiformes: Hepsetidae, Alestidae

Characiform fishes are not considered here as ‘highland’ representatives as they are more generally associated with downstream riverine and floodplain habitats. However, it is noted that representatives, such as the southern pike (*Hepsetus cuvieri*), are present in the Cuanza and the Cunene; several alestids including *Brycinus lateralis* are in the Cuanza; the silver robber, *Micralestes argyrotaenia*, possibly conspecific with the widespread *M. acutidens*, is in the Cunene. The tigerfish (*Hydrocynus vittatus*) is in the Okavango but is generally absent from the HEAN.

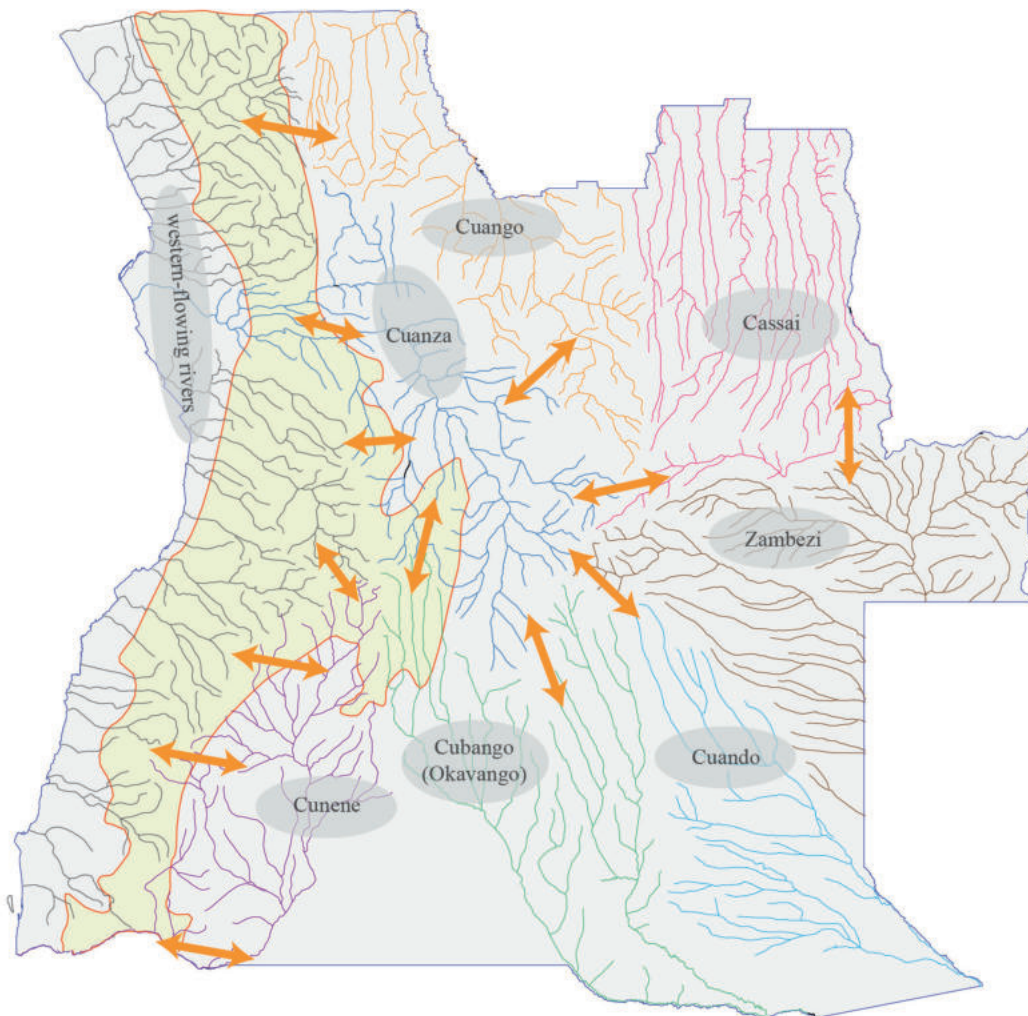


Figure 3: Western escarpments and highlands of Angola, showing rivers and the dynamic divide between the interior basins of the Cunene and the Cuanza systems and adjacent catchments. The outline of the highlands and escarpments is shown in orange. Orange bidirectional arrows indicate the interactive zones across the divides between the interior basins and rivers.

BIOGEOGRAPHY

Freshwater fishes are excellent biogeographic indicators as they are firmly tied to hydrographic evolution. While the hydrographic evolution of the highlands is not yet comprehensively understood, certain features have been exposed that begin to explain the history of the fauna. The HEAN represent the elevated eastern scarp of the rift between Africa and South America. Since rifting, the escarpment has been retreating eastward under the erosional force of coastal river systems, with a few notable breaches of the divide, namely, the Cuanza and the Cunene (Figure 2). Each of these two systems has tapped into major Kalahari sedimentary sub-basins (Cuanza–Luando and Cunene–proto-Etосha, respectively) and is actively expanding the respective basin rim by captures across the divide (Leturmy *et al.* 2003, Miller *et al.* 2010). Other rivers have penetrated deeply into the scarp and breached the coastal–interior watershed in less spectacular fashion, e.g., the Longa, the Queve and the Catumbela (Figure 2).

The northwestern drainages of the elevated ‘Kalahari plateaus’ are generally north–south in alignment along the base of the highlands and there are clear instances of drainage capture between systems along the interior (east) of the highlands (Figure 3). These captures have played a major role in faunal mixing and transfer and have imparted a clear ‘West Zambezan’ character to the faunal composition of these systems (e.g., Trewavas 1936, Schwarzer *et al.* 2012, Musilova *et al.* 2013). Typical West Zambezan indicator species in this respect include the southern pike (*Hepsetus cuvieri*) and the Zambezi grunter (*Parauchenoglanis ngamensis*), both of which also have Congo Basin associations. Other groups such as the serranochromine cichlids, the *Synodontis* catfishes and mastacembelid spiny eels have East African ‘Rift’–Lake Tanganyika affinities (Schwarzer *et al.* 2009, 2012, Schedel *et al.* 2019). In addition, strong East African affinities are indicated by the presence of widespread species like the three-spot minnow (*Enteromius trimaculatus*) and the straightfin minnow (*E. paludinosus*). The north–south alignment of interior eastern adjacent drainages (see Figure 3, Cubango (Okavango) catchment) is a key element in the deposition of the deepest sediments of the Kalahari Basin within the Etosha Basin (Thomas & Shaw 1991). This alignment extends into the south–north drainage of the Upper Cuanza. A possibly earlier linkage from west to east across the Kalahari Basin to Central (Congo and Rift) and East Africa is still evident in the drainage lines of the Upper Cassai and the Lungwe–Bungwe–Upper Zambezi. The ichthyofaunal elements derived from this earlier west–east linkage (e.g., *Enteromius mattozi*, *E. paludinosus*, *E. trimaculatus*, kneriid species, rock-dwelling clariids, *Orthochromis machadoi*) are characteristic components of the

ichthyofauna of the HEAN. This drainage connection probably existed prior to the Miocene desertification of the Kalahari Basin (Senut *et al.* 2009). Freshwater connections downstream along the coastal reaches have also contributed to the fauna of the Atlantic coastal rivers (Skelton 2019), but these involve species not generally encountered in the upland escarpment streams and rivers and are thus excluded from consideration here.

The affinities of fishes in the HEAN strongly reflect the north–south alignment of the interior drainage connections from the Cunene through to the Cuanza, as well as reflecting links across the Cuanza–Cuango–Cassai–southern Congo belt of rivers. In the north this west–east link reaches across the East African Rift System and its associated highlands to the rivers of East Africa. The postulated palaeo-drainage lines from the Okavango–Cuango–Upper Zambezi south and east to the Limpopo and southeastern coastal systems (Moore & Larkin 2001) is also reflected in the circum-Kalahari distributions of several lineages (such as *Enteromius mattozi* and *E. breviceps* chubby-head minnow lineage; *Engraulicypris* and *Kneria*). It is evident that the highlands and escarpments of Angola and Namibia have served as a geo-climate sanctuary or refuge for fishes (and likely other aquatic groups) since at least the Miocene.

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