Chapter 11
The Freshwater Fishes of Angola

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Abstract The discovery and exploration of Angolan freshwater fishes was largely effected by foreign scientists on expeditions organised by European and North American parties. Current knowledge of Angolan freshwater fishes is briefly described according to the main drainage systems that include Cabinda, Lower Congo, Angolan Coastal region including the Cuanza, the southern Congo tributaries, the Zambezi, Okavango, Cunene and Cuvelai drainages. A biogeographic model to explain the freshwater fish fauna of Angola is presented. The need for the conservation of Angolan freshwater fishes will rise with rapidly increasing pressures on aquatic ecosystems from urbanisation, dams for power, agriculture and human needs, habitat destruction from mining and deforestation, pollution, the introduction of alien species and overfishing.

Keywords Africa · Cuanza · Cunene · Cuvelai · Okavango · Southern Congo · Zambezi

Historical Review

> Despite Poll's work (1967) over a very limited area, Angola remains a poorly known region in which there remains much to be discovered (Lévêque and Paugy 2017a: 93)

The quotation above sums up the current state of knowledge for the freshwater fishes of Angola. Poll (1967) is a landmark publication that reviews the historical literature and records the known species and their distribution within the major river basins of the country at that time. No other account of Angolan fishes as a whole has been published. The current situation of a poorly known region is due to a number of factors including the historical neglect of scientific exploration by the colonial

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authorities, widely dispersed collections in international institutions from various expeditions, the relative inaccessibility to scientists and collectors of the inland rivers and biologically rich areas, and the difficulties of aquatic exploration relative to terrestrial fauna. The fact that there is no national Angolan depository for wet collections such as fishes fostered by local expertise is a further hindrance to discovery. This aspect is fundamental to effective and sustained scientific productivity in any endeavor such as ichthyology (Skelton and Swartz 2011). This accentuates the situation for Angolan freshwater fishes when it is recognised that Poll's (1967) account rested largely on the collection in the Diamond Company of Angola (DIAMANG) museum in Dundo, which to a large extent is a product of the industrial diamond mining activity in the mainly local drainages.

There are four distinct phases of scientific discovery of Angolan freshwater fishes, Phase 1 – early explorations in the second half of the nineteenth century; Phase 2 – scientific expeditions in the twentieth century until World War II; Phase 3 – post WWII to Angolan independence in 1975; and, Phase 4 – post independence investigations.

Although several of Castelnau's (1861) Lake Ngami fishes occur in the Angolan reaches of the Okavango River system, the discovery and scientific description of Angolan freshwater fishes was initiated by Steindachner (1866) describing a collection derived from the Atlantic coastal rivers. Steindachner's species include some iconic species such as his *Kneria angolensis, Clarias angolensis* and *Enteromius kessleri* that help define the Angolan Atlantic coastal fauna. Guimarães (1884) working with specimens in the Lisbon Museum (subsequently lost in the fire of 1978) (Saldanha 1978) submitted by the Portuguese explorer José Alberto de Oliveira Anchieta provided detailed descriptions and illustrations of three species taken from the Cunene and the Curoca Rivers from 1873–1884, viz. *Schilbe steindachneri, Mormyrus anchietae* and *Enteromius mattozi.*

The second phase of discovery (early twentieth century) is marked by a series of expedition reports that include freshwater fishes. Boulenger's (1909–1916) catalogue of fishes in the British Museum (Natural History) provided the basis of Angolan freshwater fish fauna. Again the fauna included collections such as Woosnam's Okavango collection described by Boulenger (1911) that includes species which occur in Angolan reaches. Boulenger (1910) described a collection by Ansorge from the Cuanza and Bengo Rivers that set the scene for considering the uniqueness of the fauna of these rivers of the Atlantic coast. Other notable expeditions that included descriptions of freshwater fishes are the Vernay Angola Expedition of 1925 (Nichols and Boulton 1927), the Gray African Expedition of 1929 (Fowler 1930), the Vernay-Lang Kalahari Expedition of 1930 (Fowler 1935), the Swiss Scientific Mission to Angola 1928–1929 and 1932–1933 (Pellegrin 1936), and Karl Jordan's Expedition to South West Africa and Angola of 1933–1934 (Trewavas 1936). All these expeditions realised new species but were somewhat limited in geographical scope to the southern Atlantic coastal rivers and to the upland western reaches of the Cubango (Okavango) tributaries, the Oshana-Etosha system and the plateau reaches of the Cuanza. This restriction emanates from the

access realised by the Benguella Railway constructed from 1903 to 1928 from Lobito port to Huambo and beyond (Ball 2015).

The third phase of scientific exploration of the freshwater fishes of Angola after the WWII up until independence in 1975 is significant in that studies into ecological aspects as well as the beginnings of a synthesis of the Angolan fauna occurred. Ladiges and Voelker (1961) studied the fish fauna of the Longa River in the Angolan watershed highlands. In addition to providing an ecological description and zonation of the river they described a few new species – *Kneria maydelli* from the Cunene, *Enteromius* (as *Barbus*) *roussellei* and *Chiloglanis sardinhai*. Ladiges (1964) followed up this article with an account of the zoogeography and ecology of Angolan freshwater fishes based on a present/absent list of fishes in the Angolan Coastal region, the Cunene, the Okavango Basin, and the Zambezi. Trewavas (1973) recorded the cichlids of the Cuanza and Bengo Rivers that exposed the independent derivation of the cichlid fauna of the Cuanza River in terms of the inland and coastal reaches. An unpublished collection by Graham Bell-Cross from the Okavango and the Cunene basins was deposited in the NHM in 1965, and this together with collections made by Mike Penrith from the State Museum in Windhoek, Namibia, provided specimens essential for Greenwood's (1984) revision of serranochromine species. Mike Penrith's collections from the Cunene and Okavango in the early 1970s led to a few descriptions of new species by Penrith (1970) and Penrith (1973).

A major milestone account of Angolan freshwater fishes was Max Poll's (1967) *Contribution à la Faune Ichthyologique de l'Angola* – based largely on the extensive collections made by Barros Machado and others and lavishly illustrated with excellent fish drawings as well as a gallery of photographs drawn from the Dundo Museum in Lunda-Norte. Poll (1967) summarised the history of freshwater ichthyology and provided a full checklist of 264 species in 18 families and 54 genera as then recorded from the inland waters of the country (excluding the Cabinda enclave). A faunistic and zoogeographical account considered five ichthyological regions (see below). Acknowledging a clearly incomplete inventory Poll listed the diversity of his regions as follows: The Congo tributaries with 121 species are richest and most diverse with characteristic families and genera known from the Congo Basin. Next in diversity was the western Atlantic coastal region with 109 species, followed by the Zambezi (62 species) but Poll pointed out that Bell-Cross had then recently recorded 77 species from the upper Zambezi, also of tropical diversity but distinct in character from the Congolean rivers. The Okavango-Cubango (57 species) reflected its close connections to the Zambezi as well as to the Cunene (55 species) in the west. The Cunene presented a mixed fauna of both the Zambezian elements as well as Atlantic coastal nature.

Poll (1967) pointed out and summarised a few notable ichthyological characteristics of the Angolan fauna – there was no pronounced endemic character to the fauna as a whole. The occurrence of lungfish (*Protopterus*) in Angola is known only from records in Congo tributaries and from Cabinda, but Poll mentions that he was shown a photograph by Ladiges of *Protopterus annectens brieni* from the Cubango region (see this recorded in Ladiges 1964: 265). Such occurrence of lungfish in the Cubango or Okavango system has not yet been confirmed in spite of

extensive collecting in that drainage. Polypterids are restricted to Congo tributaries as are freshwater clupeids (however marine or estuarine species also occur in coastal Atlantic rivers). The presence of kneriids is a distinct feature of the fauna especially of the escarpment reaches of rivers of the coastal region. Mormyrid diversity (36 species) is relatively high, most especially in the southern Congo rivers. Characins (17 species) are less diverse but there is an equivalent representation of Citharinids (16 species). The largest family represented in the country is the Cyprinidae (79 species) and this is especially notable for the Atlantic coastal drainages (43 species) that is even richer than the Congo tributaries (27 species). However the chedrins (*Raiamas* and *Opsaridium* and *Engraulicypris*) are poorly represented – two species in Congo tributaries, one in the Zambezian region and one in the Atlantic coastal drainages. Of the catfishes, the claroteids (10 species) are a presence as are the clariids (17 species) of which the majority (11 species) are represented across different provinces. Other catfish families present include schilbeids (eight species) mochokids (15 species), amphiliids (six species) and one malapterurid. Cyprinodonts are relatively few (eight species) but show a particular relationship across the Cassai-Zambezi watershed. Cichlids (31 species) are well represented but not as well as the cyprinids. They are however more endemic in nature, in particular the Atlantic coastal fauna (19 species with eight endemic). The anabantids (three species) and mastacembelids (three species) are poorly represented.

The last phase of ichthyological exploration informing on the fishes of Angola, since independence in 1975, includes several taxonomic or systematic articles (e.g. Greenwood 1984, Musilová et al. 2013); published river faunal accounts (Skelton et al. 1985; Hay et al. 1997) and several unrestricted informal fish survey reports emanating from specific projects (Bills et al. 2012, 2013; Skelton et al. 2016). These surveys have exposed several new species to the fauna and together with phylogenetic studies on a wide range of lineages that include Angolan representatives, have led to a vastly improved understanding of the distributional nuances that give explanation to improved biogeographical insights.

Freshwater Drainages and Ecoregions of Angola

The drainages of Angola include southern source tributaries of the Congo, western source tributaries of the Zambezi, coastal rivers to the Atlantic from the Chiloango in Cabinda to the Cunene in the south, and the endorheic Etosha and Okavango Basin drainages in the south (Fig. 11.1). The watershed between the Congo system and the coastal Atlantic and Zambezian rivers is a major ichthyofaunal divide of considerable biogeographic significance (Poll 1967, Jubb 1967, Skelton 1994, Snoeks et al. 2011, Paugy et al. 2017).

The freshwater fishes of Angola fall within four major African ichthyological provinces (Fig. 11.1) – Lower Guinea, Congolese, Angolan (coastal) or Cuanza and Zambezian (Roberts 1975, Snoeks et al. 2011, Lévêque and Paugy 2017b).

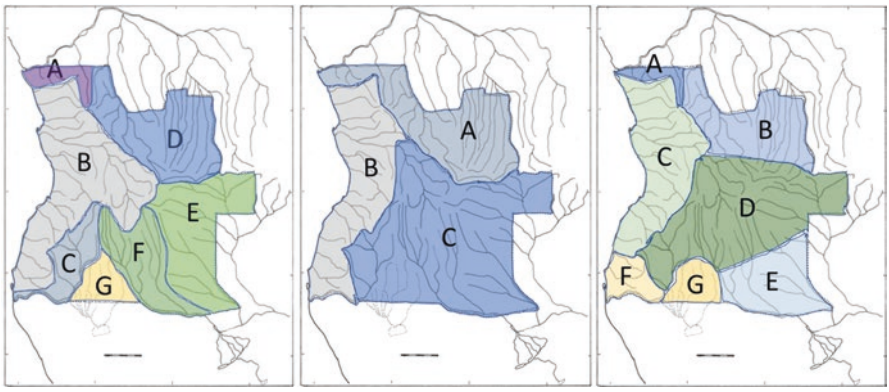

Fig. 11.1 *Left*: **Main drainage basins of Angola**. A: Lower Congo, B: Cuanzan or Atlantic Coastal, C: Cunene, D: Southwest Congo E: (west) Upper Zambezi, F: Okavango, G: Cuvelai. Chiloango in Cabinda not illustrated. *Center*: **Ichthyological provinces in Angola**, modified from Lévêque and Paugy (2017b) to include upper Cuanza and upper Cunene in the Zambezian Province. A: Congolian, B: Angolan or Cuanzan, C: Zambezian. Cabinda and the Chiloango River in the Lower Guinea Province not illustrated. *Right*: **Aquatic ecoregions in Angola**, modified, after Thieme et al. (2005). A – Lower Congo, B – Cassai, C – Cuanza, D – Zambezian headwaters, E – Okavango and Upper Zambezian floodplains, F – Namib coastal, G – Etosha. Southern West Coastal Equatorial (Cabinda) not illustrated

Previously Poll (1967) considered the freshwater fishes of Angola to be from five ichthyological regions drawn along watershed lines – Congo tributaries, Zambezi region, Angolan (western) coastal drainages excluding the Cunene, the Cubango-Okavango, and the Cunene. Thieme et al. (2005) defined ecoregions as "a large area containing a distinct assemblage of natural communities and species, whose boundaries approximate the original extent of natural communities before major land use change", and often reach across watershed lines. The Thieme et al. (2005) aquatic ecoregion map for Africa included Angolan inland waters within eight aquatic ecoregions as follows (Fig. 11.1): Floodplains, Swamps and Lakes – Region 12 Okavango Floodplains, Region 16 Upper Zambezi Floodplains; Moist Forest Rivers – Region 22 Lower Congo, Region 29 Southern West Coastal Equatorial; Savannah Dry Forest – Region 63 Cuanza, Region 76 Upper Zambezian headwaters; Xeric Systems – Region 82 Etosha, Region 88 Namib Coastal. Both the Ichthyological Provinces and the Ecoregions are convenient categories to consider the freshwater fishes of Angola.

Cabinda

Pellegrin (1928) recorded 28 species from the Chiloango River from Republic of Congo (formerly 'French' Congo). The freshwater fishes of Lower Guinea, Central West Africa that includes Cabinda were considered in detail through the two

volumes edited by Stiassny et al. (2007). This rich Central West African fauna includes 555 species in 147 genera and 38 families of which 78 species, 52 genera and 25 families have been recorded from the Chiloango (also Shiloango) River in Cabinda (Appendix 1). This Atlantic coastal river is clearly boosted by the large number of marine and estuarine species that enter freshwaters sporadically or regularly (Whitfield 2007). A number of species from here such as *Enteromius holotaenia, Enteromius musumbi, Aplocheilichthys spilauchen* and *Oreochromis angolensis*, and estuarine species of marine origin also occur in the lower reaches of Angolan Atlantic coastal rivers, some to as far south as the Cunene River (Penrith 1982, Hay et al. 1997). Fowler (1930) recorded a number of species in the Academy of Natural Sciences of Philadelphia collection taken from the Chiloango region as it was known at the time. The fauna from the Chiloango in Angolan territory is likely underrepresented in most groups due to lack of sampling.

Lower Congo

There are no records available of fishes collected in Angolan waters of the Lower Congo mainstream or of the southern bank tributaries. The largest of these tributaries is the Inkisi River of which the fish fauna is known from the studies of Wamuini Lunkayilakio et al. (2010) supplemented by the description of new species described in association with that work (Wamuini Lunkayilakio and Vreven 2008, 2010). Based on these studies it is likely that most of the species in the DRC from the reaches above the Sanga Falls at least are likely to occur in Angola as well. The nature of the likely fauna of this neglected area of Angola as far as fish exploration is concerned (Appendix 2) indicates that the species are essentially of Congolian or Lower Guinean affinity with a few endemic species indicative of the isolation of fauna in the river reaches above the Sanga Falls. The widespread presence of *Oreochromis niloticus* is attributed to introduction for aquaculture (Wamuini Lunkayilakio et al. 2010).

Cuanza and Atlantic Coastal Rivers

Poll (1967) listed 110 species in 32 genera and 15 families from the Atlantic coastal region that includes the Cuanza River, which is revised (Appendix 3) to 105 species in 45 genera and 17 families in the light of more recent surveys in the Cuanza. There are very few species recorded from the Angolan Coastal rivers other than the Cuanza, and in areas north of the Bengo to the mouth of the Congo records from Angola are practically non-existent. Devaere et al. (2007) record *Channallabes apus* as being described from this region. Fowler (1930) noted species of the Cuanza and the Bengo rivers received from the British Museum on exchange, in many instances as described by Boulenger (1910) or as recorded in Boulenger

(1909–1916). Trewavas (1936) recorded and described seven species from a headwater stream of the Cuvo River arising on Mount Moco including the only *Amphilius* species (*Amphilius lentiginosus*) described from the region. A second undescribed *Amphilius* species has been recorded in the Cuanza (South African Institute for Aquatic Biodiversity – SAIAB – collection). Both these species differ in key morphological characteristics from the *Amphilius* of the Zambezian region that indicate their faunal connections lie primarily with the Lower Guinean or Congolean regions. Trewavas (1936) also described species from the Longa (*Enteromius breviceps*), the Catumbela (*Enteromius dorsolineatus, E evansi*), and the Balombo (*Enteromius dorsolineatus*). Pellegrin (1936) described the fishes collected by two Swiss expeditions (1928–1929 and 1932) made under the direction of Monard from the *Musée d'Histoire Naturelle de la Chaux-de-Fonds* included two species, *Enteromius kessleri, Clarias dumerilii*, that were drawn from the Cueve, with the bulk of the collections coming from the Cunene, the Cuvelai and the Cubango. Ladiges and Voelker (1961) described *Kneria maydelli* from the Cunene, and *Enteromius rousellei* and *Chiloglanis sardinhai* from the Longa. Poll (1967) described *Kneria sjolandersi* and *Chiloglanis angolensis* from the Bero, to the north of the Cunene. Trewavas (1973) recorded *Oreochromis angolensis* and *Tilapia cabrae* from the Bengo. Bills et al. (2012) made a small collection from the upper reaches of the Cueve River that included species of the following genera – *Petrocephalus, Enteromius, Labeobarbus, Micralestes, Amphilius, Chiloglanis, Clarias, Pharyngochromis, Thoracochromis, Tilapia, Coptodon,* and *Mastacembelus*. The list is typically 'Zambezian' and the species positively identified are closely linked to the upper Cuanzan and Cubango fauna. The indication from these references is therefore that the Angolan Coastal fauna is a mix of Lower Guinean (along the coastal plain) and Zambezian (above the escarpment) with some Congolean elements in the upper Cuanza/Lucala (see below).

The 'Cuanzan or Angolan Coastal ' ichthyofaunal region is drawn primarily on what is known of the fishes of the Cuanza River as described by Boulenger (1910) and in Boulenger's (1909–1916) catalogue of fishes in the British Museum (Natural History) now the Natural History Museum (NHM). Fowler's (1930) account of the fishes of the Gray African Expedition in 1929 included records from the Bengo and the lower Cuanza, but also a collection of species from Chouzo on the upper reaches of the Cutato-Cuanza tributary, that provided a first strong indication that the fauna of these reaches is 'Zambezian' in character and different to those from the coastal reaches as reported by Boulenger (1910) and others. This association was later reiterated by Trewavas (1973) when considering the cichlid species of the Cuanza and Bengo rivers and has been firmly supported by the extensive surveys conducted by SAIAB and INIP (*Instituto Nacional de Investigação Pesqueira*) between 2005 and 2010. The current assessment records at least 102 species, some of which are undescribed (Appendix 3). The collections indicate that the river basin is even more heterogenous in fish faunal characteristics than simply 'lower' and 'upper' and the different zones distinguishable include (1) the lower reaches from the escarpment base to the sea, (2) the escarpment reaches, (3) the upper Cuanza and (4) the Lucala

tributary, itself probably sub-zoned into the middle and upper reaches separated by the Calandula Falls (formerly 'Duque de Bragança' Falls).

Two ecophysiological components derive the fishes of the lower Cuanza: a diverse Tropical West African or Lower Guinean brackish water or marine component, and secondly the primary and secondary freshwater fishes. The known Tropical West African brackish water fishes from the system are generally widespread species and do not include endemics. Some species such as the Bull Shark (*Carcharhinus leucas*) and the Atlantic Tarpon (*Megalops atlanticus*) are well known as gamefish from this river. Two clupeid species include the recognised freshwater species (*Pellonula vorax* and *Odaxothrissa ansorgii*) and probably other brackish water forms. One haemulid (*Pomadasys* sp.) and one polynemid threadfin, possibly *Polydactylus quadrifilis* as known from Central West Africa (Snoeks and Vreven 2007), have been recorded (SAIAB records). Mullets (Mugilidae), as yet unidentified at species level, are present as are the sleepers (Eleotridae) and gobies (*Awaous* and *Periopthalmus*). Two pipefish have been positively identified: *Enneacampus ansorgii* and *Microphis brachyurus aculeatus*. The tonguefish *Cynoglossus senegalensis* was collected in the downstream reaches.

The freshwater species of this lower zone are mostly widespread species that also occur in coastal reaches of rivers to the north, well into the adjacent Lower Guinean Province and beyond, and many probably also to the south. An example of this is *Parailia occidentalis* that has a range through to the Senegal River in West Africa (de Vos 1995). The species that occur are found generally throughout the region to the escarpment, with a few ascending into middle Cuanza sections. Other characteristic species in this zone include mormyrids of the genera *Hippopotamyrus, Marcusenius* and *Petrocephalus*, the alestid *Alestes ansorgii*, cyprinids of the genus *Labeo,* two *Enteromius* species (*E. holotaenia* and *E. musumbi*), and several distinctive claroteid catfishes (two *Chrysichthys* species *C. acutirostris* and *C. ansorgii)*, as well as *Schilbe bocagii*, and the widespread *Clarias gariepinus*. The *Chrysichthys* species confirm the West Africa coastal affinities of the assemblage as the genus is not known from the upper reaches nor from the upper Zambezian floodplain fauna. The cichlid fauna, as detailed systematically by Trewavas (1973) is in part also restricted to the zone – *Oreochomis angolensis, Hemichromis angolensis* and *Tilapia* cf. *cabrae.* The range of the procatopodid lampeye *Aplocheilichthys spilauchen* previously known from the Senegal River to the Bengo River has been extended to the Cuanza. The absence of the anabantid genus *Ctenopoma* from this zone is remarkable.

The Escarpment Zone of the Cuanza is characterised by a stepwise series of rapids, cascades and falls interspersed by rocky pools and runs. The fish fauna of this important zone for hydropower development is rich but relatively poorly known or described. The SAIAB-INIP collections are extensive and indicate that few species from the coastal zone penetrate high up into the zone. This is most probably partly an artefact of the Cambambe Dam near the base, in existence for several decades, which has likely affected the natural penetration of many species. The major freshwater families are represented; the smaller cyprinids, various catfish families, and cichlids are particularly well represented. The generic composition

includes: *Hippopotamyrus, Petrocephalus, Marcusenius, Parakneria, Enteromius, Labeobarbus, Labeo, Raiamas, Brycinus, Rhabdalestes, Hepsetus, Schilbe, Chrysichthys, Clarias, Clariallabes, Parauchenoglanis, Chiloglanis, Synodontis, Micropanchax, Hemichromis, Pharyngochromis, Pseudocrenilabrus, Serranochromis, Tilapia, Oreochromis*, and *Mastacembelus*. Only a single *Labeobarbus* species was recorded in this zone during the survey and it also occurs in the Lucala tributary. Boulenger (1910) recorded two *Labeobarbus* species from the Cuanza at Dondo – *L. rocadasi* and *L gulielmi*. A unique morphotype of *Labeobarbus* with an extremely pointed tiny mouth, collected during the Capanda pre-impoundment surveys is present in the Luanda Museum (pers. obs., Fig. 11.2) and is likely to be an undescribed species.

The Upper Cuanza extends from a waterfall on the mainstream above the Capanda dam to the watershed and consists largely of relatively low-gradient floodplain rivers on Kalahari sand formations, similar to that of the upper reaches of the Zambezi and Okavango systems in Angola. Characteristic genera from this zone are: *Hippopotamyrus, Petrocephalus, Marcusenius, Parakneria, Enteromius, Labeobarbus, Labeo, Brycinus, Rhabdalestes, Hepsetus, Schilbe, Chrysichthys, Doumea, Clarias, Clariallabes, Parauchenoglanis, Chiloglanis, Synodontis, Micropanchax, Hemichromis, Pharyngochromis, Pseudocrenilabrus, Serranochromis, Tilapia, Oreochromis,* and *Mastacembelus*. Fishes from Chouzo in the upper Cuanza described by Fowler (1930), include species such as *Marcusenius angolensis, Hepsetus cuvieri, Labeo rocadasi, Enteromius evansi* (type locality), *Enteromius lujae* (identity of this species is still debated but the same species occurs in the Okavango headwaters), *Clarias gariepinus, Clarias theodorae* (as *C. fouloni*), *Clarias ngamensis* (as *Dinotopterus prentissgrayi*), *Ctenopoma machadoi* (type locality), *Serranochromis macrocephalus* (as *Tilapia acuticeps*, see Trewavas 1973). Norman (1923) described *Synodontis laessoei*, synonymised with *Synodontis nigromaculatus* by Poll (1971), as the only species of this genus in the Cuanza, a contrast to the specious lineage in the Okavango-Zambezi region (Day et al. 2009, Pinton et al. 2013). Few species characteristic of the upper Cuanza are found beyond the zone within the basin. This agrees with the notion that the fauna in this zone is historically and biogeographically an integral part of the 'Zambezian' fauna

Fig. 11.2 An extraordinary undescribed *Labeobarbus* species from the Cuanza River in the Luanda Museum, 2005. (Photo PH Skelton)

(Trewavas 1973). Ladiges (1964) and Poll (1967) showed this to be general for the fauna as a whole, and specific studies on species like *Hepsetus cuvieri* (Zengeya et al. 2011) and cichlids like *Serranochromis* and *Tilapia sparrmanii* (Musilová et al. 2013) confirm this relationship. Recent surveys across the watershed between the Cuanza and the Okavango indicate that a number of other species like *Parakneria fortuita*, and several *Enteromius* species like *E mocoensis, E evansi, E breviceps, E brevidorsalis* occur in streams on either side and have helped to define the Upper Zambezi headwaters ecoregion that embraces this trans-system conformance.

An early indication that the Lucala River, a major tributary that joins the system in the lower reaches, is exceptional for its fishes was the fauna collected by Ansorge using a wide range of methods including explosives (Boulenger 1910). It is however only in the escarpment and upper reaches that such exception occurs. An assemblage of large fishes of the genus *Labeobarbus* in particular is outstanding, and Boulenger (1910) described 12 species now in *Labeobarbus* (Vreven et al. 2016), all of which remain valid at this time. In addition to these species, unpublished barcode studies conducted by SAIAB on the fauna indicates that several lineages in the system are restricted to the Lucala, including an *Alestes, Pharyngochromis, Serranochromis, Tilapia,* two *Enteromius species*, a *Parakneria, Hippopotamyrus*, and a undescribed *Congoglanis*.

The significance of the use of explosives in assembling Ansorge's collection described by Boulenger (1910) is that it included a number of large mainstream species that otherwise are extremely difficult to collect. The assemblage of large *Labeobarbus* described in the paper has defined the Cuanza Basin since that time. The overall faunal characteristics of the Lucala include species of the following genera: *Hippopotamyrus, Petrocephalus, Kneria, Alestes, Enteromius, Labeobarbus, Labeo, Raiamas, Amphilius, Congoglanis, Schilbe, Clarias, Chiloglanis, Synodontis, Micropanchax, Pharyngochromis, Serranochromis, Tilapia,* and *Mastacembelus*. The fauna of the upper reaches is poorly known. Only a single collection made by SAIAB was drawn from the Lucala above the Calandula Falls. This limited sample is not sufficient to gauge the full character of the zone, but does indicate a degree of continuity with the Middle Lucala zone, and differing through the absence of major elements like the *Labeobarbus* species so characteristic of the latter. The physical character of the upper reaches suggests there is a zonal distinction in the ecological character and thus the faunal elements. The known fauna includes species of the following genera: *Hippopotamyrus, Petrocephalus, Parakneria, 'Barbus', Enteromius, Amphilius, Congoglanis, Clarias, Micropanchax, Pharyngochromis, Serranochromis.* Little else can be stated at this point except that an investigation into the fauna is highly desirable given the unique nature of the Middle Lucala.

The Lucala catchment shares its watershed with tributaries of the Congo-Cuango River and is likely one of the underlying reasons for its unique character. A high degree of endemicity to this catchment is therefore evident and with further taxonomic investigation likely to be upheld and enhanced.

Cunene

Poll (1967), from the ichthyological perspective, treated the Cunene River system as a separate entity to the Atlantic coastal region, whereas it has been regarded as part of the Zambezian Province by Roberts (1975), part of the 'Angola' ichthyofaunal province by Lévêque and Paugy (2017a, b), and divided as part of the Namib aquatic ecoregion and part upper Zambezian headwaters ecoregions by Thieme et al. (2005). The reason for these varied treatments is that the river system is geo-eco-historically complex. Thus it has a dual geomorphological origin (the upper reaches being a natural part of the Kalahari Basin that has been captured by an Atlantic coastal river) and environmentally the lower reaches sit within the 'xeric' Namib region and the inland upper reaches within the savanna dry forest environs.

The fishes of the Cunene River are relatively well documented, starting with *Schilbe steindachneri* (a synonym of *S. intermedius)* and *Mormyrus anchietae* (a synonym of *M. lacerda*) described by Guimarães (1884), and summarised in the most recent checklist by Hay et al. (1997). Excluding the more strictly marine families there are 82 species recorded from the Cunene (Appendix 3). Hay et al. (1997) also record the broad distribution of species within the system according to three sections, the upper reaches down to Ruacana Falls, a middle section down to Epupa Falls and the lower river from below Epupa Falls to the mouth. Of 65 species recorded above Ruacana Falls 13 are restricted to that section. At least one species, *Marcusenius deserti*, is restricted to the lower reaches close to the coast (Kramer et al. 2016). Apart from the several marine species recorded in the extreme lower reaches by Penrith (1970) and Hay et al. (1997) that reflect a southernmost extension of the tropical (Lower Guinean) fauna, the general composition is clearly Zambezian in character. There are few representatives indicative of the Angolan (Cuanzan) Province, e.g. *Enteromius mattozi* (described by Guimarães (1884) from the Curoca River to the north of the Cunene). Pellegrin's (1921) *Enteromius* (formerly *Barbus) rohani*, probably a synonym of *E. mattozi,* was likely taken from the Caculovar River, a tributary of the Cunene, and not from the Lomba (neither the Zambezi as Pellegrin claimed, nor the Longa coastal Atlantic as suggested by Poll 1967). *Enteromius argenteus* is another minnow that has been reported from the Cunene but whose identity is unconfirmed – and is likely to be juveniles of *E. mattozi* (Skelton Unpublished Data).

There are also several isolated endemics from the system such as *Marcusenius deserti, Marcusenius magnoculis, Marcusenius multisquamatus, Hippopotamyrus longilateralis, Engraulicypris howesi, Zaireichthys cuneneensis, Orthochromis machadoi, Thoracochromis albolabrus, Thoracochromis buysi*, that suggests a degree of isolation probably reflecting older biogeographic connections. The absence of certain conspicuous families or genera such as *Parakneria, Labeobarbus, Opsaridium, Hydrocynus, Parauchenoglanis, Amphilius, Hemichromis,* and *Mastacembelus* is also noteworthy and perhaps indicative of a lack of more recent connections with the Zambezian and Cuanza systems.

Cassai and Southern Congo Rivers

Collections from the Lulua River, a tributary of the Cassai in Congo by Fowler (1930) whilst not strictly in Angola, probably pertain to Angola as well. Thus although not the only source, Poll (1967) is the current practical published source for the fishes of the southern Congo river tributaries in Angola. There are three main tributaries draining the region, from the east the Cassai including the Luangwe, the Cuilu (or Kwilu) and the Cuango. Poll (1967: 18–23) plotted the records of the fishes of each of these in his distribution table, recording 108, 28 and 37 species respectively and in the addendum supplemented the Cassai with three species and the Cuango with 24 species. The figure for the southern catchments of the Congo in Angola is now estimated at around 162 species (Appendix 3). The Cuilo and Cuango faunas are most evidently far from well explored. The Cassai fish fauna is better represented but still poorly explored, and includes species both typical of the Congo (e.g. *Polypterus ornatipinnis, Channallabes apus,* several mormyrid species*, Bryconaethiops microstoma, Alestes grandisquamis, Distichodus fasciolatus, Distichodus lusosso, Mastacembelus congicus*), and many species found also in the Upper Zambezi or the Okavango (e.g. *Hydrocynus vittatus, Hepsetus cuvieri, Pollimyrus castelnaui, Enteromius brevidorsalis, Parauchenoglanis ngamensis, Clarias stappersii, Clarias theodorae, Schilbe yangambianus, Micropanchax katangae, Oreochromis andersonii, Coptodon rendalli, Tilapia sparrmanii, Tilapia ruweti, Hemichromis elongatus, Serranochromis microcephalus, Serranochromis robustus jallae, Pseudocrenilabrus philander, Ctenopoma multispine, Microctenopoma intermedium*). The presence of *Dundocharax bidentatus* in the Cassai and the rare Zambezian endemic not yet found in Angola, *Neolebias lozii* are further good indicators of geographical connection. The strong Cassai-Zambezian faunal association is attributed to the clear evidence of hydrological pattern that the upper Cassai was formerly part of the Upper Zambezi system (Bell-Cross 1965).

Zambezian-Cuando-Cubango Headwaters and Floodplains

There is sufficient direct connection between the Zambezi, the Cuando and the Okavango river basins and similarity of the fish faunas in each to consider these under a single heading.

The Zambezi headwaters in Angola drain the Kalahari sand formation over an extensive divide with the Cassai to form major floodplains known as the Bulozi Floodplains. There are a number of lakes associated with the drainage including the largest freshwater lake in Angola, Lake Dilolo. The Okavango drainage is divided into two branches, the Cuito-Cuanavale in the east and the Cubango in the west. The Cuito-Cuanavale drains Kalahari sand formations giving rise to extensive low-gradient seepage bog and floodplain rivers in slump valleys extending into miombo savanna woodlands in the upper reaches. There are several lakes in these headwaters.

The Cubango branch arises as several relatively steep gradient rocky rivers in the Angolan highlands on the Bié plateaux before descending to the low-gradient reaches along the Namibian border to join with the Cuito before crossing to Botswana and forming the mostly endorheic Okavango Delta. The watershed of the system is shared with the Cuando, the Zambezi (mainly the Lungwe-Bungo), the Cueve-Cuanza, and the Cuanza as well as the Cunene and Cuvelai oshanas in the west.

The fishes of the Upper Zambezi are well studied and documented (e.g. Jackson 1961, Jubb 1961, 1967, Balon 1974, Bell-Cross and Minshull 1988, Tweddle 2010) with numbers now estimated at around 100–120 species (Appendix 3; Tweddle et al. 2004), possibly with as many as 20–25 undescribed. However published records from the Angolan territory are sparse, and limited in the published literature to Poll's (1967) 41 species (against his checklist of 62) taken mostly from two localities close to the watershed (Lagoa Calundo and the Longa-Luena tributary). Recent collections from the source reaches of Zambezian tributaries in Angola made by the National Geographic Okavango Wilderness Project (NGOWP 2018) are still being assessed but include 39 species from 12 families that have been included in the checklist of fishes from this region (Appendix 3). One notable new record is *Enteromius chiumbeensis* described by Poll (1967) from the Chiumbe River a tributary of the Cassai, reinforcing the close connections between these adjacent trans-watershed systems.

The upper Zambezian fish fauna is distinctive in several respects, most notably for the relatively speciose endemic *Synodontis* catfishes and the serranochromine cichlids (Trewavas 1964, Bell-Cross 1975, Greenwood 1993, Day et al. 2009; Pinton et al. 2013). To a large extent, in Angola, the fauna is ecologically tuned to the extensive seepage and floodplain drainages within a band of miombo savanna woodland on Kalahari sand deposits. Overall the known Angolan Upper Zambezi fish fauna is similar to that of the better-studied (in Angola) Okavango Basin fishes (often with the same or closely related species e.g., mormyrids of the genera *Hippopotamyrus, Marcusenius, Petrocephalus, Pollimyrus* – Kramer et al. 2003, 2004, 2012, 2014, and *Zaireichthys* species – Eccles et al. 2011). Whilst there are a few endemics, only one, *Paramormyrops jacksoni* Poll 1967 is restricted to Angola. The isolated *Neolebias lozii* is known only from the Barotse floodplains in Zambia.

Fishes of the Cuando-Linyanti-Chobe system have not been reported on from the Angolan section of that Zambezi tributary but van der Waal and Skelton (1984) provided a checklist of fishes in the Cuando River in Namibian waters. The 56 species recorded were all also found in the Zambezi system in Namibia. The Pallid Sand Catlet, *Zaireichthys pallidus* Eccles et al. (2011) is described from the Cuando but is not restricted to that system. Kramer et al. (2014) described a new species of *Pollimyrus* from the Cuando, a species possibly endemic to that tributary. Recent collections by the National Geographic Okavango Wilderness Project (NGOWP/SAIAB) from the upper reaches of the Cuando in Angola further inform the list of species (Appendix 3).

The fishes of the Okavango Basin have been studied and reported on in the literature for over 150 years since Castelnau (1861) described 14 species from Lake

Ngami, including the iconic Tigerfish (*Hydrocynus vittatus*) the Southern African Pike (*Hepsetus cuvieri*), the large Blunttooth Catfish (*Clarius ngamensis*) and the Three Spot Bream (*Oreochromis andersonii*). Fifty years later Boulenger (1911) reported on a collection from the Okavango-Lake Ngami made by RB Woosnam and described six new species including one named for Castelnau – *Pollimyrus castelnaui*. These fishes were all included in Gilchrist and Thompson (1913, 1917) and Boulenger (1909–1916). Fowler (1935) described a collection made from the Delta by the Vernay-Lang Expedition of 1930. Pellegrin (1936) described fishes collected by two Swiss expeditions of 1929 and 1933 from the Cunene, the Cuvelai and the Cubango. Barnard (1948) described in detail a collection from Rundu, Namibia. The results of all these efforts were summarised in checklists published by Poll (1967), Jubb (1967), Jubb and Gaigher (1971) and Skelton et al. (1985). More recently surveys of Angolan Okavango Basin rivers have been made (Bills et al. 2012, 2013, Skelton et al. 2016) that have reached little-explored areas, encountered additional species and provide for a more complete assessment of the fishes and their intra-basin distributions.

The additional species recently discovered include new species of *Clariallabes,* several serranochromine cichlids, and a dwarf climbing perch (*Microctenopoma* sp). Recent distribution records extend the range of several species from the Congo tributaries or in the case of *Clypeobarbus bellcrossi* from Zambezi headwaters in Zambia to the Okavango. Congolean species such as *Marcusenius moorii* (Günther) and *Enteromius chicapaensis* (Poll), and *Nannocharax lineostriatus* (Poll), and several *Micropanchax* as *M. luluae, M. nigrolateralis, M. lineolateralis*. The known range of a number of species from the Atlantic Coastal and Cuanza systems has been extended to the Okavango, e.g. *Enteromius breviceps, E. brevidorsalis, E. evansi, E. mocoensis, E. greenwoodi*. A new understanding of the complex distribution of the twin species *Enteromius trimaculatus* and *E. poechii* has also been reached – the former being found in the Cunene and the extreme upper reaches of the Cubango in place of the latter which is widespread in the downstream floodplain reaches of the Okavango and Upper Zambezi system.

Cuvelai

The Cuvelai drainage lies in a triangle between the Okavango in the east and the Cunene in the west and the streams known as ‘iishanas’ are intermittent, only flowing during periods of sustained rainfall into the endorheic Etosha Pan in Namibia (van der Waal 1991, Hipondoka et al. 2018). The 1929 and 1932–1933 Swiss expeditions to Angola collected the following species from Mupa (Pellegrin 1936): *Marcusenius altidorsalis* (?)*, Mormyrus lacerda, Enteromius paludinosus, Tilapia sparrmanii*, and *Pseudocrenilabrus philander*. Seventeen species, all conforming to Cunene fauna, have been confirmed from the western iishanas of the system by Hipondoka et al. (2018), and connections with the Cunene substantiated through remote sensing techniques. Four widespread pioneering species are consistently

present in collections, viz., *Clarias gariepinus, Enteromius paludinosus, Oreochromis andersonii* and *Pseudocrenilabrus philander* and several others are common – *Clarias ngamensis, Schilbe intermedius* and *Enteromius trimaculatus*.

Biogeography

The biogeography of Angolan freshwater fishes is closely tied to the geomorphology and the geomorphological history of the territory. In brief, Angola consists of a narrow coastal plain, a distinct escarpment and an interior plateau that is being eroded most rapidly from the Congo Basin. The coastal plain consists of a series of rivers flowing from the escarpment or – in the case of the Congo in the north, the Cuanza in the middle and the Cunene in the south – where the escarpment has been penetrated, from the interior plateau or the Congo Basin. The fish fauna of the coastal plain is primarily a southern extension of the tropical coastal fauna of West Africa and Central West Africa. River connections along this narrow strip are either via sea-level fluctuations or via river captures between watersheds, either as adjacent systems or via extended reaches through captured inland drainages that are not determined by the coastal gradients and processes. According to Lévêque and Paugy (2017a,b) the primary direction of dispersal of the coastal west African fauna was northwards from the Congo. Present day ocean currents off Angola are counter clockwise (http://oceancurrents.rsmas.miami.edu) and it is possibly only inshore counter currents that might have facilitated faunal dispersal southwards from the Congo, especially after the capture and penetration of the Congo Basin by the Lower Congo in the late Cretaceous (Flügel et al. 2015). Such would certainly explain much of the marine derived elements of the region. Given favourable currents it is likely also that the considerable volumes of freshwater entering the sea from the Congo at various times would facilitate even freshwater fishes down the coast and might explain the presence of such species as *Enteromius musumbi, Physailia occidentalis, Chysichthys spp, Oreochromis angolensis* and *Aplocheilichthys spilauchen* in the Angolan region. An alternative and complementary explanation for some freshwater faunal elements such as *Marcusenius deserti* and *Raiamas ansorgii* of the Angolan Coastal reaches is that it is primarily derived via the Cuanzan and Cunene gateways through capture of portions of the Kalahari Basin drainage. It is not only the Cuanza and the Cunene that have breached the escarpment but also the Cuvo and the Longa and possibly others, as is evident in the list of freshwater fishes reported from these lesser rivers (see above).

The evolution of the extensive Kalahari Basin is certainly key to understanding the majority of the freshwater fish fauna of Angola. Haddon and McCarthy (2005), Key et al. (2015), Moore and Larkin (2001), and Moore et al. (2012) sketch the evolution of the Kalahari Basin and its drainage since the breakup of Gondwanaland and the isolation of Africa in the late Cretaceous. Following rifting, the continental margins were probably elevated and this formed an escarpment that separated the narrow coastal plain from the elevated Kalahari sedimentary basin that was drained

primarily by the palaeo-upper Zambezi, the predominant system in the Angolan region (Fig. 11.3). The western portion of the system flowed from the escarpment highlands of the extreme northwest of the basin, now part of the Cuanza, generally southeast through the Limpopo valley to the Indian Ocean. The eastern parts of the upper Zambezi reached northeastwards to as far as pre-rift East African plateaus and

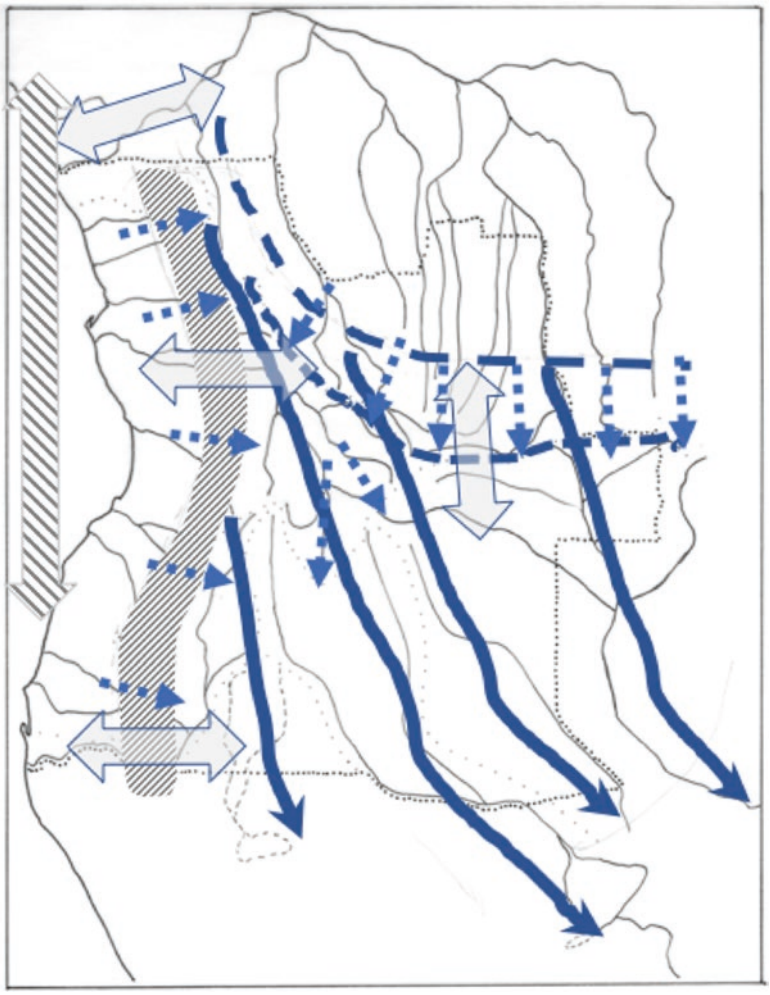

Fig. 11.3 A diagrammatic model for the post-Cretaceous biogeography of Angolan freshwater fishes. Angolan border – fine dotted line; present day drainage – thin lines; present day inter basin watersheds – open dotted lines; paleo drainage lines – thick extended arrows; paleo and present escarpment retreat – dashed arrows; paleo and present south and southwestern Congo Basin watershed – thick dashed lines; Angolan escarpment – right slanted hash; gateway drainage captures – large open bi-directional arrows. Coastal dispersal of fishes – large left-slanted bi-directions arrow. The model is based on geomorphological interpretations by Flügel et al. (2015), Haddon and McCarthy (2005), Moore and Larkin (2001), Moore et al. (2012), and others

included the proto-Luangwa and the proto-Chambeshi-Kafue-upper Zambezi as well as the Okavango. These drained into an interior basin to form, at times, a mega palaeo lake – Palaeolake Magadigadi (Burroughs et al. 2009, Moore and Larkin 2001, Moore et al. 2012, Podgorski et al. 2013). The proto-Cunene consisted of an upper portion draining endorheically to the Etosha basin. The most significant events in the history of the Kalahari Basin were firstly the downwarping and back-tilting of drainage coupled with upwarping along the southern margins that severed the initial Indian Ocean outlet via the Limpopo; the tapping of the Congo Basin by the lower Congo River that advanced the erosion and southern retreat of the northern watershed of the basin, especially in the northeast (Luapula-Chambeshi) and, in the Angola area, the Cassai-Zambezi. The dismemberment and tapping of drainage portions from the Kalahari Basin to coastal outlets including the Cuanza, the Cunene, and the Zambezi also affects the biogeographical history significantly (Moore and Larkin 2001, Moore et al. 2012, Key et al. 2015).

The most profound biogeographic significance to emerge from this geomorphological narrative is that the Kalahari Basin has been an evolutionary basin for fishes over a long period of time. The evidence is exemplified in the serranochromine cichlid radiation and the clade of *Synodontis* catfish and the radiation of several mormyrid genera that characterise the Zambezian fauna (Bell-Cross 1975, Greenwood 1984, Kramer et al. 2003, 2004, Day et al. 2009, Kramer and Swartz 2010, Kramer et al. 2012, Schwarzer et al. 2012, Pinton et al. 2013, Kramer and Wink 2013). The strong identity of the upper Zambezian fauna further exemplifies this notion. That the fauna has been supplemented with species from neighbouring ichthyological provinces, especially the Congo, is also evident in species or genera with internally restricted distributions such as *Hepsetus cuvieri, Hydrocynus vittatus, Parauchenoglanis ngamensis, Mastacembelus, Hemichromis elongatus*, *Amphilius* and others. The broader distributions of some species into basins like the east coast rivers (e.g. *Enteromius bifrenatus, Microctenopoma intermedium, Clarias theodorae, Brycinus lateralis*) gives biological credence to the former east coast linkage and subsequent drainage dismemberment on the proto-upper Zambezi (Skelton 1994, 2001).

There are other emerging details of biogeographical interest to Angola that will in time lead to a detailed accounting of the origins and development of the freshwater fishes. Thus the presence of doumeine catfishes in the Cuanza, southwest of the Congo, indicates clearly insemination from the Congo. The flock of *Labeobarbus* species in the Lucala-Cuanza probably also indicates a Congolian insemination. However the assumption that all traffic was from the Congo is not necessarily correct and *Neolebias bidentatus* in the Cassai, for example, as with other ‘Zambezian’ elements in that system, more likely reflects a Zambezian (i.e. Kalahari) insemination to the Congo. This, in essence, is the basis of the ‘Upper Zambezi headwater’ freshwater ecoregion (Fig. 11.1: basin C).

Conservation

Angola is an emerging African economy with a rapidly growing human population and increasing demand on freshwater resources. The rapid population growth and expansion of urban areas in places such as Luanda but also in the more rural districts (Mendelsohn and Weber 2015) is placing an ever increasing stress on the environment, especially that of the rivers for which such urban growth centres are dependent on for water and power. Although many Angolan rivers are relatively unregulated there are dams on several systems such as the three major hydroelectric dams on the Cuanza. A further four hydroelectric dams are planned for the escarpment section of this system alone. In the case of certain transboundary rivers like the Okavango, the threat of increased river regulation is of serious concern to the integrity of the Okavango Delta in Botswana, a World Heritage and Ramsar site (King and Chonguic 2016).

Diamond mining activities along the southern Congo tributaries have had environmental impacts of unknown severity as practically no public investigations or information is available.

With human populations, urbanisation and development comes pollution and other direct threats to aquatic life such as fishing and the introduction of invasive alien species. Few alien fishes have been recorded from Angola, but two species that have been introduced are *Oreochromis mossambicus* (SAIAB, in the Cuanza) and *Oreochromis niloticus* in Cabinda and, as recently confirmed, in the upper Cubango. The threats these particular species pose as aliens is well documented (e.g. Wise et al. 2007, Zengeya et al. 2013, Bbole et al. 2014). This is the first record of an alien species with high impact potential in the Okavango system and the threat posed is transboundary in nature. Potential transboundary threats from outside Angola include that of alien crayfish from the Zambezi (Nunes et al. 2016).

Indigenous fishery practices in Angola include a range of gear ranging from simple traps to elaborate fishing fences and walls (Poll 1967, Mendelsohn and Weber 2015). In places such traditional practices are still in evidence (Fig. 11.4 *top*), but elsewhere traditional practices are being replaced by modern gear such as monofilament gillnets and mosquito-net seines (Fig. 11.4 *bottom*) that are excessively destructive and unsustainable (Tweddle et al. 2015).

The current IUCN redlist assessments for Angolan freshwater fishes (Appendix 3) reflects the relatively weak knowledge of the species – a third of the known species are either not assessed or are Data Deficient (DD). One species (*Oreochromis lepidurus*) is listed as Endangered (see Moelants 2010), three are Vulnerable (1%) and 185 (65%) are Least Concern. The endangered species is a Lower Congo endemic found mainly in the DRC and is primarily threatened by oil pollution derived from boats. The Vulnerable species are also cichlids of the genus *Oreochromis* – *O. andersonii* (see Marshall and Tweddle 2007) and *O. macrochir* (see Marshall and Tweddle 2007), both are threatened through hybridisation from the alien invasive species *Oreochromis niloticus*. The latter species has recently been confirmed as present in Angola, within the Okavango catchment and its impact

Fig. 11.4 *Top* – traditional fishing fence on the Cacuchi River, 2012 (Photo PH Skelton). *Bottom* – Drying fish caught with monofilament gillnets on the Cuito River, 2015. (Photo G Neef)

on the native *Oreochromis* is now an imminent threat. Given the situation of rapidly escalating changes to the natural aquatic environment in Angola it is likely that the IUCN redlist score for the country will rise rapidly.

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Appendices

Appendix 1

Freshwater and brackish water fishes of Shiloango River, Cabinda, as recorded by Stiassny et al. (2007)

Species	Author & Date
Clupeidae	
Pellonula vorax	Günther, 1868
Mormyridae	
Isichthys henryi	Gill, 1863
Marcusenius moorii	Günther, 1863
Paramormyrops kingsleyae	(Günther, 1863)
Brienomyrus brachyistius	(Gill, 1862)
Hepsetidae	
Hepsetus lineatus	(Pellegrin, 1926)
Alestidae	
Brycinus longipinnis	(Günther, 1864)
Brycinus macrolepidotus	Valenciennes, 1850
Brycinus kingsleyae	(Günther, 1896)
Nannopetersius ansorgii	(Boulenger, 1910)
Distichodontidae	
Distichodus notospilus	Günther, 1867
Eugnathichthys macroterolepis	Boulenger, 1899
Nannaethiops unitaeniatus	Günther, 1872
Nannocharax parvus	Pellegrin, 1906
Neolebias ansorgii	Boulenger, 1912
Neolebias spilotaenia	Boulenger, 1912

(continued)

Species	Author & Date
Cyprinidae	
Enteromius carens	(Boulenger, 1912)
Enteromius jae	(Boulenger, 1903)
Enteromius guirali	(Thominot, 1886)
Enteromius callipterus	(Boulenger, 1907)
Enteromius camptacanthus	(Bleeker, 1863)
Enteromius rubrostigma	(Poll & Lambert, 1964)
Enteromius holotaenia	(Boulenger, 1904)
Labeobarbus aspius	(Boulenger, 1912)
Labeobarbus cardozoi	(Boulenger, 1912)
Labeobarbus roylii	(Boulenger, 1912)
Labeobarbus batesii	(Boulenger, 1903)
Labeobarbus sandersi	(Boulenger, 1912)
Labeo batesii	Boulenger, 1911
Labeo lukulae	Boulenger, 1902
Opsaridium ubangiense	(Pellegrin, 1901)
Ariidae	
Arius latiscutatus	Günther, 1864
Claroteidae	
Anaspidoglanis macrostoma	(Pellegrin, 1909)
Parauchenoglanis altipinnis	(Boulenger, 1911)
Chrysichthys auratus	(Geoffroy Saint-Hilaire, 1809)
Chrysichthys nigrodigittatus	(Lacépède, 1803)
Schilbeidae	
Parailia occidentalis	(Pellegrin, 1901)
Pareutropius debauwi	(Boulenger, 1900)
Clariidae	
Clarias angolensis	Steindachner, 1866
Clarias gabonensis	Günther, 1867
Malapteruridae	
Malapterurus beninensis	Murray, 1855
Procatopodidae	
Aplocheilichthys spilauchen	(Duméril, 1861)
Plataplochilus loemensis	(Pellegrin, 1924)
Nothobranchiidae	
Epiplatys singa	(Boulenger, 1899)
Aphyosemion escherischi	(Ahl, 1924)
Anabantidae	
Ctenopoma nigropannosum	Reichenow, 1875
Microctenopoma ansorgii	(Boulenger, 1912)
Microctenopoma nanum	(Günther, 1896)
Microctenopoma congicum	(Boulenger, 1887)

(continued)

Species	Author & Date
Cichlidae	
Pelvicachromis subocellatus	(Günther, 1872)
Chilochromis duponti	Boulenger, 1902
Coptodon tholloni	(Sauvage, 1884)
Pelmatolapia cabrae	(Boulenger, 1899)
Coptodon guineensis	(Günther, 1862)
Oreochromis schwebischi	(Sauvage, 1884)
Sarotherodon nigripinnis	(Guichenot, 1861)
Lutjanidae	
Lutjanus dentatus	(Duméril, 1861)
Monodactylidae	
Monodactylus sebae	(Cuvier, 1829)
Polynemidae	
Polydactylus quadrifilis	(Cuvier, 1829)
Mugilidae	
Mugil bananensis	(Pellegrin, 1927)
Neochelon falcipinnis	(Valenciennes, 1836)
Chelon dumerili	(Steindachner, 1870)
Eleotridae	
Eleotris daganensis	Steindachner, 1870
Eleotris senegalensis	Steindachner, 1870
Eleotris vittata	Duméril, 1861
Bostrychus africanus	(Steindachner, 1879)
Dormitator lebretonis	(Steindachner, 1870)
Gobiidae	
Periopthalmus barbarus	(Linnaeus, 1766)
Gobionellus occidentalis	(Boulenger, 1909)
Bathygobius soporator	(Valenciennes, 1837)
Bathygobius casamancus	(Rochebrune, 1880)
Nematogobius maindroni	(Sauvage, 1880)
Microdesmidae	
Microdesmus aethiopicus	(Chabanaud, 1927)
Mastacembelidae	
Mastacembelus shiloangoensis	(Vreven, 2004)
Mastacembelus niger	Sauvage, 1879
Syngnathidae	
Enneacampus ansorgii	(Boulenger, 1910)
Microphis aculeatus	(Kaup, 1856)
Cynoglossidae	
Cynoglossus senegalensis	(Kaup, 1858)
Citharichthys stampflii	(Steindachner, 1894)

Appendix 2

Freshwater fishes of the Inkisi River DRC, from above the Sangha waterfalls, after Wamuini Lunkayilakio et al. (2010)

Species	Author & Date
Mormyridae	
Hippopotamyrus cf. ansorgii	(Boulenger, 1905)
Paramormyrops cf. kingsleyae	(Günther, 1896)
Paramormyrops cf. sphekodes	(Sauvage, 1879)
Cyprinidae	
Enteromius miolepis	(Boulenger, 1902)
Enteromius unitaeniatus	(Günther, 1867)
Enteromius vandersti	(Poll, 1945)
Garra congoensis	Poll, 1959
Labeo macrostomus	Boulenger, 1898
Labeobarbus sp. nov.	
Labeobarbus boulengeri	Vreven, Musschoot, Snoeks & Schliewen, 2016
Labeobarbus robertsi	(Banister, 1984)
Raiamas kheeli	Stiassny, Schelly & Schliewen, 2006
Alestidae	
Nannopetersius mutambuei	Wamuini Lunkayilakio & Vreven, 2008
Claroteidae	
Parauchenoglanis balayi	(Sauvage, 1879)
Clariidae	
Clarias angolensis	Steindachner, 1866
Clarias buthupogon	Sauvage, 1879
Clarias camerunensis	Lönnberg, 1895
Clarias gariepinus	(Burchell, 1822)
Clarias gabonensis	Günther, 1867
Schilbeidae	
Schilbe zairensis	de Vos, 1995
Cichlidae	
Haplochromis snoeksi	Wamuini Lunkayilakio & Vreven, 2010
Hemichromis elongatus	(Guichenot, 1861)
Oreochromis niloticus	(Linnaeus, 1758)
Sarotherodon galilaeus	(Linnaeus, 1758)
Coptodon tholloni	(Sauvage, 1884)
Anabantidae	
Ctenopoma nigropannosum	Reichenow, 1875
Chanidae	
Parachanna obscura	(Günther, 1861)

Appendix 3

Freshwater fishes of the (A) Cuanza (Atlantic coastal), (C) southern Congo, (Z) Upper Zambezian, (O) Okavango, and (K) Cunene basins in Angola, after Poll (1967) with updated adjustments for taxonomy and known records by the author

Species	Author & Date	A	C	Z	O	K	I[a]
Protopteridae							
Protopterus aethiopicus	Heckel, 1851		x				DD
Protopterus dolloi	Boulenger, 1900		x				LC
Polypteridae							
Polypterus ornatipinnis	Boulenger, 1902		x				LC
Clupeidae							
Pellonula vorax	Günther, 1868	x	x				LC
Odaxothrissa ansorgii	Boulenger, 1910	x	x				LC
Kneriidae							
Kneria angolensis	Steindachner, 1866	x	x	?			LC
Kneria maydelli	Ladiges & Voelker, 1961					x	LC
Kneria polli	Trewavas, 1936	x	x				LC
Kneria sjolandersi	Poll, 1967	x					DD
Kneria ansorgii	(Boulenger, 1910)	x	x				DD
Parakneria marmorata	(Norman, 1923)	x					DD
Parakneria vilhenae	Poll, 1965		x				DD
Parakneria fortuita	Penrith, 1973	x		x	x		DD
Mormyridae							
Mormyrops attenuatus	Boulenger, 1898		x				LC
Mormyrops anguilloides	(Linnaeus, 1758)		x				LC
Petrocephalus okavagoensis	Kramer et al., 2012			x	x		NE
Petrocephalus magnitrunci	Kramer et al., 2012				x		NE
Petrocephalus magnoculis	Kramer et al., 2012					x	NE
Petrocephalus longicapitis	Kramer et al., 2012			x	x		NE
Petrocephalus christyi	Boulenger, 1920		x				NE
Petrocephalus cunganus	Boulenger, 1910	x					DD
Petrocephalus micropthalmus	Pellegrin, 1909		x				LC
Petrocephalus simus	Sauvage, 1879	x	x	?			LC
Hippopotamyrus ansorgii	(Boulenger, 1905)	x		x	x		LC
Hippopotamyrus longilateralis	Kramer & Swartz, 2010					x	NE
Pollimyrus brevis	(Boulenger, 1913)		x				LC
Pollimyrus castelnaui	(Boulenger, 1911)			x	x	x	LC
Pollimyrus cuandoensis	Kramer, van der Bank & Wink, 2013			x			NE
Pollimyrus marianne	Kramer et al., 2003			x			NE
Cyphomyrus cubangoensis	(Pellegrin, 1936)			x	x		NE

(continued)

Species	Author & Date	A	C	Z	O	K	I[a]
Cyphomyrus psittacus	(Boulenger, 1897)		x				LC
Paramormyrops jacksoni	(Poll, 1967)			x			DD
Marcusenius altisambesi	Kramer et al., 2007		x	x	x		LC
Hippopotamyrus pappenheimi	(Boulenger, 1910)	x					LC
Heteromormyrus pauciradiatus	(Steindachner, 1866)	x					DD
Pollimyrus tumifrons	(Boulenger, 1902)		x				NE
Marcusenius desertus	Kramer, vanderBank & Wink, 2016					x	NE
Marcusenius multisquamatus	Kramer & Wink, 2013					x	NE
Marcusenius angolensis	(Boulenger, 1905)	x	x	x	x	x	LC
Marcusenius cuangoanus	(Poll, 1967)		x				VU
Marcusenius dundoensis	(Poll, 1967)		x				DD
Marcusenius moorii	(Günther, 1867)		x				LC
Marcusenius stanleyanus	(Boulenger, 1897)		x				LC
Campylomormyrus alces	(Boulenger, 1920)		x				LC
Campylomormyrus cassaicus	(Poll, 1967)		x				DD
Campylomormyrus elephas	(Boulenger, 1898)		x				LC
Campylomormyrus numenius	(Boulenger, 1898)		x				LC
Campylomormyrus luapulaensis	(David & Poll, 1937)		x				DD
Campylomormyrus rhynchophorus	(Boulenger, 1898)		x				LC
Campylomormyrus tshokwe	(Poll, 1967)		x				LC
Gnathonemus barbatus	Poll, 1967		x				DD
Gnathonemus petersii	(Günther, 1862)		x				LC
Mormyrus caballus	Boulenger, 1898		x				NE
Mormyrus lacerda	Castelnau, 1861	x		x	x	x	LC
Mormyrus rume	Valenciennes, 1847		x				NE
Cyprinidae							
Garra dembeensis	(Rüppell, 1835)		x				LC
Clypeobarbus bellcrossi	(Jubb, 1965)			x	x		DD
Coptostomabarbus wittei	David & Poll, 1937			x	x		LC
Enteromius afrovernayi	(Nichols & Boulton, 1927)		x	x	x	x	LC
Enteromius amphigramma	(Boulenger, 1903)	x					
Enteromius ansorgii	(Boulenger, 1904)		x				LC
Enteromius argenteus	(Günther, 1868)	x				x	LC
Enteromius barotseensis	(Pellegrin, 1920)			x	x	x	LC
Enteromius barnardi	(Jubb, 1965)			x	x	x	LC
Enteromius bifrenatus	(Fowler, 1935)			x	x	x	LC
Enteromius breviceps	(Trewavas, 1936)	x			x	x	LC
Enteromius brevidorsalis	(Boulenger, 1915)	x	x	x	x	x	LC
Enteromius brevilateralis	(Poll, 1967)	x	x				DD
Enteromius caudosignatus	(Poll, 1967)		x				DD

(continued)

Species	Author & Date	A	C	Z	O	K	I[a]
Enteromius chicapaensis	(Poll, 1967)		x		x		LC
Enteromius chiumbeensis	(Pellegrin, 1936)		x		x		LC
Enteromius dorsolineatus	(Trewavas, 1936)	x				x	LC
Enteromius eutaenia	(Boulenger, 1904)	x	x	x	x	x	DD
Enteromius evansi	(Fowler, 1930)	x			x		LC
Enteromius fasciolatus	(Günther, 1868)	x	x	x	x	x	LC
Enteromius greenwoodi	(Poll, 1967)	x			x		DD
Enteromius haasianus	(David, 1936)	x	x	x	x		LC
Enteromius holotaenia	(Boulenger, 1904)	x	x				LC
Enteromius kerstenii	(Peters, 1868)			x	x	x	LC
Enteromius kessleri	(Steindachneri, 1866)	x	x	x	x		LC
Enteromius lineomaculatus	(Boulenger, 1903)		x	x	x	x	LC
Enteromius lujae	(Boulenger, 1913)	x	x	x	x	x	DD
Enteromius machadoi	(Poll, 1967)		x				DD
Enteromius mattozi	(Guimarães, 1884)	x	x			x	LC
Enteromius mediosquamatus	(Poll, 1967)		x				DD
Enteromius miolepis	(Boulenger, 1902)		x	x	x		LC
Enteromius mocoensis	(Trewavas, 1936)	x			x		DD
Enteromius multilineatus	(Worthington, 1933)		x	x	x	x	LC
Enteromius musumbi	(Boulenger, 1910)	x					LC
Enteromius paludinosus	(Peters, 1852)	x	x	x	x	x	LC
Enteromius petchkovski	(Poll, 1967)		x				DD
Enteromius poechii	(Steindachneri, 1911)		?	x	x	x	LC
Enteromius radiatus	(Peters, 1853)	x	x	x	x	x	LC
Enteromius rousellei	(Ladiges & Voelker, 1961)		x				DD
Enteromius thamalakanensis	(Fowler, 1935)			x	x	x	LC
Enteromius trimaculatus	(Peters, 1852)	x	x		x	x	LC
Enteromius unitaeniatus	(Günther, 1867)	x	x	x	x	x	LC
Enteromius cf viviparus	(Weber, 1897)			x	x	x	NE
Enteromius wellmani	(Boulenger, 1911)	x					DD
Labeobarbus caudovittatus	(Boulenger, 1902)		x				LC
Labeobarbus codringtonii	(Boulenger, 1908)		x	x	x		LC
Labeobarbus ensis	(Boulenger, 1910)	x					LC
Labeobarbus gulielmi	(Boulenger, 1910)	x					DD
Labeobarbus girardi	(Boulenger, 1910)	x					DD
Labeobarbus jubbi	(Poll, 1967)		x				DD
Labeobarbus lucius	(Boulenger, 1910)	x					DD
Labeobarbus marequensis (Cassai)	(Smith, 1841)		x				LC
Labeobarbus nanningsi	de Beaufort, 1933	x	x				DD
Labeobarbus rhinophorus	(Boulenger, 1910)	x					DD
Labeobarbus rocadasi	(Boulenger, 1910)	x					DD
Labeobarbus rosae	(Boulenger, 1910)	x					DD

(continued)

Species	Author & Date	A	C	Z	O	K	I[a]
Labeobarbus ansorgii	(Boulenger, 1906)	x					LC
Labeobarbus ensifer	(Boulenger, 1910)	x					LC
Labeobarbus boulengeri	Vreven et al., 2016	x					NE
Labeobarbus macrolepidotus	(Pellegrin, 1928)		x				LC
Labeobarbus steindachneri	(Boulenger, 1910)	x					LC
Labeobarbus stenostomata	(Boulenger, 1910)	x					DD
Labeobarbus varicostoma	(Boulenger, 1910)	x					DD
Labeo annectens	Boulenger, 1903	x	x				LC
Labeo ansorgii	Boulenger, 1907	x	x			x	LC
Labeo chariensis	Pellegrin, 1904		x				LC
Labeo cylindricus	Peters, 1852		x	x	x		LC
Labeo greeni	Boulenger, 1902		x		?		LC
Labeo lineatus	Boulenger, 1898		x				LC
Labeo longipinnis	Boulenger, 1898		x				LC
Labeo macrostoma	Boulenger, 1898		x				LC
Labeo parvus	Boulenger, 1902	x	x				LC
Labeo rocadasi	Boulenger, 1907	x					LC
Labeo ruddi	Boulenger, 1907					x	LC
Labeo velifer	Boulenger, 1898		x				NE
Labeo weeksii	Boulenger, 1909		x				LC
Engraulicypris howesi	Ridden, Bills & Villet, 2016					x	NE
Opsaridium zambezense	(Peters, 1852)		x	x	x		LC
Raiamas ansorgii	(Boulenger, 1910)	x					DD
Raiamas christyi	(Boulenger, 1920)		x				LC
Hepsetidae							
Hepsetus cuvieri	(Castelnau, 1861)	x	x	x	x	x	NE
Alestidae							
Bryconaethiops microstoma	Günther, 1873		x				LC
Alestes macropthalmus	Günther, 1867		x				LC
Brycinus kingsleyae	(Günther, 1896)		x				LC
Brycinus grandisquamis	(Boulenger, 1899)		x				LC
Brycinus humilis	(Boulenger, 1905)	x	x				DD
Brycinus imberi	(Peters, 1852)	?	x				LC
Brycinus lateralis	(Boulenger, 1900)		x	x	x	x	LC
Micralestes acutidens	(Peters, 1852)		x	x	x		LC
Micralestes argyrotaenia	Trewavas, 1936					x	LC
Micralestes humilis	Boulenger, 1899		x				LC
Nannopetersius ansorgii	(Boulenger, 1910)	x					LC
Rhabdalestes maunensis	(Fowler, 1935)			x	x	x	LC
Hydrocynus vittatus	Castelnau, 1861		x	x	x		LC
Distichodontidae							
Distichodus fasciolatus	Boulenger, 1898		x				LC
Distichodus lusosso	Schilthuis, 1891		x				LC
Distichodus maculatus	Boulenger, 1898		x				LC

(continued)

Species	Author & Date	A	C	Z	O	K	I[a]
Distichodus notospilus	Günther, 1867		x				LC
Distichodus sexfasciatus	Boulenger, 1897		x				LC
Nannocharax macropterus	Pellegrin, 1926		x	x	x		LC
Nannocharax procatopus	Boulenger, 1920		x				LC
Nannocharax angolensis	(Poll, 1967)		x				LC
Nannocharax lineostriatus	(Poll, 1967)		x	x	x		DD
Nannocharax machadoi	(Poll, 1967)			x	x	x	LC
Nannocharax multifasciatus	Boulenger, 1923			x	x	x	DD
Dundocharax bidentatus	Poll, 1967		x				DD
Claroteidae							
Chrysichthys ansorgii	Boulenger, 1910	x					LC
Chrysichthys bocagii	Boulenger, 1910	x					LC
Chrysichthys cranchii	(Leach, 1818)		x				LC
Chrysichthys delhezi	Boulenger, 1899		x				LC
Chrysichthys macropterus	Boulenger, 1920		x				DD
Chrysichthys nigrodigitatus	(Lacepède, 1803)	x					LC
Parauchenoglanis ngamensis	(Boulenger, 1911)		x	x	x		LC
Amphiliidae							
Zaireichthys dorae	(Poll, 1967)		x				DD
Zaireichthys flavomaculatus	(Pellegrin, 1926)		x				DD
Zaireichthys pallidus	Eccles, Tweddle & Skelton, 2011			x	x		NE
Zaireichthys conspicuus	Eccles, Tweddle & Skelton, 2011			x	x		NE
Zaireichthys kavangoensis	Eccles, Tweddle & Skelton, 2011				x		NE
Zaireichthys kunenensis	Eccles, Tweddle & Skelton, 2011					x	NE
Congoglanis alula	(Nichols & Griscom, 1917)		x				LC
Doumea angolensis	Boulenger, 1906	x					LC
Congoglanis howesi	Vari, Ferraris & Skelton, 2012		x				NE
Congoglanis sp.		x					NE
Amphilius lentiginosus	Trewavas, 1936	x	?				DD
Amphilius cubangoensis	Pellegrin, 1936			x	x		NE
Phractura macrura	Poll, 1967		x				DD
Phractura scaphyrhynchura	(Vaillant, 1886)		x				LC
Malapteruridae							
Malapterurus monsembeensis	Roberts, 2000		x				LC
Clariidae							
Heterobranchus longifilis	Valenciennes, 1840		x				LC
Channallabes apus	(Günther, 1873)	x	x				LC
Clarias angolensis	Steindachner, 1866	x	x				LC
Clarias buthupogon	Sauvage, 1879		x				LC

(continued)

Species	Author & Date	A	C	Z	O	K	I[a]
Clarias dumerilii	Steindachner, 1866	x	x			x	LC
Clarias platycephalus	Boulenger, 1902		x				NE
Clarias gariepinus	(Burchell, 1822)	x	x	x	x	x	LC
Clarias ngamensis	Castelnau, 1861	x	x	x	x	x	LC
Clarias nigromarmoratus	Poll, 1967		x				LC
Clarias stappersii	Boulenger, 1915	x	x	x	x	x	LC
Clarias liocephalus	Boulenger, 1898		x	x	x	x	LC
Clarias theodorae	Weber, 1897		x	x	x	x	LC
Clariallabes heterocephalus	Poll, 1967		x				LC
Clariallabes variabilis	Pellegrin, 1926		x				LC
Clariallabes platyprosopos	Jubb, 1965			x	x		LC
Clariallabes sp					x		NE
Platyclarias machadoi	Poll, 1977		x				DD
Schilbeidae							
Parailia occidentalis	(Pellegrin, 1901)	x					LC
Schilbe intermedium	Rüppell, 1832		x	x	x	x	LC
Schilbe angolensis	(De Vos, 1984)	x					DD
Schilbe ansorgii	(Boulenger, 1910)	x					LC
Schilbe bocagii	(Guimarães, 1884)	x					LC
Schilbe grenfelli	(Boulenger, 1900)		x				LC
Schilbe yangambianus	(Poll, 1954)		x	x			LC
Mochokidae							
Synodontis laessoei	Norman, 1923	x					DD
Synodontis leopardinus	Pellegrin, 1914			x	x	x	LC
Synodontis longirostris	Boulenger, 1902		x				LC
Synodontis macrostigma	Boulenger, 1911			x	x	x	LC
Synodontis macrostoma	Skelton & White, 1990			x	x	x	LC
Synodontis nigromaculatus	Boulenger, 1905		x	x	x	x	LC
Synodontis ornatipinnis	Boulenger, 1899	x	x				LC
Synodontis thamalakanensis	Fowler, 1935			x	x	x	LC
Synodontis woosnami	Boulenger, 1911			x	x	x	LC
Synodontis vanderwaali	Skelton & White, 1990			x	x	x	LC
Chiloglanis angolensis	Poll, 1967	x				x	DD
Chiloglanis fasciatus	Pellegrin, 1936			x	x		LC
Chiloglanis lukugae	Poll, 1944		x				LC
Chiloglanis micropogon	Poll, 1952		x				NE
Chiloglanis sardinhai	Ladiges & Voelker, 1961	x					LC
Euchilichthys astatodon	(Pellegrin, 1928)		x				LC
Euchilichthys royauxi	Boulenger, 1902		x				LC
Atopochilus macrocephalus	Boulenger, 1906		x				DD
Chiloglanis sp. (dark)				x	x		NE
Chiloglanis sp. (gold)				x	x		NE

(continued)

Species	Author & Date	A	C	Z	O	K	I[a]
Procatopodidae							
Aplocheilichthys spilauchen	(Duméril, 1861)	x					LC
Micropanchax hutereaui	(Boulenger, 1913)		x	x	x		LC
Micropanchax johnstonii	(Günther, 1894)		x	x	x	x	LC
Micropanchax katangae	(Boulenger, 1912)		x	x	x	x	LC
Micropanchax luluae	(Fowler, 1930)		x		x		NE
Micropanchax macrurus	(Boulenger, 1904)	x	x			x	LC
Micropanchax mediolateralis	(Poll, 1967)		x		x		LC
Micropanchax myaposae	(Boulenger, 1908)	x					LC
Micropanchax nigrolateralis	(Poll, 1967)		x		x		DD
Micropanchax 'pigmy'				x	x		NE
Cichlidae							
Hemichromis elongatus	(Guichenot, 1861)	x	x	x	x		LC
Hemichromis angolensis	Steindachner, 1865	x					NE
Pharyngochromis acuticeps	(Steindachner, 1866)	x		x	x	x	LC
Pseudocrenilabrus philander	(Weber, 1897)	x	x	x	x	x	LC
Oreochromis andersonii	(Castelnau, 1861)			x	x	x	VU
Oreochromis macrochir	(Boulenger, 1912)		x	x	x	x	VU
Oreochromis angolensis	(Trewavas, 1973)	x					LC
Coptodon rendalli	(Boulenger, 1897)	x	x	x	x	x	LC
Pelmatolapia cabrae	(Boulenger, 1899)	x	x				LC
Oreochromis lepidurus	(Boulenger, 1899)	x	x				EN
Oreochromis schwebischi	(Sauvage, 1884)	x	x				LC
Tilapia sparrmanii	Smith, 1840	x	x	x	x	x	LC
Tilapia ruweti	(Poll & Thys van den Audenaerde, 1965)	x	x	x			LC
Serranochromis altus	Winemiller & Kelso-Winemiller, 1991			x	x		LC
Serranochromis angusticeps	(Boulenger, 1907)		x	x	x	x	LC
Serranochromis longimanus	(Boulenger, 1911)			x	x		LC
Serranochromis macrocephalus	(Boulenger, 1899)	x	x	x	x	x	LC
Serranochromis robustus jallae	(Boulenger, 1864)		x	x	x	x	LC
Serranochromis thumbergi	(Castelnau, 1861)		?	x	x	x	LC
Sargochromis greenwoodi	(Bell-Cross, 1975)				x	x	LC
Sargochromis carlottae	(Boulenger, 1905)			x	x		LC
Sargochromis giardi	(Pellegrin, 1903)			x	x	x	LC
Sargochromis coulteri	(Bell-Cross, 1975)					x	LC
Sargochromis codringtonii	(Boulenger, 1908)			x	x	x	LC
Thoracochromis lucullae	(Boulenger, 1913)	x					LC
Orthochromis machadoi	(Poll, 1967)					x	LC
Sargochromis thysi	(Poll, 1967)		x				DD
Chetia welwitschi	(Boulenger, 1898)	x				x	DD

(continued)

Species	Author & Date	A	C	Z	O	K	I[a]
Chetia gracilis	(Greenwood, 1984)				x		LC
Thoracochromis albolabrus	(Trewavas & Thys vd Audenaerde, 1969)					x	LC
Thoracochromis buysi	(Penrith, 1970)					x	LC
Anabantidae							
Ctenopoma machadoi	(Fowler, 1930)	x					LC
Ctenopoma multispine	Peters, 1844		x	x	x	x	LC
Microctenopoma intermedium	(Pellegrin, 1920)		x	x	x		LC
Microctenopoma sp.		x			x		NE
Mastacembelidae							
Mastacembelus ansorgii	Boulenger, 1905	x					DD
Mastacembelus niger	Sauvage, 1879		x				LC
Mastacembelus congicus	Boulenger, 1896		x				LC
Mastacembelus frenatus	Boulenger, 1901			x	x		LC
Mastacembelus sp.		x					NE
Eleotridae							
Eleotris vittata	Duméril, 1861					x	LC
Dormitator lebretonis	(Steindachner, 1870)					x	NE
Gobiidae							
Awaous lateristriga	(Duméril, 1861)					x	NE
Nematogobius maindroni	(Sauvage, 1880)					x	NE
Ctenogobius lepturus	(Pfaff, 1933)					x	NE
Periophthalmus barbarus	(Linnaeus, 1766)	x					LC
Syngnathidae							
Enneacampus ansorgii	(Boulenger, 1910)	x					LC
Enneacampus kaupi	(Bleeker, 1863)	x					LC
	TOTALS	**104**	**161**	**93**	**103**	**82**	

IUCN status (I) as recorded by Darwell et al. (2011) and IUCN (2018). The table is for tentative indications of distribution and IUCN status
DD data deficient, *EN* endangered, *LC* least concern, *NE* not evaluated, *VU* vulnerable
[a]IUCN Red List Categories Codes

References

Ball P (2015) Benguela – more than just a current. The Heritage Portal, p 13. http://www.the-heritageportal.co.za/article/Benguela-more-just-current

Balon EK (1974) Fishes from the edge of Victoria Falls, Africa: demise of a physical barrier for downstream invasions. Copeia 1974(3):643–660

Barnard KH (1948) Report on a collection of fishes from the Okavango River, with notes on Zambesi fishes. Ann S Afr Mus 36:407–458

Bbole I, Katongo C, Deines AM et al (2014) Hybridization between non-indigenous *Oreochromis niloticus* and native *Oreochromis* species in the lower Kafue River and its potential impacts on fishery. J Ecol Nat Environ 6(6):215–225

Bell-Cross G (1965) Movement of fish across the Congo-Zambezi watershed in the Mwinilunga district of Northern Rhodesia. Proceedings of the Central African Scientific and Medical Congress, Lusaka, 1963, pp 415–424

Bell-Cross G (1975) A revision of certain *Haplochromis* species (Pisces: Cichlidae) of Central Africa. Occas Pap Natl Mus Monuments Rhod Ser B 5(7):405–464

Bell-Cross G, Minshull JL (1988) The fishes of Zimbabwe. National Museums and Monuments of Zimbabwe, Harare

Bills IR, Skelton PH, Almeida F (2012) A survey of the fishes of the upper Okavango system in Angola. SAIAB Investigational Report 73, 61 pp

Bills IR, Mazungula N, Almeida F (2013) A survey of the fishes of upper Okavango River system in Angola. SAIAB Investigational Report 74, 21 pp

Boulenger GA (1909–1916) Catalogue of the fresh-water of Africa in the British Museum (Natural History), Vol 1 (1909) Vol 2 (1910), Vol 3 (1915), Vol 4 (1916). Trustees of the British Museum, London

Boulenger GA (1910) LXI.–on a large collection of fishes made by Dr. W. J. Ansorge in the Quanza and Bengo Rivers, Angola. Ann Mag Nat Hist 6(36):537–561

Boulenger GA (1911) V. on a collection of fishes from the Lake Ngami Basin, Bechuanaland. Trans Zool Soc London 18(5):399–418, pls XXXVIII-XLIII

Burrough SL, Thomas DSG, Bailey RM (2009) Mega-lake in the Kalahari: a late Pleistocene record of the Palaeolake Magadigadi system. Quat Sci Rev 28:1392–1411

Castelnau F (1861) Mémoire sur les Poissons de l'Afrique Australe. J-B Baillière et Fils, Paris, p 78

Day JJ, Bills R, Friel JP (2009) Lacustrine radiation in African *Synodontis* catfish. J Evol Biol 22:805–817

De Vos LDG (1995) A systematic revision of the African Schilbeidae (Teleostei, Siluriformes). With an annotated bibliography. Annalen Zoologische Wetenschappen 271:1–450

Devaere S, Adriaens D, Verraes W (2007) *Channallabes sanghaensis* sp.n. a new anguilliform catfish from the Congo River basin, with some comments on other anguilliform clariids (Teleostei, Siluriformes). Belg J Zool 137:17–26

Eccles DH, Tweddle D, Skelton PH (2011) Eight new species in the dwarf catfish genus *Zaireichthys* (Siluriformes: Amphiliidae). Smithiana Bull 13:3–28

Flügel TJ, Eckardt FD, Cotterill FPD (2015) Chapter 15: the present day drainage patterns of the Congo river system and their Neogene evolution. In: de Wit MJ et al (eds) Geology and resource potential of the Congo basin, Regional geology reviews. Springer, Berlin/Heidelberg, pp 315–337

Fowler HW (1930) The fresh-water fishes obtained by the gray African expedition – 1929. With notes on other species in the academy collection. Proc Acad Natl Sci Phila 82:27–83

Fowler HW (1935) Scientific results of the Vernay-Lang Kalahari Expedition, March to September, 1930. The freshwater fishes. Ann Transv Mus 16(2):251–293

Gilchrist JDF, Thompson WW (1913) The freshwater fishes of South Africa. Ann S Afr Mus 11(5):321–463

Gilchrist JDF, Thompson WW (1917) The freshwater fishes of South Africa (continued). Ann S Afr Mus 11(6):465–575

Greenwood PH (1984) The haplochromine species (Teleostei, Cichlidae) of the Cunene and certain other Angolan rivers. Bull Brit Mus (Nat Hist) 47(4):187–239

Greenwood PH (1993) A review of the serranochromine cichlid fish genera *Pharyngochromis, Sargochromis, Serranochromis and Chetia* (Teleostei, Labroidei). Bull Brit Mus (Nat Hist) 59:33–44

Guimarães ARP (1884) 1. Diagnoses de trois nouveaux poisons d'Angola. J Sci Math Phys Lisboa 37:1–10

Haddon IG, McCarthy TS (2005) The Mesozoic–Cenozoic interior sag basins of Central Africa: the late-cretaceous–Cenozoic Kalahari and Okavango basins. J Afr Earth Sci 43:316–333

Hay CJ, van Zyl BJ, van der Bank FH et al (1997) A survey of the fishes of the Kunene River, Namibia. Modoqua 19:129–141

Hipondoka MHT, van der Waal BCW, Ndeutapo MH, Hango L (2018) Sources of fish in the ephemeral western iishana region of the Cuvelai–Etosha Basin in Angola and Namibia. Afr J Aquat Sci 43(3):199–214.https://doi.org/10.2989/16085914.2018.1506310

Jackson PBN (1961) The fishes of northern Rhodesia: a checklist of indigenous species. Department of Game and Fisheries, Lusaka

Jubb RA (1961) An illustrated guide to the freshwater fishes of the Zambezi River, Lake Kariba, Pungwe, Sabi, Lundi and Limpopo Rivers. Stuart Manning, Bulawayo

Jubb RA (1967) The freshwater fishes of southern Africa. AA Balkema, Cape Town

Jubb RA, Gaigher IG (1971) Checklist of the fishes of Botswana. Arnoldia, Rhodesia 5(97):1–22

Key RM, Cotterill FPD, Moore AE (2015) The Zambezi river: an archive of tectonic events linked to the amalgamation and disruption of Gondwana and subsequent evolution of the African plate. S Afr J Geol 118:425–438

King J, Chonguic E (2016) Integrated management of the Cubango-Okavango River basin. Ecohydrol Hydrobiol 16:263–271

Kramer B, Swartz ER (2010) A new species of slender Stonebasher within the *Hippopotamyrus ansorgii* complex from the Cunene River in southern Africa (Teleostei: Mormyriformes). J Nat Hist 44(35–36):2213–2242

Kramer B, Wink M (2013) East–west differentiation in the *Marcusenius macrolepidotus* species complex in southern Africa: the description of a new species for the lower Cunene River, Namibia (Teleostei: Mormyridae). J Nat Hist 47(35–36):2327–2362

Kramer B, van der Bank FH, Flint N et al (2003) Evidence for parapatric speciation in the Mormyrid fish, *Pollimyrus castelnaui* (Boulenger, 1911), from the Okavango–upper Zambezi River systems: *P. marianne* sp. nov., defined by electric organ discharges, morphology and genetics. Environ Biol Fish 77:47–70

Kramer B, van der Bank FH, Wink M (2004) The *Hippopotamyrus ansorgii* species complex in the upper Zambezi River system with a description of a new species, *H. szaboi* (Mormyridae). Zool Scr 33:1–18

Kramer B, Bills IR, Skelton PH et al (2012) A critical revision of the churchill snoutfish, genus *Petrocephalus* Marcusen, 1854 (Actinopterygii: Teleostei: Mormyridae), from southern and eastern Africa, with the recognition of *Petrocephalus tanensis*, and the description of five new species. J Nat Hist 46:2179–2258

Kramer B, van der Bank H, Wink M (2014) Marked differentiation in a new species of dwarf stonebasher, *Pollimyrus cuandoensis* sp. nov. (Mormyridae: Teleostei), from a contact zone with two sibling species of the Okavango and Zambezi rivers. J Nat Hist 48(7–8):429–463

Kramer B, van der Bank FH, Wink M (2016) *Marcusenius desertus* sp. nov. (Teleostei: Mormyridae), a mormyrid fish from the Namib desert. Afr J Aquat Sci 41(1):1–18

Ladiges W (1964) Beiträge zur zoogeographie und Oekologie der süßwasserfische Angolas. Die Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 61:221–272

Ladiges W, Voelker J (1961) Untersuchungen über die Fishfauna in Gebirgsgewässern des Wasserscheidenhochlands in Angola. Die Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 59:117–140

Lévêque C, Paugy D (2017a) General characteristics of ichthyological fauna. In: Paugy D, Lévêque C, Otero O (eds.) The inland water fishes of Africa, diversity, ecology and human use. IRD Éditions, Paris, & Royal Museum for Central Africa, Tervuren, pp 83–96

Lévêque C, Paugy D (2017b) Geographical distribution and Affinities of African freshwater fishes. In: Paugy D, Lévêque C, Otero O (eds) The inland water fishes of Africa, diversity, ecology and human use. IRD Éditions. France, & Royal Museum for Central Africa, Belgium, pp 97–114

Marshall BE, Tweddle D (2007) *Oreochromis macrochir*. The IUCN Red List of Threatened Species 2007: e.T63336A12659168

Mendelsohn J, Weber B (2015) An atlas and profile of Moxico, Angola. RAISON, Windhoek

Moelants T 2010. *Oreochromis lepidurus*. The IUCN Red List of Threatened Species2010: e.T182875A7991695

Moore AE, Larkin PA (2001) Drainage evolution in south-Central Africa since the break-up of Gondwana. S Afr J Geol 104:47–68

Moore AE, Cotterill FPD, Eckardt FD (2012) The evolution and ages of Makgadikgadi palaeolakes: Consilient evidence from Kalahari drainage evolution. S Afr J Geol 115:385–413

Musilová Z, Kalous L, Petrtýl M et al (2013) Cichlid fishes in the Angolan headwaters region: molecular evidence of the ichthyofaunal contact between the Cuanza and Okavango-Zambezi systems. PLoS One 8(5):e65047

NGOWP – National Geographic Okavango Wilderness Project (2018) Initial findings from exploration of the upper catchments of the Cuito, Cuanavale and Cuando Rivers in Central and South-Eastern Angola (May 2015 to December 2016). National Geographic Okavango Wilderness Project, 352 pp

Nichols JT, Boulton R (1927) Three new minnows of the genus *Barbus*, and a new characin from the Vernay Angola expedition. Am Mus Novit 264:1–8

Norman JR (1923) A new cyprinoid fish from Tanganyika territory, and two new fishes from Angola. Ann Mag Nat Hist 12(72):694–696

Nunes AL, Douthwaite RJ, Tyser B et al (2016) Invasive crayfish threaten Okavango Delta. Front Ecol Environ 14(5):237–238

Paugy D, Lévèque C, Otero O (eds) (2017) The inland water fishes of Africa, IRD Éditions. Institut de Recherche pour de Developpement/RMCA Royal Museum for Central Africa, Paris/Tervuren

Pellegrin J (1921) Description d'un Barbeau nouveau de l'Angola. Bull Soc Zool Fr 46:118–120

Pellegrin J (1928) Poissons du Chiloango et du Congo receuillis par l'expédition du Dr Schouteden (1920–1922). Annales du Musée Royal du Congo Belge, Zoologie Série 1 3(1):1–50

Pellegrin J (1936) Contribution à l'ichthyologie de l'Angola. Arquivos do Museu Bocage 7:45–62

Penrith M-L (1970) Report on a small collection of fishes from the Kunene River mouth. Cimbebasia Series A 1:165–176

Penrith MJ (1973) A new species of *Parakneria* from Angola (Pisces: Kneriidae). Cimbebasia Series A 11:131–135

Penrith MJ (1982) Additions to the checklist of southern African freshwater fishes and a gazetteer of south-western Angolan collecting localities. J Limnol Soc South Afr 8(2):71–75

Pinton A, Agnèse J-F, Paugy D, Otero O (2013) A large-scale phylogeny of *Synodontis* (Mochokidae, Siluriformes) reveals the influence of geological events on continental diversity during the Cenozoic. Mol Phylogenet Evol 66:1027–1040

Podgorski JE, Green AG, Kgotlhang L et al (2013) Paleo-megalake and paleo-megafan in southern Africa. Geology 11:1155–1158

Poll M (1967) Contribution à la Faune Ichthyologique de l'Angola. Publicações Culturais 75 75. Companhia dos Diamentes de Angola (DIAMANG), Lisbon, 381 pp

Poll M (1971) Révision des *Synodontis* Africains (Famille Mochocidae). Annales Musée Royal de l'Afrique Centrale Serie IN-8 Sciences Zoologiques No. 191. Musée Royal de l'Afrique Centrale, Tervuren, 497 pp

Roberts TC (1975) Geographical distribution of African freshwater fishes. Zool J Linnean Soc 57(4):249–319

Saldanha L (1978) Museu Bocage. Copeia 1978(4):739–740

Schwarzer J, Swartz ER, Vreven E et al (2012) Repeated trans-watershed hybridization among haplochromine cichlids (Cichlidae) was triggered by Neogene landscape evolution. Proc R Soc London, Ser B 279:4389–4398

Skelton PH (1994) Diversity and distribution of freshwater fishes in East and Southern Africa. Annales Musée Royal de l'Afrique Centrale, Sciences Zoologiques 275:95–131

Skelton PH (2001) A complete guide to the freshwater fishes of Southern Africa. Struik, Cape Town

Skelton PH, Swartz ER (2011) Walking the tightrope: trends in African freshwater systematic ichthyology. J Fish Biol 79:1413–1435

Skelton PH, Bruton MN, Merron GS et al (1985) The fishes of the Okavango drainage system in Angola, South West Africa and Botswana: taxonomy and distribution. Ichthyol. Bull. JLB Smith Inst Ichthyol 50:1–21

Skelton PH, Neef G, Costa A (2016) Into the wilderness expedition 2015: the fishes. SAIAB Investigational Report No 75, 49 pp

Snoeks J, Vreven EJ (2007) Chapter 38: Polynemidae, 445-449 in: Stiassny, MLJ, Teugels GG, Hopkins CD (eds) The fresh and brackish water fishes of lower Guinea, west-Central Africa. Collection Faune et Flore tropicales 42, vol 2. Institut de recherché pour le développement, Paris, France/Muséum national d'histoire naturelle, Paris, France/Musée royal de l'Afrique Centrale, Tervuren

Snoeks J, Harrison IJ, Stiassny MLJ (2011) Chapter 3: The status and distribution of freshwater fishes. In: Darwall WRT, Smith KG, Allen DJ, Holland RA, Harrison IJ, Brooks EGE (eds) The diversity of life in African freshwaters: under water, under threat. An analysis of the status and distribution of freshwater species throughout mainland Africa. IUCN, Cambridge/Gland, pp 42–73

Steindachner F (1866) Ichthyologische Mittheilungen. (IX.) [With subtitles I-VI.]. Verh Zool Bot Ges Wien 16:761–796

Stiassny MLJ, Teugels GG, Hopkins CD (eds) (2007) The fresh and brackish water fishes of Lower Guinea, West-Central Africa. Collection Faune et Flore Tropicales 42, Volume 1 and 2. IRD & Muséum National d'Histoire Naturelle, Paris & Musée Royal de l'Afrique Centrale, Tervuren

Thieme ML, Abell R, Stiassny ML et al (eds) (2005) Freshwater ecoregions of Africa and Madagascar, a conservation assessment. Island Press, Washington

Trewavas E (1936) Dr. Karl Jordan's expedition to south-West Africa and Angola: the fresh-water fishes. Novitates Zoologicae 40:63–74

Trewavas E (1964) A revision of the genus *Serranochromis* Regan (Pisces, Cichlidae). Annales Musée Royal de l'Afrique Centrale Serie IN-8 Sciences Zoologiques No. 125, Musée Royal de l'Afrique Centrale, Tervuren, 58 pp

Trewavas E (1973) A new species of cichlid fishes of rivers Quanza and Bengo, Angola, with a list of the known Cichlidae of these rivers and a note on *Pseudocrenilabrus natalensis* fowler. Bull Brit Mus (Nat Hist) 25(1):28–37

Tweddle D (2010) Overview of the Zambezi River system: its history, fish fauna, fisheries, and conservation. Aquat Ecosyst Health Manage 13(3):224–240

Tweddle D, Skelton, PH, van der Waal et al (2004) Aquatic biodiversity survey "four corners" transboundary natural resources management area. SAIAB Investigational Report No 71 202 pp

Tweddle D, Cowx IG, Peel RA et al (2015) Challenges in fisheries management in the Zambezi, one of the great rivers of Africa. Fish Manag Ecol 22:99–111

Van der Waal BCW (1991) A survey of the fisheries in Kavango, Namibia. Modoqua 17(2):113–122

Van der Waal BCW, Skelton PH (1984) Checklist of fishes of Caprivi. Modoqua 13(4):303–321

Vreven EJ, Musschoot T, Snoeks J et al (2016) The African hexaploid Torini (Cypriniformes: Cyprinidae): review of a tumultuous history. Zool J Linnean Soc 177(2):231–305

Wamuini Lunkayilakio S, Vreven E (2010) *'Haplochromis' snoeksi*, a new species from the Inkisi River basin, lower Congo (Perciformes: Cichlidae). Ichthyol Explor Freshwaters 21(3):279–287

Wamuini Lunkayilakio SW, Vreven E (2008) *Nannopetersius mutambuei* (Characiformes: Alestidae), a new species from the Inkisi River basin, Democratic Republic of Congo. Ichthyol Explor Freshwaters 19:367–376

Wamuini Lunkayilakio S, Vreven E, Vandewalle P et al (2010) Contribution à la connaissance de l'ichtyofaune de l'Inkisi au Bas-Congo (RD du Congo). Cybium 34(1):83–91

Whitfield AK (2007) Estuary associated fish species. In: Stiassny MLJ, Teugels GG, Hopkins CD (eds) The fresh and brackish water fishes of Lower Guinea, West-Central Africa. Collection

Faune et Flore Tropicales 42, vol 1. IRD & Muséum National d'Histoire Naturelle, Paris & Musée Royal de l'Afrique Centrale, Tervuren, pp 46-56

Wise RM, van Wilgen BW, Hill MP et al (2007) The economic impact and appropriate management of selected invasive alien species on the African continent. Final report for GISP. CSIR report number CSIR/RBSD/ER/2007/0044/C

Zengeya TA, Decru E, Vreven EJ (2011) Revalidation of *Hepsetus cuvieri* (Castelnau, 1861) (Characiformes: Hepsetidae) from the Quanza, Zambezi and southern part of the Congo ichthyofaunal provinces. J Nat Hist 45:1723–1744

Zengeya TA, Robertson MP, Booth AJ et al (2013) Qualitative ecological risk assessment of the invasive Nile tilapia, *Oreochromis niloticus* in a sub-tropical African river system (Limpopo river, South Africa). Aquat Conserv Mar Freshwat Ecosyst 23:51–64