



Species in the spotlight

The Congo blind barb: Mbanza-Ngungu's albino cave fish

Vreven, E.¹, Kimbembi ma Ibaka, A.² and Wamuini Lunkayilakio, S.²



A live specimen of *Caecobarbus geertsii* from the cave 'Grotte de Lukatu', D. R. Congo. © ROYAL MUSEUM FOR CENTRAL AFRICA

The enigmatic, Congo blind barb, *Caecobarbus geertsii*, was scientifically described by Boulenger (1921), based on four specimens collected in 1920, from the 'Grottes de Thysville' in the Lower Congo region (Roberts and Stewart 1976) of D. R. Congo. It was the first African cave fish to be discovered. The species is locally referred to as 'Nzonzi a mpofo' in Kikongo (the local Ndibu dialect) which literally means 'blind barb'.

Although the eyes are not visible, they are present. They are deeply embedded in the head, lack a lens, and have only a rudimentary retina and optical nerve (Gerard 1936). Nevertheless, Thinès (1953), contrary to Petit and Besnard (1937), notes that the species moves away from light, demonstrating a typical photonegative reaction due to the existence of extra-ocular photosensitivity.

The species also lacks pigmentation (Boulenger 1921; Heuts 1951) and is considered a true albino, as placing live animals under light for more than one month does not result in development of pigment (Gerard 1936). However, Poll (1953) reported the presence of melanophores in a specimen kept for seven months in an aquarium. The lateral vein creates a vivid red

band along the lateral line. Below the operculum the gills are visible as a purplish region, and the intestinal region is visible through the abdomen (Petit and Besnard 1937). Heuts (1951) estimated longevity at nine to 14 years; Proudlove and Romero (2001) stated the lifespan may exceed 15 years, but this needs to be confirmed. The species reaches a maximum size of 80 to 120mm total length, based on the largest specimen housed at the Royal Museum for Central Africa.

Following explorations of several caves in 1949, Heuts (1951) and Heuts and Leleup (1954) recorded *C. geertsii* from seven caves around Mbanza-Ngungu (formerly Thysville), situated on the western slope and the top of the Thysville mountain ridge (Monts de Cristal: 750 to 850m elevation). One population was reported as extirpated by the exploitation of limestone between 1930 and 1935 (Leleup 1956; see also Heuts and Leleup 1954). Indeed, a visit to the cave site in 2005 found it to have completely disappeared following excavation of the slope.

The presence of *C. geertsii* in at least four of the other caves reported by Heuts and Leleup (1954) has been confirmed by recent surveys by Kimbembi (2007) and the authors.

Statistical population surveys have been impossible because the subterranean habitat is extensive and difficult to sample (Heuts 1951); however, a gross population estimate for the seven caves reported by Heuts and Leleup (1954) would be about 7,000 individuals (based on information supplied by those authors). Kimbembi (2007) discovered seven more caves with at least small populations of *C. geertsii*, although no population estimations have been made for these.

Heuts (1951) and Heuts and Leleup (1954) previously considered *C. geertsii* to be present in only two upper tributaries of the Kwilu Basin (an affluent of the Lower Congo), namely the Fuma and the Kokosi. One of the new caves that Kimbembi (2007) identified as holding *C. geertsii* is on the Tobo River, another affluent of the Kwilu Basin. Lévêque and Daget (1984) and Banister (1986) also reported the species from the Inkisi Basin, but at the time had no evidence for this. However, inferred from mapping of the new cave localities identified by Kimbembi (2007), the species' presence in the Inkisi River basin seems to be confirmed by two of them – one on the Tubulu River and another one on the Uombe or possibly the Kela River, a tributary to the Uombe. The

¹ Royal Museum for Central Africa, Vertebrate Section, Ichthyology, Leuvensesteenweg 13, B-3080 Tervuren, Belgium

² Institut Supérieur Pédagogique de Mbanza-Ngungu, Bas-Congo, Laboratoire de Biologie, Democratic Republic of Congo

presence of *C. geertsii* in D. R. Congo, as reported by Lévêque and Daget (1984), is incorrect. Thus, the entire distribution area of the species is about 120km². Heuts (1951) noted important differences between the different populations of *C. geertsii* in the Kwilu basin. Populations present in affluents of the Kokosi River have an opercular guanine spot which may cover one third of the operculum (in addition to a few other guanine spots and marks). This spot is absent in all other populations (affluents of the Fuma River). Furthermore, within one cave the population has a serrated dorsal spine, which was not found in all other populations examined by Heuts (1951).

Traditionally, caves are sacred in the area (Laman 1962) and, as a result, access to most of the caves is restricted still today. A law, passed on 21 April 1937, protected *C. geertsii* from all hunting and fishing, except for scientific purposes (Frenchkop 1941, 1947, 1953; Duren 1943). The species was added to the CITES Annex II (on 6 June 1981), resulting in an international trade restriction which means that the species cannot be traded without appropriate export and import permits. *C. geertsii* is still the only African freshwater fish species on the CITES list. The IUCN Red List status of *C. geertsii* is Vulnerable (VU), due to a limited geographic range and a decline in the area and quality of its habitat (Moelants 2009).

Caecobarbus geertsii was found in only seven of the 45 caves explored by Heuts and Leleup in 1949. This indicates, according to Heuts (1951) and Heuts and Leleup (1954), that caves must have a specific combination of ecological conditions if they are to be populated by *C. geertsii*, and they summarised the following conditions:

1. high calcium bicarbonate concentrations in the water; and
2. a distinct periodicity of the subterranean river flow regime through the caves.

Due to this periodic inundation

of the caves inhabited by *C. geertsii*, other typical cave animals, such as terrestrial insects, are absent. Therefore, *C. geertsii* is entirely dependent on an external, exogenous, food supply to the caves during the rainy season with, as a result, important fluctuations in food resources between seasons. Moelants (2009) states that the species may feed on small crustaceans living in the caves, but this needs to be confirmed. Consequently, growth is extremely slow, and all further available data suggest a very low reproduction rate, justifying protection measurements.

A visit to the Kambu cave by the authors in August 2009 failed to find the species, although its presence had been reported by Kimbembi (2007). However, several individuals of at least one species of *Clarias* (\pm 200mm standard length) were found in the different isolated pools. This observation suggests predation of *C. geertsii* by species of *Clarias*, as previously proposed by Heuts and Leleup (1954) and by Leleup (1956).

Caecobarbus geertsii has, in the past, been traded as an aquarium fish, with large numbers having been exported to industrialized nations. Collection pressure should have been reduced through listing under CITES; however, a CITES certificate was issued to import

1,500 individuals to the United States (Proudlove and Romero 2001). Three other primary threats to the species were identified by Brown and Abell (2005): changes in hydrology of the small rivers feeding the caves; increasing human population; and associated deforestation (Kamdem Toham *et al.* 2006). Since 2003, with the attenuation of the political situation in D. R. Congo and the rehabilitation of the Matadi-Kinshasa road, there has been a significant influx of rural people towards Mbanza-Ngungu. Consequently, land use has increased around Mbanza-Ngungu for buildings as well as agriculture. One cave is now used as a quarry, with consequential loss of the *Caecobarbus* population (Leleup 1956; Poll 1956; and see above), and others are at risk of collapse due to human disturbance (Kimbembi 2007; Moelants 2009). Agriculture is practiced preferentially in the valleys near to the caves but may also occur on the hillside slopes surrounding and covering the caves, leading to increased erosion and landslides. In the past, these areas were covered with lowland rainforest and secondary grassland (White 1986), limiting erosion. Further research and conservation initiatives in the field are necessary if this unique species of fish is to survive.



Land use around the entrance of the 'Grotte de Lukatu', with subsequent landslides visible (9 March 2007). The entrance to the cave is directly below the largest trees in the middle of the photograph. © ROYAL MUSEUM FOR CENTRAL AFRICA



Species in the spotlight

A unique species flock in Lake Tana – the *Labeobarbus* complex

Getahun, A.¹

Lake Tana, in Ethiopia, and the rivers that drain into it, are home to a unique, endemic species flock belonging to the cyprinid genus *Labeobarbus*. The lake, which has a surface area of 3,150km², is the largest in Ethiopia. It is situated in the north-western highlands at an altitude of approximately 1,800m. It was formed during the early Pleistocene when a 50km-long basalt flow blocked the course of the Blue Nile near its source (Mohr 1962; Chorowicz *et al.* 1998). Today, several rivers drain into Lake Tana, which itself forms the headwaters of the Blue Nile – the only river flowing out of the lake, contributing more than 80% of the total volume of the Nile River at Khartoum, Sudan.

The wetlands and floodplains that surround most of the lake form the largest wetland area in Ethiopia and are an integral part of the complex Tana ecosystem. The wetlands to the east of the lake serve as breeding grounds for *Oreochromis niloticus* (Nile tilapia) and *Clarias gariepinus* (North African catfish), both of which are important for the lake fisheries (Vijverberg *et al.* 2009).

There are 28 species of fish in Lake Tana, of which 20 are endemic to the lake and its catchments (Vijverberg *et al.* 2009). The fish fauna includes representatives of the genera *Oreochromis*, *Clarias*, *Labeobarbus* (i.e., the ‘large African barbs’), *Barbus* (i.e., the ‘small *Barbus* group’; see De Weirtd and Teugels 2007), *Garra*, *Varicorhinus* and *Nemacheilus*. The population of *O. niloticus* in Lake Tana was described as a separate sub-species, *Oreochromis*



Labeobarbus macrophthalmus is a benthopelagic species that forms an important component of the Lake Tana fishery. © LEO NAGELKERKE

niloticus tana. Two exotic species, *Gambusia holbrooki* and *Esox lucius*, were reported to have been brought from Italy during the late 1930s and introduced into the lake (Tedla and Meskel 1981); there is, however, no trace of these fishes from the lake in recent times.

The *Labeobarbus* species flock

The Cyprinidae are the most species-rich family in the lake, represented by four genera, *Barbus*, *Garra*, *Labeobarbus* and *Varicorhinus*. Within the *Labeobarbus* is a unique complex of 17 species (Getahun and Dejen in prep.). It is thought that the lake is able to support such a large number of closely related species because, when it first formed, it offered several new habitats that may have promoted adaptive radiation among the original colonising species, and it has since remained isolated due to the Tissisat Falls, located 30km downstream from the outflow of the lake. Most interesting is the speed of evolution for so many new species, as historical evidence suggests the lake dried out completely as recently as 16,000

years ago (Lamb *et al.* 2007), meaning the evolution of the *Labeobarbus* species complex may have taken fewer than 15,000 years (Vijverberg *et al.* 2009).

Eight of the *Labeobarbus* species are piscivores, and most of them periodically migrate into the rivers for spawning. *L. intermedius* and *L. tsanensis* are abundant in the inshore habitats and are the predominant species at the river mouths. *L. tsanensis* and *L. brevicephalus* are the dominant species offshore.

Spawning behaviour

Limited surveys around Lake Tana indicate that the Ribb, Megech and Dirma Rivers and their tributaries provide ideal breeding grounds for these species in the northern and eastern parts of the lake. Five species were found to migrate from Lake Tana up both the Megech and Dirma rivers to spawn (Anteneh 2005), although slightly greater numbers migrate up the Megech, which has more tributaries with gravel beds, and a slightly higher dissolved oxygen content. Three categories of spawning behaviour are

¹ Department of Biology, Addis Ababa University, Ethiopia

observed (Anteneh 2005), obligate river spawners, lake spawners and generalists (spawning in both the lake and its tributary rivers).

At least seven species spawn in the headwaters of the main rivers draining to the lake. As yet, there is no evidence of river-specificity, but this cannot be discounted. After a brief pre-spawning aggregation at the river mouths, the adults migrate upstream in July and August, at the onset of the rainy season. Final maturation and spawning occur in the tributaries of the major rivers, or possibly in gravel reaches in the main channels. After spawning, the adults return to the lake for feeding until the next cycle of breeding. Highly oxygenated water and gravel beds are important for development of the eggs and larvae. Deposition of eggs in gravel beds prevents them from being washed away, and clear water is required to ensure they are free of sediments that might obstruct the diffusion of oxygen.

The juveniles start to return to the lake in September and October as flows reduce, where they feed and grow to sexual maturity. There is good evidence that, during their return to the lake, the juveniles may remain in the pools of the main river segments for an extended period, probably until the next rainy season, at which time they will be carried into the lake.

The lake fisheries

The lake fishery is clearly very important to the local population, employing more than 3,000 people in fishing, marketing, and processing (Anteneh 2005). Traditionally, the main fishery has been a subsistence reed boat fishery targeting a range of species, sometimes including the *Labeobarbus* species. This was conducted throughout the lake until the 1980s; since then it has been replaced in many areas by other methods. The fishery remains important in the more remote areas of the lake, with the catch being sold at small markets or used for household consumption. It mainly

employs gillnets, and the main target species is Nile tilapia (*O. niloticus*). However, the reed boat (*tankwa*) fishermen also use hooks and lines, and traps, as well as spears to catch catfish.

In 1986, motorised boats and nylon gill nets were introduced as part of the Lake Tana Fisheries Resource Development Program (LTFRDP) (Anteneh 2005). Data collected from all commercial fisheries recognizes only four species groups: *Labeobarbus* spp., African catfish (*C. gariepinus*), Nile tilapia (*O. niloticus*) and beso (*Varacorhinus beso*). This fishery mainly supplies larger markets, using 100m long gillnets. There are around 25 motorised fishing boats, most of which land their catch in Bahir Dar, the main town on the shore of Lake Tana. The fishery is, however, expanding to all 10 Woredas (districts) bordering the lake, including the Gorgora area (on the northern shore).

Total annual catches increased from 39 tonnes in 1987 to 360 tonnes in 1997 (Wudneh 1998). However, the catch per unit effort for the commercial gill net fishery targeting *Labeobarbus* species dropped by more than 50% over the period 1991 to 2001 (de Graff *et al.* 2004).

The same authors have reported a 75% decline (in biomass) and 80% (in number) of landed fish of the species of *Labeobarbus* (*L. acutirostris*, *L. brevicephalus*, *L. intermedius*, *L. macrophthalmus*, *L. platydorsus* and *L. tsanensis*) in the southern gulf of Lake Tana. The most plausible explanation for the decline is recruitment overfishing by the commercial gillnet fishery (de Graff *et al.* 2004), and poisoning of the spawning stock in rivers using the crushed seeds of 'birbira' (*Milletia ferruginea*) (Nagelkerke and Sibbing 1996; Ameha 2004).

The commercial gill net fishery for species of *Labeobarbus* is highly seasonal and mainly targets spawning aggregations, as more than 50% of the annual catch is obtained in the river mouths during August and September. There is also a chase and trap fishery based in the southern part of the lake, and longlines, cast nets and traps are occasionally used but contribute little to the total fish catch.

Threats to Lake Tana and its *Labeobarbus* species

Overfishing

Although a fishery policy has been developed both at federal and regional levels, it is not effectively



Fishermen cast their lines from papyrus boats ("tankwas") on Lake Tana in northern Ethiopia. Behind them lies the source of the Blue Nile. Near Bahir Dar, Ethiopia.

© A. DAVEY

implemented. Lakes and rivers are, unofficially, considered to be resources that are freely available to everyone. There are still many illegal, unregistered fishermen exploiting the fish resources, and there is little regulation of fishing gears. As reported above, this has led to overfishing of *Labeobarbus* in some parts of the lake, especially in the south around the town of Bahir Dar.

Habitat disturbance

As seasonal flooding recedes, many people use the shores of the lake for 'floodplain recession agriculture'. Human encroachment on the wetlands increases every year, with the subsequent depletion of emergent macrophytes through harvesting and burning, while there is an expansion of submerged macrophyte stands in other areas.

Over the last 15 years, deforestation has become very widespread, facilitating conditions for soil erosion, resulting in sediments draining into the lake and smothering upstream spawning areas. The soil loss rate from areas around the lake is between 31 and 50 tonnes per hectare per year (Teshale *et al.* 2001; Teshale 2003). These huge deposits of sediment into the lake have led to a reduction in the lake's area, a drop in water levels, and a loss of water holding capacity. This reduction in the water level has resulted in fragmentation of the available aquatic habitat, especially around shores. Some of the exposed land is now used for cultivation and excavation of sand.

Water pollution

Run-off from small-scale agriculture around the lake is bringing agricultural fertilizers, pesticides (including DDT), and herbicides into the lake. The use of these agricultural products by farmers is still relatively limited; however, a lack of effective regulation on their use presents a potential threat to water quality in the lake. Other chemicals, such as 'birbira' (*Milletia*



Many of the *Labeobarbus* species migrate up the rivers flowing into Lake Tana to spawn in gravel beds, such as seen here in the Gumara River. © LEO NAGELKERKE

ferruginia) seed powder (used as an ichthyocide; see above), may also pollute the lake and kill the aquatic fauna, including *Labeobarbus* species. Domestic waste water from the town of Bahir Dar is, in most cases, discharged directly into Lake Tana – the development of an appropriate sewage system could solve or mitigate these pollution threats.

Water abstraction and impoundment

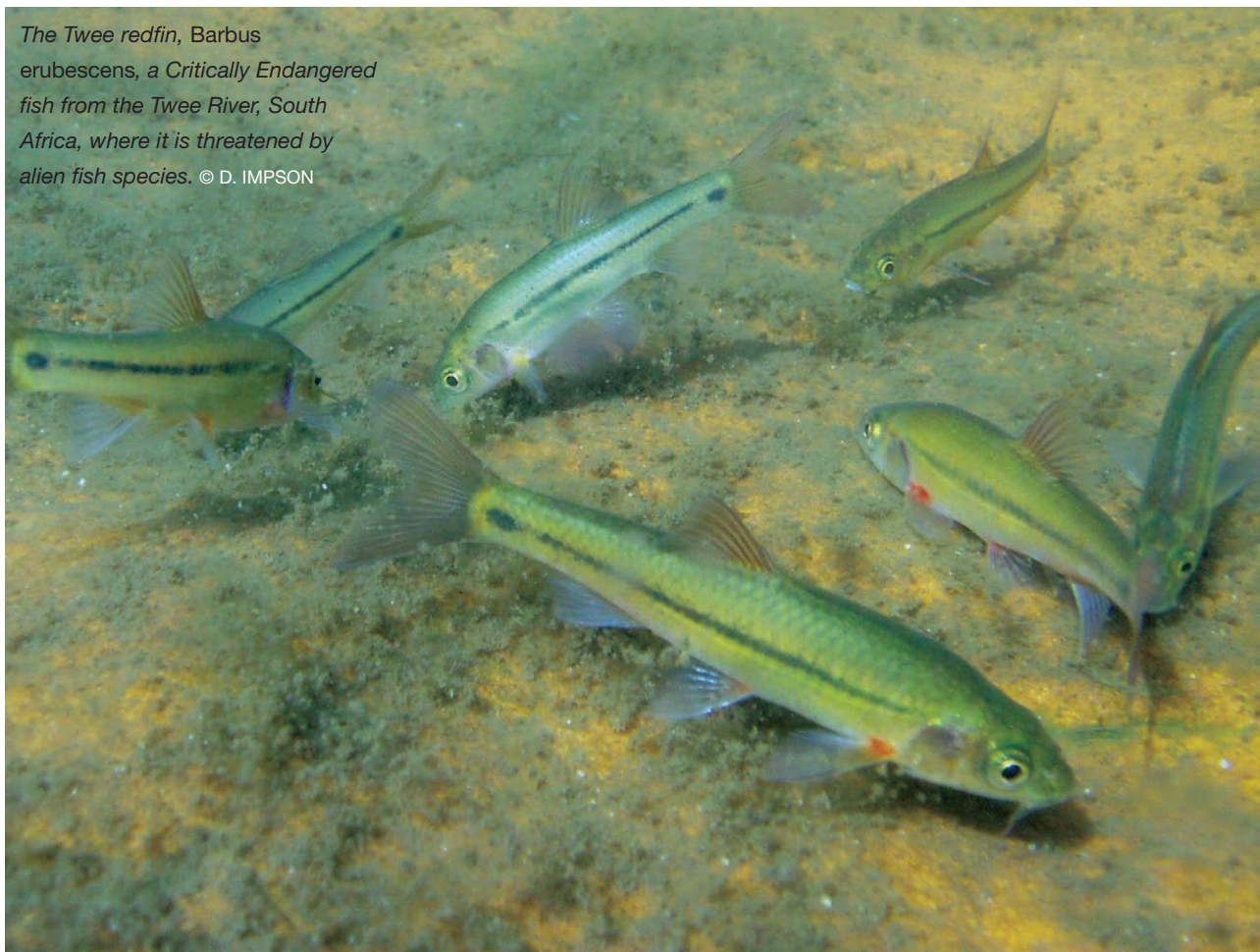
Water abstraction occurs at some points around the lake as a result of privately run, small-scale irrigation projects. However, because the Lake Tana and Beles sub-catchment is considered a growth corridor by the federal and regional governments, there are several other dam and irrigation projects under consideration or being implemented. These include the Tana Beles inter-basin water transfer project, and the Koga, Ribb, Megech, Gilgel Abay and Gumara dams and irrigation projects. Some of these are intended to impound the lake's tributaries to store water; some to pump water through tunnels from the lake to a hydropower facility before discharging the water into the Beles River; and some to pump water directly from the lake for irrigation purposes. These projects may lower the water level and quality in Lake Tana and its tributaries, with

subsequent impacts to biodiversity. As reported above, many species of *Labeobarbus* undergo spawning migrations that, without effective measures to allow passage past newly constructed dams, may be blocked, potentially leading to the extinction of this unique flock of cyprinids. Environmental impact assessment (EIA) studies have been conducted for many of these projects, so it is hoped that the recommended mitigation measures and the management plans suggested will be strictly followed and implemented.

Lack of information and institutional capacity

Comprehensive scientific studies on the biology, behaviour, and ecology of the different species of *Labeobarbus* are still lacking. This makes it difficult to recommend mitigation measures in some of the EIA studies and follow up with implementation. In addition, the implementing agencies for EIAs still lack the strength and capacity to enforce and implement any recommendations made. The development of a Lake Tana sub-basin authority is an option for solving this problem. Concerted action by all stakeholders is required if the unique fish fauna of this lake is to be conserved for the future.

The Twee redfin, *Barbus erubescens*, a Critically Endangered fish from the Twee River, South Africa, where it is threatened by alien fish species. © D. IMPSON



Species in the spotlight

The Twee River redfin – a Critically Endangered minnow from South Africa

Skelton, P.H.¹

The Twee River redfin (*Barbus erubescens* Skelton) was described in 1974, following an investigation that included extensive field observations. The species is named for the bright reddish breeding dress assumed by spawning males, with females being less intensely coloured. The common name indicates that the species' distribution is restricted to one tributary system of the Olifants River in the Cedarberg Mountains of the Western Cape, South Africa. This tributary system includes the Twee and some of its affluents, the

Heks, Suurvlei and Middeldeer rivers.

At the time of discovery, only one other fish species was known to be indigenous to the Twee River, and both species were isolated by a vertical waterfall of about 10m, located close to the confluence of the Twee and Leeu rivers. This other indigenous fish is a species of South African *Galaxias*, formerly named as the Cape galaxias (*Galaxias zebratus*); however, more recently it has become evident that a number of populations of *G. zebratus* might represent distinct species. The population of *Galaxias*

in the Twee River is one of these distinct populations. The Cape galaxias is currently assessed in the IUCN Red List as Data Deficient, due to the taxonomic confusion associated with the species complex. Below the falls several other indigenous freshwater fish species are found, most of them endemic to the Olifants system. One of these species, *Barbus calidus*, is the sister species of *B. erubescens* (i.e., it is the phylogenetically most closely related species to *B. erubescens*). *Barbus calidus*, the Clanwilliam redfin, itself classified as Vulnerable, due to threats

¹ South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown 6140, South Africa

from invasive species, and habitat degradation caused by agriculture, is discussed below.

Much has been learnt about the Twee River redfin since its original description. In common with a disproportionately large number (80%) of barbine minnows from the temperate reaches of southern Africa, the Twee River redfin is tetraploid (that is, it has four sets of each chromosome), with 100 chromosomes in total. Its most distinctive external character is the high number of branched anal fin branched rays – six or, more usually, seven – more than any other African barbine species. It has several other distinctive features, such as small scattered nuptial tubercles on both sexes, two pairs of well developed mouth barbels, and an unbranched ray in the dorsal fin that shows either incipient or vestigial serrations.

The species' breeding behaviour features males congregating and forming a dense, swarming, nuptial school against rock surfaces to which individual breeding females are attracted and enticed to spawn over cobbles or rock crevices with several pursuant males. This occurs in spring or early summer (October to December) when streams are swollen by frontal rains. The species is a 'broadcast spawner' (releasing the gametes into the water) and does not practice any form of parental care. It can live for up to five or six years. The species feeds on drifting insects and other invertebrates or from rocks and other benthic surfaces.

Conservation concerns

When first discovered, the species was common and widespread in the tributary system – with larger adults occupying open water habitats in pools and runs, and juveniles shoaling along marginal zones. Since the 1970s, the population has declined markedly and is absent from large sections of its former range. The reasons for this decline are several, including



The Twee River in the Cedarburg Mountains, the Western Cape, South Africa.

© SAIAB/P. SKELTON

likely impacts from agricultural developments (riparian fruit orchards) impacting both water quality and quantity, and alien invasive fish species. The first alien fish species to be recorded was a South African anabantid, the Cape kurper (*Sandelia capensis*) which, although not a large fish, is widespread throughout most of the tributary and an avid predator on small fishes and invertebrates. The Clanwilliam yellowfish (*Labeobarbus capensis*), a large cyprinid of the Olifants River system, was introduced to the Twee River above the barrier waterfall by Nature Conservation authorities seeking to conserve that species in the face of threats from other introduced species! The Clanwilliam yellowfish is found mainly in the downstream reaches of the Twee and, although its precise impact is not known, it is a predator and grows much larger than the Twee River redfin. Bluegill sunfish (*Lepomis macrochirus*), a North American centrarchid species, and another predator on small fishes and invertebrates, have also invaded the system. Rainbow

trout (*Oncorhynchus mykiss*) have been recorded from the Twee River but are not common.

The Twee River has been extensively surveyed on several occasions to determine the conservation status of the redfin and the *Galaxias* species. The decline in their populations is of great concern, as the tributary system is restricted in size and subject to increasing agricultural pressures as well as the invading alien species. There are few natural sanctuary reaches and, unless determined action to remove the alien species is taken, the fate of the threatened indigenous species might be sealed forever. Two things are essential for conservation action – political will by the authorities to do what they must in the face of contrary perceptions by the public (who, for example, may support introductions of species for fishing), and a properly informed public, especially the local landowning public. If those elements are in place, the survival of these and other indigenous species in South Africa might be secured.



Species in the spotlight

Tilapia in eastern Africa – a friend and foe

Nyingi, D.W.¹ and Agnès, J.-F.^{2,3}

Tilapia form the basis for much of the aquaculture industry that is important to so many people across Africa. Its success as a commercially fished and cultured species is attributed to several characteristics: its ability to establish and occupy a wide variety of habitats; its wide food spectrum from various trophic levels (Moriarty 1973; Moriarty and Moriarty 1973; Getachew 1987; Khallaf and Aln-Na-Ei 1987); high growth rate; large maximum size; and high fecundity (Ogutu-Ohwayo 1990). All of these factors accord *O. niloticus* with great competitiveness over other tilapia, which can become a problem where they have been introduced, or escaped, to areas outside of their native range. Aquaculture is also one of the most common sources of invasive species in many parts of the world, and the famous Nile tilapia (*Oreochromis niloticus niloticus*), in particular, is recognised as a significant threat to other native fish species. The popularity of tilapia in Africa is indicated by their high market value and, consequently, the high fishing pressure in most lakes and rivers (Abban *et al.* 2004; Gréboval *et al.* 1994).

The Nile tilapia

Eastern Africa is endowed with six sub-species of Nile tilapia: *O. niloticus niloticus* (Linnaeus, 1758), originally from the White Nile Basin but now widely introduced elsewhere; *O. niloticus eduardianus* (Boulenger, 1912) in Lakes Edward, Kivu, Albert and George; *O. niloticus vulcani* (Trewavas, 1933) in Lake Turkana; *O. niloticus sugutae* Trewavas, 1983 in the Suguta



The Nile tilapia, *Oreochromis niloticus*, (LC), a highly favoured species for aquaculture. © LUC DE VOS

river basin; *O. niloticus baringoensis* Trewavas, 1983 in Lake Baringo; and one other recently discovered (Nyingi *et al.* 2009), but still undescribed subspecies from the Lake Bogoria Hotel spring near the Lobo swamp, between Lake Baringo and Bogoria in the Kenyan Rift Valley.

Oreochromis niloticus was introduced to Lake Victoria for the purpose of improving tilapia fisheries in several phases between 1954 and 1962, due to decreasing stocks of native tilapia species *O. esculentus* and *O. variabilis*. *Oreochromis niloticus* rapidly colonized the entire lake and by the end of the 1960s was well established in inshore habitats (Mann 1970; Ogutu-Ohwayo 1990; Twongo 1995). It is thought that the introduction of *O. niloticus* caused the disappearance of the two native tilapia species (*O. variabilis* and *O. esculentus*) from the main part of the lake – *O. esculentus* having once represented the bulk of the fisheries in the lake. It was initially hypothesised that hybridization with subspecies of *O. niloticus* was the main driver of the decline of *O. variabilis* and *O. esculentus*, because *O. niloticus* is well known for its ability to hybridize

with other tilapiines (Welcomme 1988; Mwanja and Kaufman 1995; Rognon and Guyomard 2003; Nyingi and Agnès 2007). However, the competitive superiority of *O. niloticus* subspecies over the two former native species was demonstrated to be the most likely contribution for their extinction (Balirwa 1992; Agnès *et al.* 1999).

Tilapia and aquaculture

The greatest limitation to development of aquaculture in eastern Africa has been financial, with all new activities in the sector initiated and dependent on foreign financing. In Kenya, the government has stepped up efforts to promote aquaculture under the Economic Stimulus Programme. The government's intention has been to highlight fish farming as a viable economic activity in the country by raising the income of farmers and other stakeholders in the fishing industry. The project, worth 1,120 million Kenya shillings (EUR 10.67 million) was launched by the Ministry of Fisheries Development to construct 200 fish ponds in 140 constituencies by June 2013. According to existing plans, each constituency is geared to receive 8 million Kenya shillings (EUR 70,000) for ponds. In Kenya, the Sagana Fish farm, under the Fisheries Department, provides fingerlings for warm water freshwater species. So far, the centre has been efficient in provision of seed fish to farmers and in research and production of suitable feed. Despite these advances, considerable investment is still needed to ensure the provision of suitable species for

¹ National Museums of Kenya, P.O. Box 40658 Nairobi, 00100, Kenya

² Département Biologie Intégrative, CNRS UMR 5554, Université de Montpellier II CC 63 Place Eugène Bataillon F- 34095 Montpellier Cedex 5, France

³ Institut de Recherche pour le Développement, 213 rue La Fayette 75180 Paris Cedex 10, France

the various regions, ensuring development of the industry.

With the government supporting new initiatives, the greatest challenge is to identify a suitable species that will ensure high yield, while also safeguarding native species from the impacts of introduced aquaculture species. Unfortunately, in Africa the search for suitable species for aquaculture has often disregarded potential impacts on the native species. The most important culture species are still mainly taken from the wild, and populations are often translocated to basins far beyond their native range, potentially bringing closely related but formerly isolated species or populations into contact with each other. Where there has been inadequate research and planning, an introduced cultured species may directly compete with native species, or may hybridize with them, as noted above for *O. niloticus*

when it was introduced to Lake Victoria. Unfortunately, *O. niloticus* has, in many cases, been the species of choice for aquaculture, therefore leading to further problems of competition and hybridisation.

Oreochromis leucosticus was originally known from drainages near the border of Uganda and the D. R. Congo, specifically Lakes Edward, and Albert, and associated affluents. However, it was introduced to Lake Naivasha in Kenya in 1957 (Harper *et al.* 1990). About 150km away from Lake Naivasha is Lake Baringo, in the Kenyan Rift Valley, home to the endemic subspecies of Nile tilapia, *O. niloticus baringoensis*. Nyingi and Agnèse (2007) note that *O. niloticus baringoensis* share genetic characteristics of *O. leucosticus*, suggesting that *O. leucosticus* might have been introduced also to Lake Baringo, with some subsequent transfer of genetic material through hybridization with *O. niloticus*

baringoensis. Even though impacts of the possible introduction of *O. leucosticus* are still unknown, introductions of tilapiines continue to be made within the region, either intentionally or accidentally through escape from culture ponds. Such issues are a clear indication of a failure of well-defined policies, or implementation of the existing regulations, for the management of natural fisheries resources in Kenya. Through lack of awareness, and desperation to increase yield, fish farmers are breeding alien species of tilapia that could naturally hybridize in a similar manner – as seems to have occurred in Lake Baringo. Consequently, native species may be lost in several parts of eastern Africa, as already observed in Lake Victoria.

As noted above, a new subspecies of *Oreochromis* was recently discovered from the Lake Bogoria Hotel spring near the Lobo swamp. This population was formerly



Fish farms, such as this one in Malawi, represent an important source of food and income for people throughout Africa. However the traits that make species such as *Oreochromis niloticus* suitable for aquaculture mean that they pose a significant threat to local species should they escape. © RANDALL BRUMMETT

thought to have been introduced, but genetic and morphological analysis demonstrated its originality (Nyingi 2007; Nyingi and Agnès 2007). The main body of the Loboï swamp acts as a physical and chemical barrier between the warm water springs (where the new sub-species is found) that flow into the swamp, and the Loboï River, which drains from it to Lake Baringo. The swamp has a significantly low dissolved oxygen level (around 4% saturated dissolved oxygen, compared to around 60% in the springs and groundwater discharges), which is a consequence of high oxygen consumption during aerobic decomposition of detritus from macrophytes in the swamp (Ashley *et al.* 2004).

The new apparent sub-species from the springs draining into the Loboï swamp offers interesting new possibilities for aquaculture development, if managed properly. The sub-species inhabits high temperatures (approximately 36°C) and may have developed hypoxic resistance mechanisms as dissolved oxygen levels may also be low. This sub-species may also have developed special mechanisms to regulate its sex-ratio, since sex determination is known to be influenced by high temperatures (Baroiller and D'Cotta 2001; Tessema *et al.* 2006). Therefore, the new sub-species may be a model for the study of sex determination in *Oreochromis*.

However, the population from the Loboï swamp and associated rivers is under threat from human encroachment. The Loboï swamp itself has receded by around 60% over the last 30 years due to water abstraction for irrigation since 1970 (Ashley *et al.* 2004; Owen *et al.* 2004). In addition, periodic avulsions have caused changes in the course of rivers in this region. The most recent was during the El Niño-induced heavy rains of 1997, which caused changes in the courses of the Loboï and Sandai Rivers. The Sandai River now partly flows into Lake Baringo and partly to Lake Bogoria.

“...many challenges still lie ahead, and it will be critical to reinforce policy and management action with programmes of public awareness and education.

Similarly, the Loboï River, which used to feed Lake Baringo, has changed its course and now flows to Lake Bogoria. These changes of flow were also due to intensive agricultural encroachment by local farmers leading to weakening of the river banks (Harper *et al.* 2003; Owen *et al.* 2004). This situation is not unique to the Loboï swamp but is common in almost all lakes and river systems in Kenya. The National Environment Management Authority in Kenya has been actively involved in ensuring rehabilitation of the Nairobi River, which had been greatly impacted due to solid waste disposal, sewage, run-off from car washes, and other human activities within the city and suburbs of Nairobi (Nzioka 2009). The success of this project is a clear indication that the National Environment Management Authority is able to protect hydrological systems in Kenya. There is, however, a need to replicate these successes elsewhere.

Management of tilapia fisheries

A significant challenge has existed where freshwater resources are shared by different countries. For example, fisheries management of Lake Victoria was highly compromised in the early 1960s following independence of the countries bordering the lake (Kenya, Uganda and Tanzania), when they adopted different fishing regulations based on the stocks targeted for exploitation (Marten 1979). These different regulations and priorities for exploitation have made it difficult to manage the lake as a complete

ecosystem (Ntiba *et al.* 2001; Njiru *et al.* 2005). Ironically, this lack of management has contributed to declines in the introduced *O. niloticus*, which was previously responsible for the decline in the native sub-species (see above). Stock analyses for *O. niloticus* surveys of 1998 to 2000 and 2004 to 2005 show that artisanal catches were dominated by immature fish, most being below the legally allowed total length of 30cm (Njiru *et al.* 2007). The paucity of mature individuals observed in commercial catches (Njiru *et al.* 2005) may be partly due to the increased numbers of introduced Nile perch (*Lates niloticus*) (Lubovich 2009), but is also probably due to overexploitation. In the past, this overexploitation has been possible because of the laxity and weakness in enforcement of the Fisheries Act of 1991, which is highly explicit on the manner in which fishing activities should be conducted. Significant efforts are being made to address the challenge of providing a comprehensive, consistent set of policies and programs for sustainable management of the lake's fishery resources. For example, in March 2007, Kenya, Tanzania, and Uganda adopted a Regional Plan of Action for the Management of Fishing Activity; this plan called on the respective governments to review their national policies and develop a harmonized fishing framework (LVFO 2007; Lubovich 2009). Nevertheless, many challenges still lie ahead, and it will be critical to reinforce policy and management action with programmes of public awareness and education.



Species in the spotlight

Forest remnants in western Africa – vanishing islands of sylvan fishes

Moritz, T. ¹

A significant part of western Africa is covered by differing types of savanna that are drained by a few large rivers, like the Niger, Volta and the Senegal. The vegetation reflects climatic conditions including a cycle of dry and wet seasons. Closer to the coast, partly bordered by the Guinean highlands (from the highlands of the southern Fouta Djallon in south-eastern Guinea, through northern Sierra Leone and Liberia, to north-western Côte d'Ivoire), the climate is more humid, allowing different types of forest to grow. These forests are inhabited by animals closely resembling or even identical to those of the central African forests. Thus, many sylvan (forest dwelling) fish species and species-groups find their most westerly distributions within the western Africa coastal forests. A number of these westerly sub-populations may be discrete sub-species, or separate species within species complexes, showing distinct colour morphs, or other unique features.

The high number of unconnected coastal rivers in western Africa is thought to have promoted these speciation processes, which have led to noticeably high levels of endemism, such as for characids, barbs and cichlids. Furthermore, several remarkable fishes, which are sometimes called 'relict' species, occur in the Guinean regions. These species belong to phylogenetically old groups previously represented by more numerous and widespread species but, following evolutionary events, now represented by only a few, often locally restricted



Lokoli swamp forest in southern Benin. This small forest fragment serves as one of the last refuges for many forest dwelling species. © T. MORITZ

species. Examples include the fourspine leaf-fish (*Afromonandus sheljuzhkoii*) and the African leaf-fish (*Polycentropsis abbreviata*), with their closest relatives in Asia and South America, and the enigmatic denticle herring (*Denticiceps clupeoides*), which is the only extant representative of the family Denticipetidae, the sister group of all other clupeomorphs. The climatic conditions of the Guinean region not only provide good conditions for forest ecosystems, but also support a more diverse and reliable agriculture compared with the Sahelo-Sudan region. This promotes better livelihood opportunities which, in turn, lead to increased population densities and a greater demand for land. With increased demands for agricultural land, deforestation continues, leaving only forest fragments in some areas.

Lokoli forest – a refuge

An exemplary forest remnant is the Lokoli swamp forest in southern Benin. This small, (approximately 500ha) piece of forest is permanently flooded by a network of channels from the Hlan River, an affluent of the Ouémé River. It is approximately 20km east of Bohicon and 100km north of Cotonou and can only be crossed by boat. The forest is densely vegetated with high tree density, and the tree cover is usually closed above the channels. Most channels are less than a metre wide and are only navigable using small dugout canoes. Water depth varies by less than one metre within a year, and is usually around 1 to 2.5 metres. The water has a dark brown colouration due to leaf litter decomposition, a moderate acidic pH of 6 to 7 and a temperature of around 26°C. The channel substrate is predominantly

¹ Deutsches Meeresmuseum, Museum für Meereskunde und Fischerei – Aquarium, Stralsund, Germany



Barboides britzi, one of Africa's smallest freshwater fish, is a newly described species endemic to Lokoli forest in Benin.

© T. MORITZ

sand, with small patches of gravel where the current is stronger; most places have a mud and leaf litter layer of variable depth.

The Lokoli forest serves as one of the last refuges for forest dwelling animals in the Dahomey Gap, including pangolins, flying squirrels and the red-bellied monkey (*Cercopithecus erythrogaster*), which is endemic to Benin. While herpetological surveys have shown relatively few exclusive forest species of reptiles and amphibians (Rödel *et al.* 2007; Ullenbruch *et al.* 2010), the situation for fishes is very different. Despite a direct connection to the main channel of the Ouémé River, fishes of the Lokoli are, to a high degree, typical forest species, otherwise known from the coastal forested rivers of the Niger Delta and the connected network of lagoons parallel to the coast. The reedfish (*Erpetoichthys calabaricus*), butterfly fish (*Pantodon buchholzi*), and elephant nose fish (*Gnathonemus petersii*) in Lokoli are at the most western points of

their ranges (Montchowui *et al.* 2007; pers. obs.). The cyprinid genus *Barboides*, consisting of two of the smallest African freshwater species, is also at the most westerly point of its range, with *B. britzi* endemic to the Lokoli forest itself. This miniature fish becomes sexually mature at a smaller size than any other freshwater fish in Africa, at 12.6mm standard length (Conway and Moritz 2006). It is likely that more fish species, especially of smaller body size, await discovery in such unusual habitats. For example, the bottom dwelling distichodontid *Nannocharax signifer* was only recently described, from a small affluent of the Lokoli forest (Moritz 2009).

Impacts to this small forest fragment are significant, with extensive clearance for agriculture along the forest margins. Within the forest itself, despite religious taboos prescribing at least some regulations for hunting, the bush meat trade remains an important source of income and bush meat

is openly sold along the main road leading to Cotonou. Palm wine and secondary products are produced by cutting off the tops of the palm *Raphia hookeri*, with evident impacts to the plants themselves. As a result, the abundance of this formerly dominant palm has been significantly reduced through over-harvesting. The forest flora has been further impacted through introduction of alien species such as the taro (*Colocasia esculenta*), an introduced plant valued for its root tubers, which is widely planted, even within clearings in the swamp forest.

Forested coastal rivers, although more spacious than some of the Guinean forested rivers, face similar threats. In addition to pollution, which is heavily impacting certain areas, the primary problem is, once more, habitat degradation due to expanding agriculture. The Iguidi River at the border of Benin and Nigeria provides a good example. The course of this small coastal river is clearly visible on aerial or

satellite images, due to its bordering gallery forest. The forest stands out in stark contrast to neighbouring, and continuously expanding, fields. The Iguidi River flows in a north-south direction, starting out as a small forested stream that develops into a swamp. As is typical for a forest stream, the water is brown to dark brown in colour, although the pH is not especially acidic, at 6.5 to 7.5; water temperature is commonly 26 to 29°C; and conductivity is low at 50 to 65µS (Moritz 2010). Despite the river's low salt content, fishes characteristic of brackish environments are also present, such as the freshwater pipefish of the genus *Enneacampus*, and the sleeper goby (*Eleotris daganensis*). The majority of fishes from the Iguidi are, however, typically freshwater, forest-dwelling species such as the dotted catfish (*Parauchenoglanis monkei*), the small distichodontid, *Neolebias ansorgii*, and the cryptic mormyrid (*Isichthys henryi*). This small river represents an outpost of the Lower Guinean forest, and holds the most westerly distributions of several Lower Guinean species, such as the aforementioned *Neolebias ansorgii*, the Niger tetra (*Arnoldichthys spilopterus*), and the catfish *Schilbe brevianalis* (Moritz 2010). Furthermore, the Iguidi River is the type locality for the rare, miniature *Barbus sylvaticus*, the even smaller *Barboides gracilis*, and the denticle herring (*Denticeps clupeioides*), all of which are assessed as Vulnerable or Endangered.

In conclusion, at first glance, small forest fragments seem to be of minor importance for the conservation of forest dwelling species – often being too small to sustain endemic species, or even too small to harbour a discrete population of a sylvan species. Many inhabitants of forest remnants are, therefore, non-specialist or even savanna species. A closer view of the fishes, however, reveals a quite different picture. Forest remnants, such as

the Lokoli, can sustain a number of small endemic species. What is more important, however, is the complexity of biodiversity that is found and that needs to be conserved. Forest fragments and remnants of gallery forests are focal points of habitat complexity, edge effects and ecological interactions – and as outposts for species

distributions, they may be of high importance for maintaining genetic variability within a species and in ongoing evolutionary processes. Therefore, despite their small size, forest fragments deserve greater focus within conservation plans; their inclusion will help to ensure preservation of biodiversity in all its forms.



The freshwater butterflyfish, *Pantodon buchholzi* (LC), a widespread species in Africa, reaches the most westerly point of its range in Lokoli forest, Benin. This species is capable of jumping out of the water to search for insects or to escape from predators. It is not a glider, but a ballistic jumper, with tremendous jumping power. © T. MORITZ



Species in the spotlight

Cauldrons for fish biodiversity: western Africa's crater lakes

McGregor Reid, G.¹ and Gibson, C.¹

Globally, crater lakes are comparatively rare, usually small and specialised freshwater habitats formed in geological depressions, such as the Ojos del Salado in the Andes mountains, bordering Argentina and Chile – probably the highest altitude permanent lake of any description (68°32'W, 27°07'S, elevation 6,390m, diameter 100m, depth perhaps 5 to 10m). Crater lakes are well represented in tropical Africa, especially in the Guinean rainforest zone of Cameroon, where there may be 36 or more. The entire region is a celebrated 'biodiversity hotspot' for both lacustrine and riverine fishes (Reid 1989; 1996; Teugels *et al.* 1992; Schliewen 2005; Stiassny *et al.* 2007). Contemporary general studies on the world's crater lakes address important topics such as: lake formation; physical, chemical, geological, geographical and biological evolution; paleoecology; historical biotic colonisation; and recent ecology – including the assessment of conservation status and threats to the survival of the contained habitats and species. The potential for (and impacts from) human use is studied, including water supply, agriculture, fisheries and also recreation and ecotourism – such lakes often being scenic locations.

Crater lakes everywhere may contain a substantial number of endemic fishes and other aquatic and amphibious taxa. Among African fishes endemic to craters, small phyletic and trophic assemblages of species and genera representing the family Cichlidae



Stomatepia mongo, a Critically Endangered cichlid endemic to Lake Brombi Mbo, Cameroon. © OLIVER LUCANUS/BELOWWATER.COM

have attracted much international scientific attention. Crater lake cichlids, their taxonomy, phylogeny and ecology were documented early on in Cameroon, notably in Lake Barombi Mbo (Trewavas 1962; Trewavas *et al.* 1972; see below); and they continue to be discovered – for example, the recently documented 'flock' of eight new species of *Tilapia* from Lake Bermin or Beme (5°9'N, 9°38'E; diameter around 700m, depth around 16m, and age probably far less than 1 million years) (Stiassny *et al.* 2002; Schliewen 2005). Such Cameroonian assemblages are often regarded as small-scale tilapiine counterparts to the better known large haplochromine and other cichlid 'species flocks' of the East African Great Lakes (Klett and Meyer 2002; Salzburger and Meyer 2004).

Formation

Whatever the location, all craters on earth are formed either by *impact* of extraterrestrial bodies or

by *vulcanism* (Decker and Decker 1997; Sigurðsson 1999). They are often visible in photographic, radar and other imagery taken from space (Hamilton 2001).

Impact crater lakes

The impact of a meteorite, asteroid or comet creates a depression. This can be a simple bowl (depth to diameter ratio typically 1:5 to 1:7) or a larger, shallower, more complex depression (depth to diameter ratio 1:10 to 1:20) sometimes incorporating a central island or islands. Such islands are caused by a gravitational collapse of the rim and a rebound of material to the centre, analogous to the splash effect seen when raindrops hit water. An island may itself incorporate a hollow that later forms a 'lake within a lake', as in Lake Taal, Philippines (Reid pers. obs.). In geological terms, impact depressions occur frequently but are often temporary, and only some 120 are currently known

¹ North of England Zoological Society, Caughall Road, Upton, Chester CH2 1LH, UK



Lake Barombi Mbo, Cameroon. This lake is considered to be the oldest radiocarbon-dated crater lake in Africa. © U. SCHLIEWEN

worldwide, most commonly from North America, Europe and Australia. Their occasional occurrence in Africa is therefore of considerable scientific interest. It is postulated that multiple terrestrial impacts, particularly large ones, are of importance in both geological and biological terms and are likely associated with periodic species extinction events on land and in the marine environment occurring since at least the Cretaceous period (around 60 million years ago). The nature, persistence and effects of impact depressions depend on the 'target' substrate, the velocity of the impactor, its composition and identifying 'signature' – the physical and chemical outputs, such as meteorite shards, shock metamorphism, 'rock melt' and silica rich glasses. All of this may become biotically significant at some later stage of lake evolution. Other factors determining nature and persistence include the location, scale and form of the depression, and subsequent chemical, geological, geographical and biological processes including any underlying volcanic activity, erosion, deposition of sediments and ecological colonisation.

Aorounga, in the Sahara Desert of northern Chad, contains a rare western Africa example of a large, ancient, much eroded impact

crater (19°6'N, 19°15'E; diameter 17km; age around 200 million years ago (Hamilton 2001)) which supports isolated temporary pools in rainy periods. Across the Sahelian region such pools may contain a remarkable density of life, albeit briefly, including anacostracan crustaceans ('fairy shrimps') emerging from eggs resting in the sand since previous inundations of water; and anuran (frog and toad) tadpoles which appear 'as if from nowhere' (Reid pers. obs.). However, the craters are usually dry and contribute a fine diatomaceous lake substrate to dust storms generated within the Bodélé Depression and which, in winter, amount to an average of 1,200,000 tonnes of dust per day carried for hundreds or thousands of kilometres (Todd *et al.* 2007). The Aorounga crater is one of a local series, which may have been part of the more permanent and far more extensive 'Mega Lake Chad' dating from the Pleistocene to Holocene periods (around 2 million years ago to 10,000 years ago) and persisting to some extent until a few thousand years ago. Lake Chad is now only 5% of its volume in the 1960s, mainly due to excessive human abstraction demands. The Mega Chad has been crucial in determining much of the large-scale aquatic and terrestrial patterns in

historical and recent biogeography for western Africa and the Nilo-Sudan ichthyological province (Reid 1996).

Lake Bosumtwi, Ghana is a better known, but still scarce, example of a comparatively young, permanent impact crater lake (06°32' N, 01°25'W; rim diameter 10.5km; maximum depth 75m; age 1.3 ± 0.2 million years). The largest single natural lake in sub-Saharan western Africa, it lies over crystalline bedrock of the West African Shield and research indicates that sediments associated with Lake Bosumtwi have spread to the Ivory Coast and to oceanic deposits, nearby in the Gulf of Guinea (Hamilton 2001; Embassy of the Federal Republic of Germany 2011).

Volcanic crater lakes.

Craters formed through vulcanism, and their associated lakes, are sometimes divided into two classes: *calderas* which are deep inverted cones; and *maars* which are shallower with a low profile. However, these distinctions are not always obvious, and the nature of the volcanic activity can be complex (Decker and Decker 1997). The rocky rim is often created in a gaseous explosion when hot volcanic lava or magma in a subterranean chamber makes contact with groundwater.



“By contrast, Lake Barombi Mbo is small (see above) and estimated to be biologically mature since about 25,000 to 33,000 years ago; it is considered to be the oldest radiocarbon-dated crater lake in Africa

Subsidence of materials creates a depression within the rim that may later fill with water. A diatreme often persists under the lake bed, that is, a pipe-like vertical volcanic vent that is filled with broken and cemented rock created by a single explosion. Such diatremes may remain active. Lake Nyos (around 322km north-west of Yaoundé, Cameroon, close to the border with Nigeria) is an example of a simple maar lake, but a comparatively deep one (6°26'17"N, 010°17'56"E; 1,091m above sea level; 2km long by 1.2km wide; and 208m maximum depth). Lake Barombi Mbo in south-west Cameroon is formed in a caldera, albeit a fairly small one (4°39'46"N, 9°23'52"E; 303m above sea level; 2.15km wide; and around 110m maximum depth) (Schliewen 2005; Lebamba *et al.* 2010).

Lake development

Whether formed by impact or vulcanism, craters that persist anywhere may periodically or

permanently fill up with water from snow, rainfall, groundwater, a captured drainage, spring or swamp or a larger inundation. Depending on water supply, drainage and evaporation, the lake may reach the lowest point on the rim and then overspill as a waterfall if the rim is high; or as a stream, if at the outset the rim is low or becomes water eroded. At a critical point of attrition there can be catastrophic breakout flooding. If the crater contains an active volcanic vent (see 'diatreme' above) the water will have an elevated temperature and be turbid and acidic from high concentrations of dissolved volcanic gases and distinctly green, or red-brown if iron rich. Gases include carbon dioxide (CO₂), sulfur dioxide (SO₂), hydrogen chloride (HCl) and hydrogen fluoride (HF), which may persist in solution and are lethal to invertebrate and vertebrate life.

Lake Nyos, with a diatreme some 80km below the lake bed, is one of

only three known contemporary 'exploding' and periodically lethal lakes, all of which are African (the others being nearby Lake Monoun, Cameroon (5°35'N, 10°35'E) and Lake Kivu, Rwanda). Nyos and Monoun are located within the Oku Volcanic Field near the northern boundary of the Cameroon Volcanic Line, a zone of volcanoes, maars, calderas and other tectonic activity that extends south-west to the large, inactive Mount Cameroon composite volcano (stratovolcano) and beyond to the island of Bioko in the Gulf of Guinea, which also contains an unexplored crater lake (Flesness, pers. comm.). Nyos has periodically been supersaturated with carbon dioxide (CO₂, forming carbonic acid) leaching from the underlying magma and with a peak lake density of approximately 90 million tonnes of CO₂. In 1986, there was a gaseous explosion, perhaps precipitated by an earthquake or landslide, releasing approximately 1.6 million tonnes of CO₂ into the atmosphere. This killed some 1,800 people, 3,500 livestock, and gas in solution presumably killed fishes and other aquatic life. Degassing pipes were installed in 2001 to prevent a repetition of the catastrophe (Kling *et al.* 2005). Some 2,000 times larger than Nyos, Lake Kivu has also been found to be periodically supersaturated – with evidence for outgassing every

thousand years or so. The general ability of crater lakes to store carbon dioxide at depth for long periods and also release it is clearly important when calculating lake stability, contemporary carbon sequestration and 'footprints' – and in determining the survival, ecology and evolution of fishes and other aquatic animal populations.

In the case of large mature impact craters and inactive or dormant volcano craters, the water normally becomes thermally and eventually ecologically stratified. The deep, cold, dense, aphotic and anoxic water above the lake bed is usually quite separate from the warm, less dense, sunlit surface layers which support most of the animal and plant species and biomass. Lake surface waters down to around 40m are usually life supporting and fresh but can, in some instances, be saline. The clarity or transparency (and hence transmission of sunlight, level of photosynthetic activity and primary production) can be high, but this is determined by the nature of the crater rim soil and biota above the waterline (Elenga *et al.* 2004; Lebamba *et al.* 2010), nutrients, water movements (including inflows, outflows and overturns of thermal strata), and by other limnological processes. Some crater lakes are of considerable maturity and scale, for example, the Lake Toba caldera, Danau Toba, Indonesia was formed around 70,000 years ago, with an area of over 1,000km². By contrast, Lake Barombi Mbo is small and estimated to be biologically mature since about 25,000 to 33,000 years ago; it is considered to be the oldest radiocarbon-dated crater lake in Africa (Elenga *et al.* 2004; Lebamba *et al.* 2010). The physical origin of the lake has been estimated as around 1 million years ago (Schliewen 2005). In any event, there is contemporary evidence that substantial permanent bodies of water can form very quickly in craters, for example, the lake that

“The craters represent a younger, less complex (if potentially more volatile) ecosystem – a ‘microcosm’ more easily studied than the East African Great Lakes

developed post 1991, following the eruption of Mount Pinatubo, Philippines.

Lake colonisation and the evolution of species. Western African and other small crater lakes have attracted the attention of evolutionary biologists and conservationists mainly because of their endemic cichlid fishes and the natural and anthropogenic threats to their survival. The craters represent a younger, less complex (if potentially more volatile) ecosystem – a ‘microcosm’ more easily studied than the East African Great Lakes. Such craters provide an opportunity to investigate stages in ecological colonisation from an initially lifeless environment, and the processes of population differentiation and speciation. While invariably occupied by invertebrates, not all western African crater lakes contain fishes and shrimps (Schliewen 2005). For those which contain cichlids, and which are geologically isolated, the question of how they came to occupy the crater is intriguing. In some cases, there are potentially testable hypotheses of natural migration through large-scale paleo-historical inundations of water, or via crater stream outflows (some still extant). Notions of paleo-historical introductions of fishes or eggs by humans or birds are less credible and difficult, or impossible, to test scientifically. Setting such possibilities aside, western African models of tilapiine cichlid speciation or adaptive radiation are

being tested against the classical grand-scale eastern African model (Klett and Meyer 2002; Salzburger and Meyer 2004; Seehausen 2006).

Evidently, the evolution of species flocks is not invariably an enclosed, lacustrine phenomenon or confined to cichlid taxa. However, for Salzburger and Meyer (2004): ‘Species richness seems to be roughly correlated with the surface area, but not the age, of the lakes. We observe that the oldest lineages of a species flock of cichlids are often less species-rich and live in the open water or deepwater habitats.’ Based initially on Lake Victoria, the general eastern African hypothesis is that haplochromine and other cichlid taxa evolved into lacustrine species flocks numbering in the hundreds through a process of allopatric speciation, that is, one involving periodic geographical separation of populations. It was suggested that a regular rise and fall of waters in geological time created satellite lakes to isolate cichlid populations, which then differentiated ecologically, morphologically, behaviourally and genetically into distinct species. These isolates supposedly later returned to the main lake during high paleo-historical water levels, but by that time did not interbreed with their congeners.

An alternative model is that species can arise as monophyletic flocks within the body of a lake without such total isolation, that is, through a process of sympatric speciation. In testing these competing (but not

necessarily mutually exclusive) models, Schliewen *et al.* (2001) conducted a 'gene flow' study within five tilapiine morphs endemic to Lake Ejagham, western Cameroon (5°44'59"N, 8°59'16"E; surface areas 0.49km²; maximum depth around 18m (Schliewen 2005)). Comparisons with a closely related riverine outgroup of cichlids suggest that synapotypic colouration and 'differential ecological adaptations in combination with assortative mating could easily lead to speciation in sympatry' (Schliewen *et al.* 2001). More generally, it is postulated that a dynamic network of gene exchange or hybridization among populations creates a process of 'reticulate sympatric speciation' among Cameroonian crater lake cichlids (Schliewen *et al.* 1994; Schliewen 1996, 2005; Schliewen and Klee 2004). Comparable empirical research on post-colonisation cichlids in a young crater lake in Nicaragua also supports the idea that sympatric endemic 'morphs' of individual cichlid species may diversify rapidly (say, within a hundred years or generations) in ecology, morphology and genetics and this can be interpreted as 'incipient speciation' (Elmer *et al.* 2010). Again, this is postulated to be through disruptive selection, perhaps sexual selection, mediated by female mate choice.

Conservation of crater lake fishes.

The phylogenetic and associated data on crater lake cichlid species flocks (above) are at different levels of generality and, among other criteria, important in the evaluation of conservation priorities (Stiassny and de Pinna 1994). However, a paucity of well-worked and wide-ranging studies has until recently limited such contributions (Stiassny 2002; Stiassny *et al.* 2002). Even so, western African crater lakes are included as an important biogeographic category within

standard recognised freshwater ecoregions of the world and Africa (Thieme *et al.* 2005; Abell *et al.* 2008).

Thieme *et al.* (2005) designate closed basins and small lakes as a 'major habitat type', whose ultimate conservation status within most of the western African block of ecoregions is under threat 'based on projected impacts from climate change, planned developments, and human population growth'. Recent research on pollen, biomes, forest succession and climate in Lake Barombi Mbo crater during the last 33,000 years or so suggests the persistence of a humid, dense, evergreen cum semi-deciduous forest: 'These forests display a mature character until *ca* 2800 cal yr BP then become of secondary type during the last millennium probably linked to *increased human interferences* [our emphasis]' (Lebamba *et al.* 2010).

The recent conservation status of small Cameroonian crater lakes, including Barombi Mbo, and their endemic fishes and invertebrates, is considered in detail by Reid (1989, 1990a,b, 1995, 1996) and Schliewen (1996, 2005). Such unique lake environments and endemic species are clearly of national and international importance. There is, from the outset, an inherent vulnerability of these ecosystems resulting from the geological instability in craters; their small physical size; the small size of the contained populations and their genetic isolation; and, for cichlid fishes, their methods of reproduction and limited fecundity. Actual or potential general threats are widely familiar, including: overfishing and other socio-economic factors, including pressure from external visiting tourists; the introduction of alien species (for example, crustaceans and fishes (Slootweg 1989)); siltation and a reduction or loss of allochthonous food supply of terrestrial plant material and invertebrates (both resulting from

deforestation and slash and burn agriculture within the crater rim); adverse water level fluctuation (from damming the lake outflow and from excessive abstraction); and water pollution (from natural volcanic gases, from aerial and industrial emissions travelling from a distance; and from locally applied agrochemicals, pesticides and ichthyotoxic molluscicides used to control the aquatic snail vectors of human schistosomiasis, at least endemic in Barombi Mbo).

Among conservation recommendations that have been proposed by the authors (above) are: systematic Population and Habitat Viability Analyses, as formulated by the IUCN Conservation Breeding Specialist Group; Red List threat assessments (as summarized in this volume); the formal designation of lakes as legally and practically protected aquatic nature reserves of national and international importance, with an accompanying conservation action plan (Lakes Barombi Mbo and Ejagham have now been designated as forest reserves (Schliewen 2005)); and ex situ programmes for the conservation breeding of species at risk, with the prospect of eventual reintroduction in appropriate circumstances (such ex situ aquarium breeding programmes have been in operation since 1999 through European and North American Fish Taxon Advisory Groups). Despite the persistent threats outlined above, a survey of Lake Barombi Mbo in 2002 found all fish species to still be present (Schliewen 2005). However, many of the species present are threatened (even Critically Endangered), but there have been no recorded fish or invertebrate population declines to the point of extinction in any of the crater lakes. Nevertheless, continued vigilance, conservation monitoring, threat assessment, mitigation and protective measures remain highly appropriate.