Identification of the Cichlid Fishes of Lake Malawi/Nyasa Part 3: Rhamphochromina and others.

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ABSTRACT: With an estimated 800-1000 species, the cichlid fishes of Lake Malawi represent the largest known adaptive radiation of vertebrates from common ancestry in a limited geographical area, in this case a single lake. Although they represent a major system for the study of evolution, and have considerable local economic value, the presence of so many closely-related and poorly known species presents formidable difficulties for researchers, conservationists and resource managers. At least half of the plausible species remain undescribed. The present work reports on progress in their identification, assessing evidence from examination of specimens and photographs in conjunction with studies of type material and literature. Here, we focus on the endemic subtribe Rhamphochromina ('pelagic clade'), of which 37 known species are considered, along with 10 miscellaneous 'haplochromine' species (tribe Pseudocrenilabrini) in non-endemic genera. We also consider 10 'tilapia' species (tribes Coptodonini, Oreochromini and Tilapiini), several of which have been introduced to the catchment for aquaculture and may in time become established in the wild, if they have not already done so. This work represents one of three free-standing preprints, which can be modified as identifications are improved and species formally described.

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Introduction

The cichlid fishes of the African Great Lakes have been the subject of many studies covering behaviour, morphology, genetics and systematics, but taxonomically they remain poorly known, with many undescribed species (Snoeks 2004; Konings 2016). This is a reflection of the difficulties in distinguishing among many closely-related species (Snoeks 2004), as well as the lack of interest in traditional taxonomy among researchers (Bouchet et al. 2023). A further problem is raised by the difficulty in working around old descriptions which retain taxonomic priority despite often being based on a small number of specimens which are sometimes poorly preserved and/or lack information on key diagnostic features, such live coloration or accurate collecting localities. Future progress is likely to be hindered by difficulties in obtaining access to freshly collected material by researchers based externally as a result of administrative hurdles raised in response to Access and Benefit Sharing legislation through the Nagoya Protocols (Bouchet et al. 2023; Sherman et al. 2025). At present, there is considerable interest in applying a range of modern methods to study the evolution and genetics of African lake cichlids at a large scale (e.g. Malinsky et al. 2018; Svardal et al. 2019; Ronco et al. 2020a; Meier et al. 2023). While the fauna of Lake Tanganyika is reasonably well-known (Ronco et al. 2020b), there are substantial gaps in current knowledge of the cichlid fishes of Lakes Victoria and Malawi. Identification to species-level is often problematic and uncritically labelled sequences accessioned into international databases, including the NCBI Sequence Read Archive and European Nucleotide Archive, may be storing up problems for future researchers. The purpose of the present work is to provide a primer to the identification of Lake Malawi's cichlid fauna, in particular to support recent and planned publications based on genomic data (Malinsky et al. 2018; Svardal et al. 2019; Turner et al. 2022; Ciezarek et al. 2024; Sawasawa et al. 2024, Blumer et al 2025, Camacho Garcia et al. 2025), but it is hoped that it will also assist in future field work and taxonomic studies.

Recently, a number of nomenclatural issues have been straightened out by Oliver (2024). The tribe 'Haplochromini' has been found to be a junior synonym of the tribe Pseudocrenilabrini, on the basis that the genus *Pseudocrenilabrus* is the type genus of the family-level name Pseudocrenilabrinae used for the cichlid subfamily that includes all African cichlids. A follow-on effect of this is that if the subfamily is split into further divisions using family-level names, any that contain *Pseudocrenilabrus* have to take this name, but with the ending appropriate to a particular taxonomic level. A confusing consequence of this is that any derived informal name, 'pseudocrenilabrine' could refer to the subfamily (pseudocrenilabrinae: all African cichlids), the tribe (pseudocrenilabrini: 'haplochromines') or the subtribe (pseudocrenilabrina: *Pseudocrenilabrus* and close relatives). As the term 'haplochromine' is widely used in taxonomic and other literature, it is here retained as an informal name for the tribe Pseudocrenilabrini.

Oliver (2024) also created formal subtribal names for the Lake Malawi endemic haplochromines, among others, and these will be used here. The present volume will cover the Rhamphochromina (pelagic subradiation: Oliver 2024), along with miscellaneous cichlids of non-endemic genera known from within the Lake Malawi catchment, whether naturally occurring or cultivated in aquaculture facilities (*Astatotilapia, Coptodon, Oreochromis,* *Pseudocrenilabrus, Serranochromis, Tilapia*). It is intended that this document will remain as an open access preprint that will be updated to reflect additional collections and nomenclatural changes.

Methods

Evidence useful for Lake Malawi cichlid species identification comes from photographs, either of live fish underwater, or from recently collected specimens from food fisheries or experimental surveys. Useful evidence also comes from illustrations of preserved specimens. Colour and overall body shape are the most useful features in species identification. In cases where preserved specimens are available, useful information can be obtained from examination of oral and pharyngeal dentition, cephalic lateral line pores and gillrakers. Other features are often of limited value in identification (see Turner 2025).

Where possible, in the following pages, presentation of species identification features has involved reference to original species descriptions, including text, illustrations and type specimens, although the task of investigating the latter is far from complete. Fortunately, many of the early taxonomic works are now in the public domain, particularly through the Biodiversity Heritage Library (BHL). We have also had kind permission to use original illustrations which remain the intellectual property of individuals or public institutions, such as museums.

Species including all known undescribed taxa are listed alphabetically within a taxonomic unit (tribe, subtribe). Genera containing more than one species in the area are discussed briefly before listing the species. This work is intended to remain as a permanent preprint, and as such is not considered a valid taxonomic work by the International Council for Zoological Nomenclature (despite being a permanent record), so we will make no new taxonomic proposals but retain existing published names (formal and informal) where possible. In a few cases, we have had to make a decision among competing taxonomies. In general, we have tried to follow Eschmeyer's Online Catalog (Fricke et al. 2025) which is comprehensive, regularly updated and free to access. In a few cases, we have had to coin new informal names, generally for taxa not previously recognised. At present, around half of all Lake Malawi cichlids remain undescribed, but the great majority of those are known by informal names, a practice stretching back to Ribbink et al.'s (1983) monograph on rocky shore fishes.

Photographs are credited to the photographer where known, with the following abbreviations: AK = Ad Konings; GFT = George Turner; GFT lab= George Turner and collaborators; HS= Hannes Svardal; HS lab= Lab of Hannes Svardal; MJG= Martin Genner, NHM= London Natural History Museum staff. Line drawings are mostly credited to the source publication with the artist often uncredited.

Diplotaxodon Trewavas 1935: species MC831-851.

Family: Cichlidae; **Subfamily:** Pseudocrenilabrinae; **Tribe:** Pseudocrenilabrini; **Subtribe:** Rhamphochromina.

Type species: *Diplotaxodon argenteus* Trewavas 1935

Contained valid species: *Diplotaxodon aeneus, Diplotaxodon altus, Diplotaxodon apogon, Diplotaxodon argenteus, Diplotaxodon dentatus, Diplotaxodon ecclesi, Diplotaxodon greenwoodi, Diplotaxodon limnothrissa, Diplotaxodon longimaxilla, Diplotaxodon macrops*

Proposed undescribed taxa: *Diplotaxodon* sp. 'bigeye blackdorsal', *Diplotaxodon* sp. ‘brevimanus’, *Diplotaxodon* sp. 'brevimaxillaris', *Diplotaxodon* sp. 'holochromis', *Diplotaxodon* sp. 'limnothrissa blackdorsal', *Diplotaxodon* sp. 'limnothrissa blackpelvic', *Diplotaxodon* sp. 'limnothrissa msaka', *Diplotaxodon* sp. 'macrops north', *Diplotaxodon* sp. 'ngulube', *Diplotaxodon* sp. 'offshore',

Taxa considered invalid: *Diplotaxodon* sp. ‘bigeye white belly’ (Blumer et al. 2025, Camacho Garcia et al. 2025); *Diplotaxodon* sp. ‘deep’ (Turner 1996, Turner et al. 2004); *Diplotaxodon* sp. ‘deep mottled’ (Turner et al. 2004); *Diplotaxodon* sp. 'similis white-back south' = *D. altus*; *Diplotaxodon* sp. 'similis white-back north' = *D.* sp. ‘brevimanus’.

Taxa of uncertain status: *Diplotaxodon* sp. ‘deep mozambique’ (Turner et al. 2004).

Generic reviews & diagnoses: Trewavas 1935, Eccles & Trewavas 1989; Turner et al. 2004.

Generic diagnosis: “Haplochromines endemic to Lake Malawi, without distinct bars or stripes, but sometimes showing darkening of the upper or lower part of the body, or general darkening. Mouth oblique, lower jaw projecting, moderately strong sometimes with a mental knob. Teeth all simple, in two to four rows” (Eccles & Trewavas 1989).

“Cichlid fishes endemic to Lake Malawi and associated water bodies. Apart from reproductively active males, all individuals are silvery and countershaded, lacking stripes, bars or flank spots. The premaxillae are not beaked and the teeth are simple, conical and closely-packed. The gape is strongly angled upwards” (Turner et al. 2004).

Initially, attempts were made to define the genus partly on osteological traits: “Near *Haplochromis.* Mouth oblique ; teeth conical, biserial. Paired laminar inferior apophyses extending the whole length of third or third and fourth vertebrae” (Trewavas 1935), but the inferior apophsis trait was put aside due to lack of knowledge of species subsequently added (*D.ecclesi, D. greenwoodi*) or known but undescribed (Eccles & Trewavas 1989). It is now known not to be a synapomorphy of the genus (Turner 1994a,b).

Field Diagnosis: Silvery fish coming in a variety of body shapes, but with small teeth compared to the big teeth of *Rhamphochromis,* with bigger eyes and stronger jaws than other pelagic haplochromines including *Copadichromis mloto*. Mouths usually upwardly-angled (more so than in *Pallidochromis*). Breeding males are variously marked in black and white (apart from pale yellow eggspots, and a pinkish hue in one species) but not with vertical, horizontal or oblique stripe or any kinds of flank spots.

Species diagnoses: *Diplotaxodon* species are highly problematic to identify, with many taxa showing considerable overlap in morphometrics and meristics. Many are essentially indistinguishable as females or immature individuals, but show clear differences in male breeding dress. This is not without its difficulties either, as male breeding dress can be exhibited in varying degrees of development, which may lead to spurious distinctions. Additionally, the same (or very similar) male breeding dress can be re-used by other species in the genus with different body shapes. Further difficulties lie in past species descriptions: *D. altus, D. argenteus, D. dentatus, D. greenwoodi* and *D. longimaxilla* were all described from specimens lacking clear information on male breeding dress. *Diplotaxodon ecclesi* was described from a single specimen, and although it appears to show some male breeding coloration in the photograph of the type specimen, this has proved particularly problematic to identify since. *Diplotaxodon limnothrissa* was described from a large number of specimens, including males in breeding dress, but the holotype was a female, which is not helpful as it now appears that there are 2 or 3 species that are essentially indistinguishable except on the basis of male breeding dress. *Diplotaxodon aeneus* was described from a few mature males, but they were not photographed fresh, and had been deep-frozen prior to preservation, which may have altered their colours. Really only *D. apogon* and *D. macrops* were described from a reasonable number of specimens, including males photographed freshly collected in breeding dress, taken as holotypes. Proper resolution of the group will require extensive sampling focussed on whole genome sequencing of males photographed and preserved in various stages of breeding dress: from this it may (or may not) prove possible to calibrate morphological or simpler genetic methods of identification of females and immatures. For now, identification is very dependent on a small number of experienced workers operating from ‘eyeballing’ similarities and differences in shape, partly calibrated with information on male breeding dress, where known. We have tried and failed to make progress using a range of statistical analyses of a range of measurements and counts: generally with a reasonable sample size, every species overlaps with a least one other species in any given trait. Lower gillraker counts and visual inspection of the size of jaw teeth have some utility in a few cases.

Phylogenetic comments: *Diplotaxodon* + *Pallidochromis* forms a clear clade in all molecular analyses to date. Along with *Rhamphochromis*, they are resolved as the first endemic subradiation to have diverged from the stem *Astatotilapia*. Phylogenetic analysis of whole genome sequences (Camacho Garcia et al. 2025) tends to confirm that when adequate samples are available, *Diplotaxodon* can be split into clearly genetically distinct species. In many cases, morphologically-similar species pairs that differ largely in male breeding dress have not been resolved as sister taxa. It appears *Diplotaxodon* is comprised of multiple ‘good’ genetic species, but there is a lot of morphological parallelism.

MC831. *Diplotaxodon aeneus* Turner & Stauffer 1998

Diplotaxodon aeneus was described by Turner & Stauffer (1998) from six specimens collected to the north-east of Nkhata Bay: they were not actually seen or photographed fresh by the authors, but had been deep-frozen. They are deep-bodied with large eyes, large mouths and a prominent premaxillary pedicel. The mature males were dark with an overlying coppery cast, and completely lacked any white margin to the dorsal fin (in contrast to other short-bodied, big-eyed species). They have 18-20 lower gillrakers, two rows of simple jaw teeth, Dorsal fin XIII-XV, 11-12; Anal fin III, 10-12; Longitudinal line scales 33-35, Cheek Scale rows 2-3. They are known to attain 14cm SL (larger than *D. macrops* and *D. apogon*), and are recorded mainly from deep water in the northern half of the lake, although a few specimens were reported from Domira Bay (Turner et al. 2004). The species has not been positively identified since 2004. The full genome of this species not been sequenced.

Fig. 831.1: *Diplotaxodon aeneus*, holotype.

MC832. *Diplotaxodon altus* Stauffer, Phiri & Konings 2018

Diplotaxodon altus was described by Stauffer et al. (2018) from five specimens collected in the SW Arm, from midwater Chirimila nets in 2013 (fig. 832.1). No fresh photographs or details of male breeding dress were presented. The body is relatively deep, the mouth not particularly large or upwardly angled and the eyes of moderate size. There are 21-26 lower gillrakers on the outer arch, which is higher than *D. greenwoodi, D. longimaxilla* and *D.* sp. 'brevimaxillaris'. Stauffer et al. (2018) suggested that specimens recorded *D.* sp. 'similis whiteback south' (Genner, in Konings 2016), *D.* sp. 'deep' (Turner 1996, Turner et al. 2004; fig. 832.2), *D.* sp. 'deep mottled', *D.* sp. 'deep white-top' and *D.* sp. 'deep Mozambique' (all Turner et al. 2004) might also be *D. altus*. Re-examination of photographs and specimens suggests that this is very likely to be correct, although we have not yet located material for 'deep Mozambique'. In addition, specimens collected in 2025 in the south of the lake appear to be males in full breeding colour (figure 832.3). From a combination of the information on specimens recorded under these various names, it appears that *D. altus* is widespread in Lake Malawi, often collected by bottom trawling in waters of depths of 50-90m, but occasionally deeper. It was not collected by sampling in the middle of the lake, over the anoxic zone, and appears to be a midwater-feeding member of the benthic community rather than a truly pelagic species. Turner et al. (2004) report a maximum size of 224mm SL, although that is from one exceptional specimen (and probably needs to be checked); the majority were less than 190mm SL.

The full genome of a single specimen has been sequenced under the name *D.* sp. 'big eye white dorsal' (Blumer et al. 2025; Camacho Garcia et al. 2025). This was obtained from Chipoka in 2004 from a batch of fin clips from the same species put in the same vial; representative specimens are shown in figure 832.4. One of this batch of specimens is illustrated in Konings (2016) as *D.* sp. 'similis whiteback south', and those individuals appear to be males with partially developed breeding dress. From phylogenetic analyses of the genome-wide data, the species appears closely-related to *D.* sp. 'ngulube' and to a specimen provisionally assigned to *D.* cf. 'holochromis' (Camacho Garcia et al. 2025).

Fig. 832.1: *Diplotaxodon altus*, holotype, 162mm SL.

Fig. 832.2: *Diplotaxodon altus*, #1996.752, trawl catch, Maldeco Fisheries, SE Arm, 1996 [GFT].

Fig. 832.3: *Diplotaxodon altus*, mature male, southern arms, pair trawl catch 2025 [Monkey Bay Capture Fisheries Centre]

Fig. 832.4: *Diplotaxodon altus,* males with developing breeding dress, 2004-342, 28 July 2004, Chipoka. Sequenced. [MJG]

MC833. *Diplotaxodon apogon* Turner & Stauffer 1998.

Diplotaxodon apogon was described from 22 types in 1998. It is a small species (largest of the types was 117mm SL) with a short body and large eye. Adult males are distinguished by their pale underside and broad white dorsal fin margin, contrasting with the dark bellied males of *D. macrops, D. aeneus* and *D. ecclesi*. Konings (2016, citing Genner pers. comm.) has suggested that it might be a junior synonym of *D. ecclesi*. However, the single type of *D. ecclesi* is a black-bellied male with a narrow white dorsal fin margin and a size out of the range of the *D. apogon* material, 145.7mm SL (Burgess & Axelrod 1973). *D. apogon* also has 12-14 dorsal spines (mode 13) compared to 15 in *D. ecclesi*. Ceratobranchial gillraker counts also differ: 16-20 v 22. Body depth of *D. ecclesi* was given as 33.3% SL, compared to 32.4-37% SL in *D. apogon*, but only individuals less than 80mm SL had such slender bodies. In addition to male breeding colour, a number of meristic and morphological differences were also noted to differentiate the species from *D. macrops*, for example, *D. apogon* has a relatively longer lower jaw. The type series specimens are all from the southern arms of the lake, where the species seems to be common at depths of around 100m. Elsewhere, large-eyed specimens with similar breeding colours are often found but these are generally larger and their relationship to *D. apogon* is unclear. These are treated herein as *Diplotaxodon* sp. ‘offshore’.

The full genomes of two mature males have been sequenced (Blumer et al. 2025, Camacho Garcia et al. 2025), both collected from the south and both showing characteristic body shape and male breeding dress of *D. apogon* (fig. 833.3-4). Phylogenetic analysis based on these genome data indicates *D. apogon* is relatively distantly related to other sequenced ‘big-eyed’ *Diplotaxodon* species, but is sister to a clade comprised of *D. greenwoodi, D. longimaxilla* and *Pallidochromis tokolosh* (Camacho Garcia et al. 2025). These are all much larger species with strongly predatory facies.

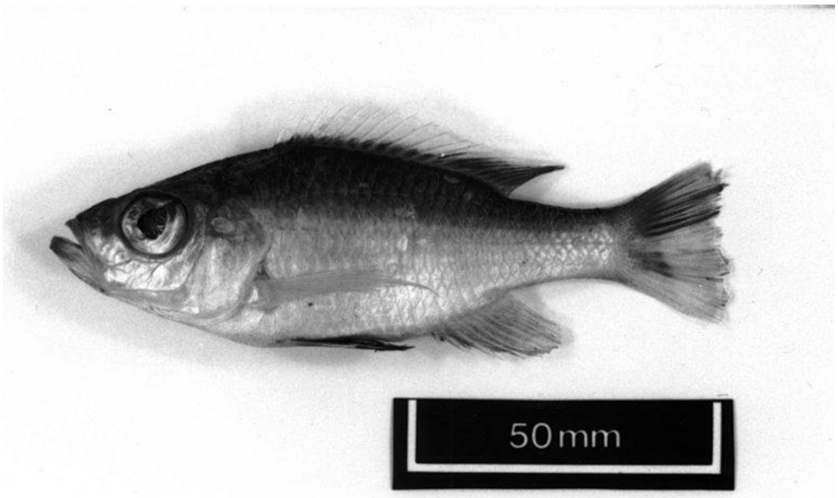


Figure 833.1: Type of *D. apogon*, mature male, 87.8mm SL , trawled from 100m depth off Monkey Bay, 28 Feb 91 [GFT].

Figure 833.2: Freshly collected mature male paratypes of *D. apogon*, trawled from 100-105m depth off Chinyankwazi Island, 21 Jan 91 [GFT].

Fig. 833.3: *Diplotaxodon apogon*, sequenced male, D13-I04 trawled off Cape Maclear, 4 March 2016 [HS].

Fig. 833.4: *Diplotaxodon apogon*, sequenced male, D14-A03, trawled off Cape Maclear, 4 March 2016 [HS]

MC834. *Diplotaxodon argenteus* Trewavas 1935

The type species of *Diplotaxodon* was described by Trewavas in 1935 from three whole specimens, and a skeleton collected from the southern end of the lake, by Cuthbert Christy and accessioned into the Natural History Museum London (fig. 834.1). These do not show male breeding dress. They are slightly predatory in appearance with relatively large upwardly-angled mouths, strong teeth, and a long premaxillary pedicel, but they have a relatively high lower gillraker count, of 23-25 (non-types, which may not be correctly identified, showed a wider range of 20-27). A high gill-raker count is often consistent with a diet of small prey. The high gillraker count helps to distinguish them from the broadly similar *D. longimaxilla*, which also tends to have a larger eye, stronger jaws and a less upwardly-angled snout. The types of *D. argenteus* range from 145.5 to 150mm SL, but specimens from the 1990s collections (again with caveats of identification) were up to 180mm SL, although few exceeded 160mm (fig. 834.2). Male breeding dress was characterised by silvery flanks but black dorsally and on the upper part of the snout, the lips and throat, unpaired fins and pelvics (fig. 834.3). The species was common in trawl catches in the southern arms from 34-114m, but was it was not common in the offshore catches from above the anoxic layer, suggesting the species was more benthic than truly pelagic. The genome of a single specimen (fig. 834.4) from Nkhata Bay has been sequenced (Camacho Garcia et al. 2025; Blumer et al. 2025), but reported under the name *D.* sp. 'holochromis' (sequence code cichlid6978788). It was a large female of 177mm SL, which is rather large for *D.* sp. 'holochromis' and a gillraker formula of 7/1/24, which is outside the range for *D. longimaxilla*. We now think that this is *D. argenteus*. In a phylogenetic analysis, this specimen clusters with *D. altus* and *D.* sp. 'ngulube' and not with the other specimen identified as *D.* sp. 'holochromis' (Camacho Garcia et al. 2025).

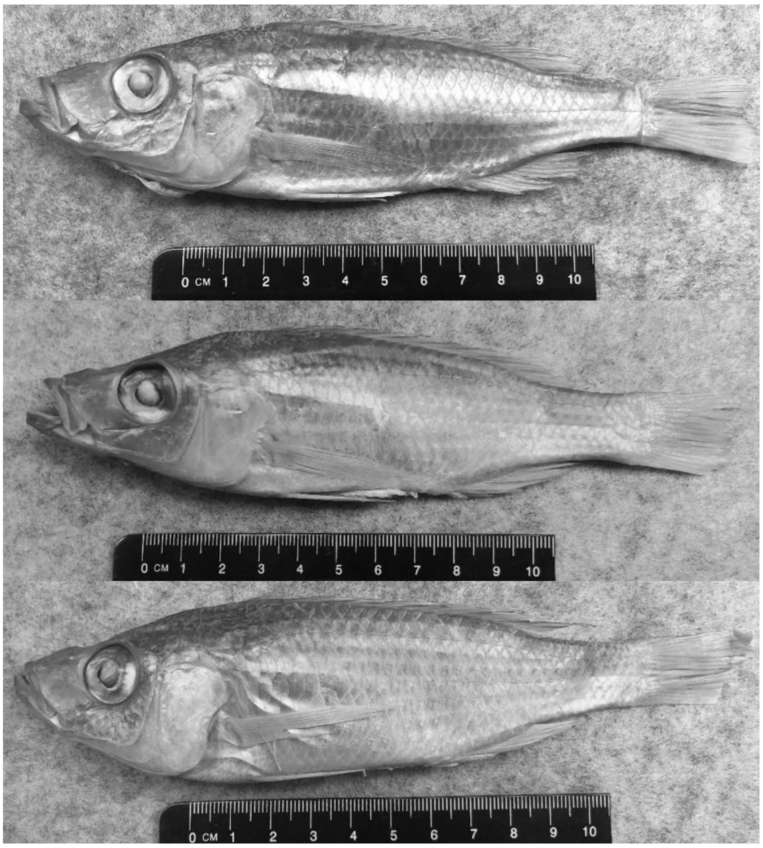


Fig. 834.1: Types of *Diplotaxodon argenteus*, with lectotype above, London Natural History Museum 2023 [GFT].

Fig. 834.2: *Diplotaxodon argenteus*, #1996.769, Maldeco commercial trawl, 1996 [GFT].

Fig. 834.3: *Diplotaxodon argenteus?* (or *D. dentatus*?) mature male #1996.766, Maldeco commercial trawl, 1996 [GFT].

Fig. 834.4: *Diplotaxodon argenteus*, D03-A03, bought from fishermen, Nkhata Bay, 21 Feb 2016 [HS].

MC835. *Diplotaxodon dentatus* Stauffer & Konings 2021

The species was described from eight specimens collected together off Monkey Bay in the south of the lake at a depth of 73m (fig. 835.1). Initially identified as *D. argenteus*, they were distinguished on the basis of their shorter snouts, 26.6–29.2 % HL v 31.7–34.2 % HL for *D. argenteus*. The types are 97-120mm SL, considerably smaller than those of *D. argenteus* (145.5 to 150mm). Like *D. argenteus*, they have large teeth that are visible when the mouth is closed (fig. 835.4). They have a similar lower gillraker count of 23-27. They appear to conspecific with *D.* sp. 'blackfin' (Turner et al. 2004), collected from Likoma Island, Nkhata Bay and SE Arm, at depths of 50-70 m. Although many specimens were collected and preserved, no fresh photographs were presented, but it was found that specimens had similar male breeding colours to *D. argenteus* but matured at smaller sizes, with no specimens above 132mm SL. Many specimens showed dark lappets and a dark area in the middle of the caudal fin, like the types, along with dark pelvic and anal fins and dark areas on the snout. A full genome of this species has not yet been sequenced. One specimen collected in 2023 potentially available for sequencing has the appropriate phenotype and may represent this species (fig. 835.3).

Fig. 835.1: *Diplotaxodon dentatus*, holotype from original description.

Fig. 835.2: *Diplotaxodon dentatus* specimens collected from 1996-98 as *D.* sp. 'blackfin'. #758 from SE Arm, Maldeco, #4085 Karonga [GFT]

Fig. 835.3: *Diplotaxodon dentatus,* BMNH 1988.1.22:141-149, adult male, 115mm SL, trawl off Monkey Bay at 40 fathoms (~75m) 24 May 1985 [GFT].

Fig. 835.3: *Diplotaxodon dentatus*, MWA2891, Nkhata Bay Station NKB66, -11.781, 34.278, 4 Nov 2023 [HS lab].

Fig. 835.4: *Diplotaxodon dentatus,* holotype, jaws and teeth, from original description.

MC836. *Diplotaxodon ecclesi* Burgess & Axelrod 1973

Diplotaxodon ecclesi was described in 1973 from a single specimen, about 145mm SL. It is a slender fish with a large eye and relatively small jaws, dark overall with a thin white dorsal fin margin and hints of an eggspot or two on its anal fin. It has not been positively identified since its original description, although it was collected from a very well-sampled area: bottom trawling at a depth of about 80m just off Monkey Bay. There are two taxa with an overall dark male breeding dress and a white dorsal fin margin, that we have considered for comparative purposes. The first of these is *Diplotaxodon macrops*, which has a stockier body (for 22 *D. macrops*: 30-36.8 %SL v 31.6% for *D. ecclesi*, a relatively larger eye (32.6-39.7 % Head Length v 32.9% in *D. ecclesi*), a much wider white dorsal fin margin, and is not known to attain sizes of more than 12cm SL. Although the morphometric ranges just overlap, taken together with the overall specimen length and the dorsal fin margin width, it seems unlikely that *D. ecclesi* and *D. macrops* are conspecific. The second option is *D.* sp. 'holochromis', which gets larger, up to 160mm SL and has a similarly narrow white dorsal fin margin, but it has a relatively deep body, with the deepest point well behind the pectoral fin base, in contrast to *D. ecclesi*, where they are about level. The type of *D. ecclesi* has a lateral line count of 32 which is lower than has been recorded for *D. macrops* or *D.* sp. 'holochromis', but perhaps this this is due to observer differences in methods. We consider it possible that *D. ecclesi* is a small male *D.* sp. 'holochromis' that had finished breeding and lost body condition, resulting in its overall slender 'big-headed' look. Equally, it may represent a further species that has not been recorded in breeding dress in the subsequent 50-odd years since its description.

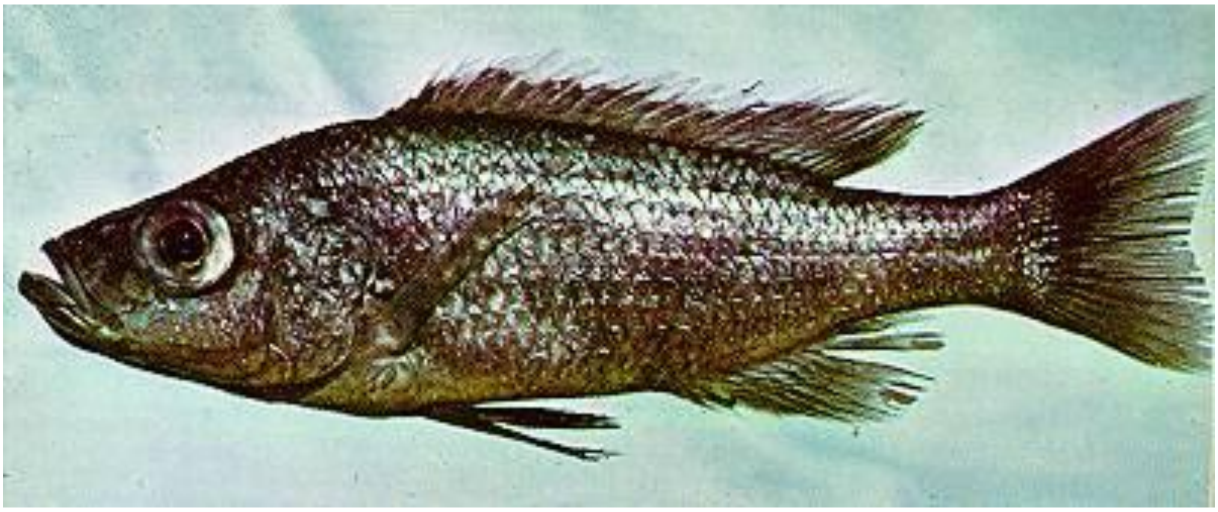


Fig. 836.1: Holotype of *Diplotaxodon ecclesi*, from the original description.

MC837. *Diplotaxodon greenwoodi* Stauffer & McKaye 1986

This large, deep-bodied *Diplotaxodon* was described from four specimens collected at 86m depth off Mumbo Island in the south of the lake. The largest type, the holotype, was a female of 198mm SL (fig. 837.1). The species is distinguished by its large laterally compressed body, huge mouth and steeply-angled gape (57-66º). The description states that the species is prognathous, which is certainly rather dramatically clear on the illustration of the type and on specimens in the London Natural History Museum collected in the 1950s as intended types of a new species to be called 'Diplotaxodon eugnathus' (fig. 837.2), but this trait seems to be quite a variable trait. Males in breeding dress were first illustrated by Turner et al. (2004), showing darkening on the dorsal surface, much of the head and all of the fins, with a number of yellow eggspots on the anal fin, but with silvery flanks and belly (fig. 837.3). Maximum size is at least 244mmSL, perhaps 27cm. The species is mainly found in deepwater, from 50m to at least 148m depth. In the original description, it was suggested that the species was a paedophage, based on (i) the finding of eggs in the stomach of the type, although it was admitted they could have been swallowed in the chaos of the trawl landing and (ii) the steeply angled gape and the distribution of the jaw teeth deeply embedded along the outer anterior end of the jaws. However, the species seems very common compared to other paedophagous species, it has much longer jaws and the drawing of the lower pharyngeal bone in the description shows rather large sharp widely-spaced teeth of a kind that would seem unnecessary for processing soft eggs or embryos (fig. 837.5). Allison et al. (1996) found that stomachs of *D. greenwoodi* contained the remains of larger juvenile cichlids. The full genome of a single specimen has been sequenced (Blumer et al. 2025, Camacho Garcia et al. 2025), which was one of a pair of adult males collected at Nkhata Bay in 2004, a representative specimen is shown in figure 837.4. Phylogenetic analysis of this genome sequence indicates that the species is sister to *Pallidochromis tokolosh*, with *D. longimaxilla* as sister to this pair (Camacho Garcia et al. 2025). Both *P. tokolosh* and *D. longimaxilla* are large predators from the same habitat, but with more slender bodies and less upwardly-angled mouths.

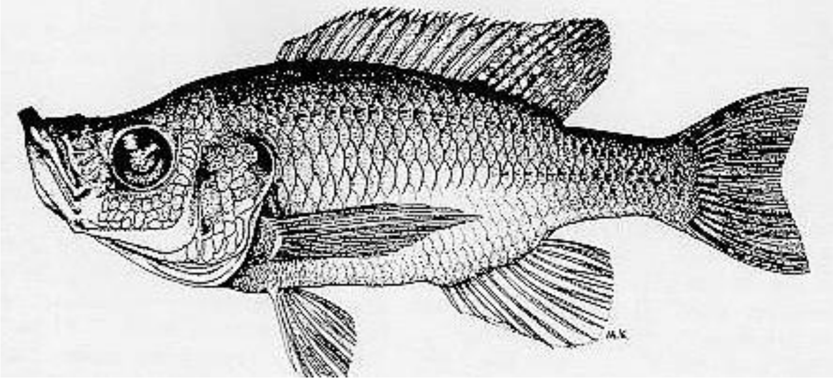


Fig. 837.1: Type of *D. greenwoodi,* from original description (cropped).

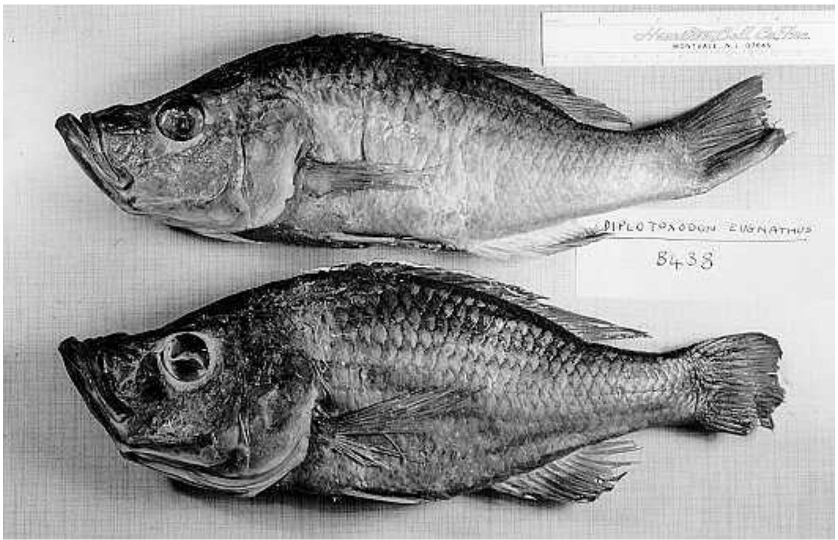


Fig. 837.2: Specimens of *Diplotaxodon greenwoodi* collected by T.D. Iles in the 1950s, intended as types of 'D. eugnathus' which was never described. Deposited in the London Natural History Museum. Uncatalogued at the time they were photographed by M.K. Oliver in 1971 (and apparently still so at the time of writing).

Fig. 837.3: Mature male *Diplotaxodon greenwoodi*, collected from trawl in SE Arm, 1996 [GFT]

Fig. 837.4: *Diplotaxodon greenwoodi*, #2004-117 bought from fishermen at Nkhata Bay, 15 April 2004, [MJG].

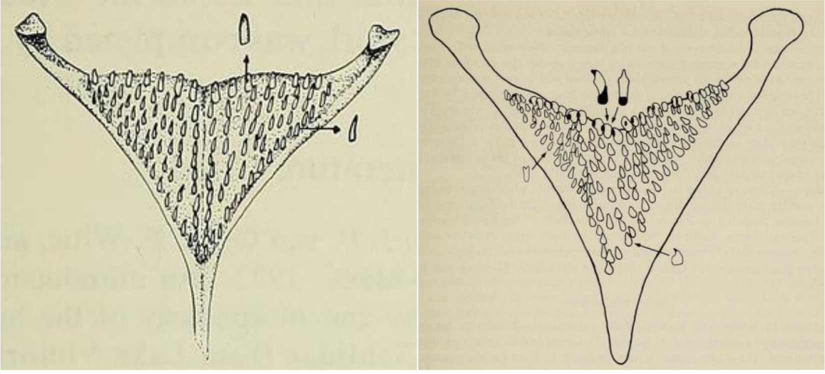


Fig. 837.5: Lower pharyngeal bones showing larger, more widely spaced teeth, especially on posterior rows of *Diplotaxodon greenwoodi* (left) compared to *Caprichromis liemi*, a known paedophage, from original descriptions.

MC838. *Diplotaxodon limnothrissa* Turner 1994.

This species was described from numerous specimens from the southern part of the lake (Turner 1994a). The species was distinguished by its elongate body shape, small mouth, relatively small eye and small teeth (fig. 838.1). Several males in breeding dress were included in the type series and they all exhibited a similar phenotype, dark dorsally with a white dorsal fin and pale pelvic fins (fig. 838.2). Some individuals exhibited a pale 'blaze' on the upper part of the head. The decision to choose a female as the holotype was unfortunate, as it has subsequently been found that there are up to three further species with very similar body shapes and meristics, that cannot really be distinguished except on male breeding colours. When these are described, a male paratype should probably be selected as the neotype for *D. limnothrissa*. It seems that *D. limnothrissa* is the most common of the similar species in the southern part of the lake, so the current holotype is probably conspecific with the male paratypes with white dorsal and pelvic fins. Members of the *D. limnothrissa* phenotype are ecologically very important and dominate the fish biomass in the open waters of the lake, with an estimated 87,000 tonnes present in the lake (Menz 1995). Their diet is dominated by crustaceans such as the copepods *Tropodiaptomus, Mesocyclops*, and cladoceran *Diaphanosoma*, but occasionally also *Chaoborus* fly larvae and pupae, fry of the danionid fish *Engraulicypris*, as well as filamentous diatoms, particularly *Aulacoseira* (Turner et al. 2004).

A total of 33 specimens of *D. limnothrissa* have had full genomes sequenced (Blumer et al. 2025, Camacho Garcia et al. 2025), with phylogenetic analyses of those data showing all individuals form a single clade. Of these, all males in breeding dress corresponded to the white dorsal, white pelvic phenotype (fig. 838.3-6), while other specimens were identified by their position in the phylogeny (fig. 838.7-8). These came from a wide range of locations: SW Arm 16, SE Arm 1, Cape Maclear 3, Chiofu Bay 2, Nkhata Bay 4, Chilumba 4. There was minimal geographic structure, consistent with previous studies using microsatellite DNA (Shaw et al. 2000). In the phylogenetic analysis, *D. sp.* 'limnothrissa black dorsal'was resolved as the sister species to *D. limnothrissa*, while *D.* sp. 'limnothrissa black pelvic' was more distantly related (Camacho Garcia et al. 2025).

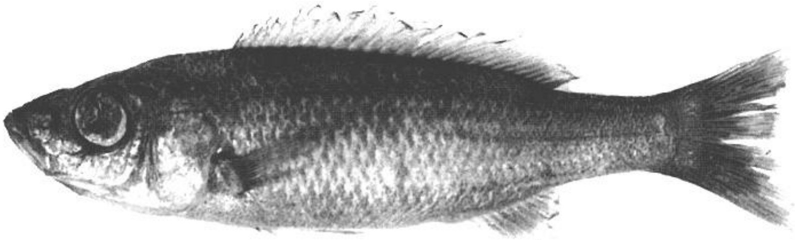


Fig. 838.1: *Diplotaxodon limnothrissa*, female holotype, SE Arm [GFT].

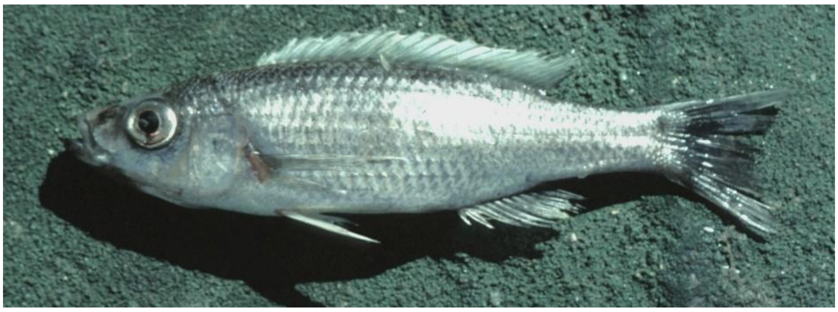


Fig. 838.2: *Diplotaxodon limnothrissa*, male paratype, SE Arm, 1991 [GFT].

Fig. 838.3: *Diplotaxodon limnothrissa* 3 males n breeding dress D04-I05 (top), D04-I06 (bottom left), D05-A02, bought from traders, Chilumba main beach, 23 Feb 2016 [HS].

Fig. 838.4: *Diplotaxodon limnothrissa*, D11-D09, D11-G01, D11-I04, mature males trawled from 85-95m depth, off Monkey Bay, 2 March 2016 [HS]

Fig. 838.5: *Diplotaxodon limnothrissa*, 3 males, D14-A05, D14-A06, D14-A07, trawled off Cape Maclear, 4 March 2016 [HS].

Fig. 838.6: *Diplotaxodon limnothrissa*, mature males D22-J02, D23-A01, D23-A02, D23-A04, trawled in SW Arm, 27 Jan 2017 [HS].

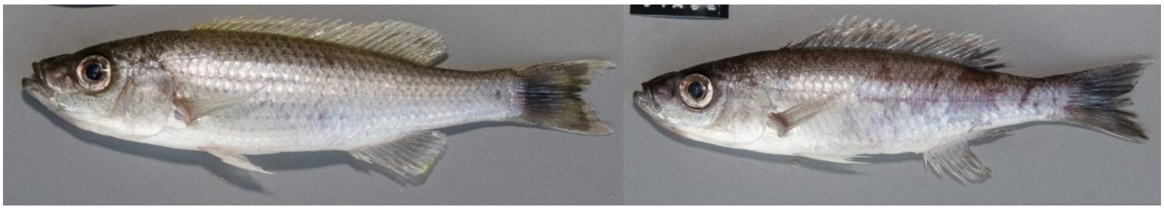


Fig. 838.7: *Diplotaxodon limnothrissa*, D01-A01, D01-A02, bought from traders, Nkhata Bay, 19 Feb 2016 [HS].

Fig. 838.8: *Diplotaxodon limnothrissa*, D10-C04, C07, bought from fishermen, Chiofu, 29 Feb 2016 [HS].

MC839. *Diplotaxodon longimaxilla* Stauffer, Phiri & Konings 2018

Diplotaxodon longimaxilla was described from 12 specimens collected together in a deep water trawl off Mbenji Island, Domira Bay, the largest of which was just under 180mm SL. The species is similar to *D. argenteus* but has slightly larger eyes, fewer gillrakers (usually 16-19, but occasionally 20-21, v 20-27 for *D. argenteus*), a more arched back and a less upwardly-angled gape (fig. 839.1). Stauffer et al. (2018) suggested that taxa discussed by Turner et al. (2004) as *D.* 'similis' (fig. 839.2), *D.* sp. 'similis fat', and *D.* sp. 'brevimaxillaris' were the same as *D. longimaxilla*. We are agree with the first two, but *D.* sp. 'brevimaxillaris' (MC842) has a much more steeply angled gape. We also suggest *Diplotaxodon* sp. 'large black' (fig. 839.3) and *Diplotaxodon* sp. 'black argenteus' (fig. 839.4) as conspecific with *D. longimaxilla*. Based on this combination of previously reported taxa, we conclude that the species is found all around the lake in suitable habitats, usually near the bottom at depths from 70m to 145m. Smaller specimens can sometimes be found as shallow as 50-60m. It is not known from the true pelagic habitat over the anoxic zone. It is a piscivore, growing to at least 203mm SL. Four clear-cut specimens have had their full genomes sequenced (Blumer et al. 2025; Camacho Garcia et al. 2025), from Monkey Bay, Nkhata Bay and Chilumba (fig. 839.5). All individuals cluster together on the phylogeny generated with these genome data. A slightly more problematic individual that has been genome sequenced was collected from near Chinyamwezi Island (fig. 839.6). It is difficult to judge its head shape because the throat is puffed out, and unfortunately there is no preserved voucher specimen. Nevertheless, it resolves phylogenetically sister to the main group of four specimens (Camacho Garcia et al. 2025), and most parsimoniously belongs to this species.

Fig. 839.1: *Diplotaxodon longimaxilla* holotype, from original description.

Fig. 839.2: *Diplotaxodon longimaxilla*, SE Arm Maldeco commercial trawler, shown as *D.* sp. 'similis' by Turner et al. 2004 [GFT].

Fig. 839.3: *Diplotaxodon longimaxilla*, purchased from fishers, near Salima, 1996, shown as *D.* sp. 'large black' by Turner et al. 2004 [GFT].

Fig. 839.4: *Diplotaxodon longimaxilla*, trawled from Cape Maclear between Thumbi West and Mumbo, 1996, shown as *D.* sp. 'black argenteus' by Turner et al. 2004 [GFT].

D02-B01, bought from traders, Nkhata Bay, 21 Feb

D04-H03, bought from traders, Chilumba, 23 Feb.

D12-B03, trawled at 85-95m off Monkey Bay, 3 Mar

D12-B04, trawled at 85-95m off Monkey Bay, 3 Mar.

Fig. 839.5: *Diplotaxodon longimaxilla*, sequenced specimens collected from three widely separated locations in the lake in 2016 [HS].

Fig. 839.6: *Diplotaxodon cf. longimaxilla*, D24-H09, Trawled at Chinyankwazi, 2 Feb 2017 [HS].

MC840. *Diplotaxodon macrops* Turner & Stauffer 1998

Diplotaxodon macrops was described from 21 specimens from the South East Arm of Lake Malawi. The holotype and several paratypes are mature males which were dark all over (black when freshly collected in full breeding dress), apart from a broad white margin to the spiny area of the dorsal fin (fig. 840.1). Males that are not fully ripe can be paler ventrally, but do not show the strongly white belly of *D. apogon* or *D.* sp. 'offshore' males. Females and immatures were distinguished from co-occurring *D. apog*on largely on basis of head shape, shorter lower jaw (37-41% SL v 42-46%), greater lower gillraker count (20-25 v 16-20), and dorsal spine count (14-16 v 12-14). They were deeper bodied than *D. ecclesi* and had relatively smaller heads than *D. aeneus*. However, no comparison has been made with undescribed taxa, such as *D.* sp. 'bigeye blackdorsal' (MC841), *D.* sp 'macrops ngulube' (MC849), *D.* sp 'macrops north' (MC848) or *D.* sp. 'offshore' (MC850). All of those species can be differentiated on male breeding dress, but females or immature individuals cannot be reliably assigned to this species. Eight specimens have had their genomes sequenced (Blumer et al. 2025; Camacho Garcia et al. 2025), all mature males from the south of the lake around Monkey Bay and Cape Maclear (figures 840.2-5). In phylogenetic analyses, all formed a clade, with *D.* sp 'ecclesi white dorsal' (MC843) as sister species (Camacho Garcia et al. 2025).

Fig. 840.1: mature male *Diplotaxodon macrops*, unsequenced paratype freshly collected off Monkey Bay in SE Arm on 28th Feb 1991. From original description (location mislabelled as off Chinyamwezi Island) [GFT].

Fig. 840.2: *Diplotaxodon macrops*, D11-H01, sequenced male, trawled from 85-95m off Monkey Bay, 2 March 2016 [HS].

Fig, 840.3: *Diplotaxodon macrops*, D13-I07, sequenced male, trawled from Cape Maclear, 4 March 2016 [HS].

Fig. 840.4: *Diplotaxodon macrops*, DMS_SE_1, sequenced male, one of a batch of finclips placed in a shared vial, trawled from SE Arm, 30 April 2014 [MJG].

D13-J09.

D13-J10.

D14-A01.

D14-A02.

Figure 840.5: An additional five sequenced males were obtained from a trawl catch in deep water off Cape Maclear (including D14-A04, not shown) on 4 March 2016. All seemed consistent with the phenotype of *D. macrops*.

MC841. *Diplotaxodon* sp. 'bigeye blackdorsal'

This species was first distinguished by Genner et al. (2007a) as *D.* 'macrops black dorsal', and by Genner et al. (2010) as *D.* 'macrops black back'. It is a medium-sized species, up to 139.1mm SL, and like the other bigeye/macrops types, is relatively short-bodied with a large eye. Given the instability of previous nomenclature, we take the opportunity to report the species as 'bigeye blackdorsal' as it is not particularly close to *D. macrops* either genetically or in male phenotype. Genner et al. (2007a) reported male breeding colours as being dark dorsally, including the upper part of the caudal fin and all of the dorsal, except for white lappets. Pelvic and anal fins were translucent / hyaline (fig. 841.1). Genner et al. (2010) reported breeding males from the north of the lake at Ngara, Chilumba and Nkhata Bay; the Ngara and Nkhata Bay populations showed small genetic differences using a suite of microsatellite loci. The male breeding dress is very similar to that of *D.* sp. 'limnothrissa blackdorsal' but body proportions are generally different. No quantitative comparison has been made of the morphology of this species versus the others of the bigeye/macrops group, and at present there is no reliable way to identify the females and immatures other than by whole genome sequencing.

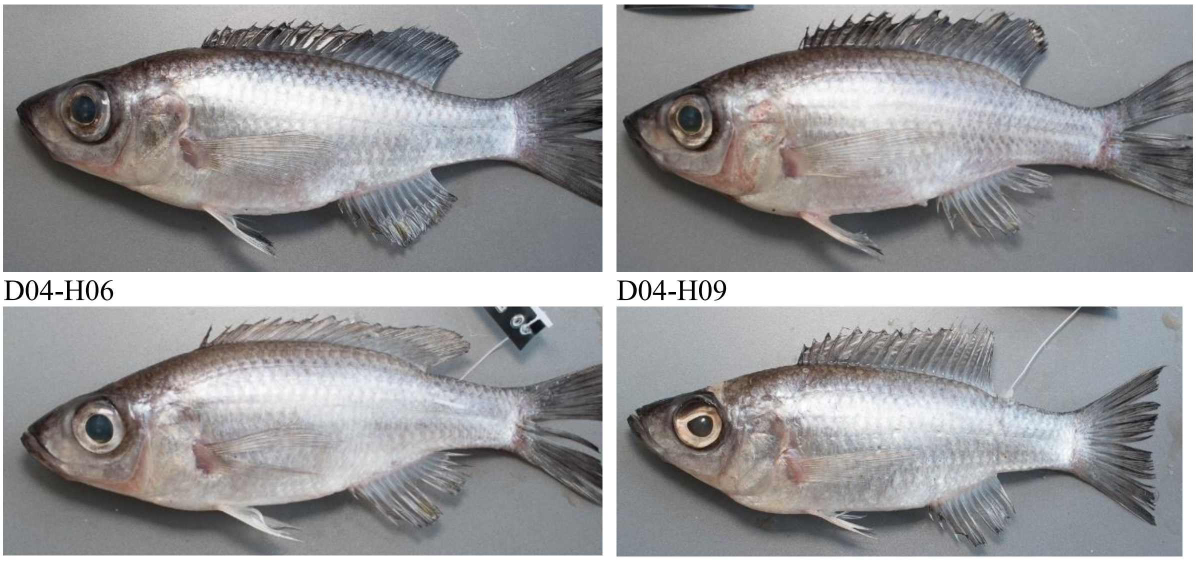
For the studies of Blumer et al. (2025) and Camacho Garcia et al. (2025), 20 specimens have had their full genomes sequenced, including three from Nkhata Bay (fig. 841.2-4), 15 from Chilumba (fig. 841.5), one from Ngara (fig. 841.6) and one from Chiofu Bay (fig. 841.7). All showed a similar phenotype of large eye, deep body and smooth head profile. Some individuals showed hints of a male breeding dress of a dark dorsal and caudal fin. In a phylogenetic analysis based on the genome-wide sequence data, these specimens formed a clade, along with three specimens sequenced that did not show clear-cut male breeding dress (Camacho Garcia et al. 2025). This clade was resolved as sister group to a diverse clade comprised of *D. altus, D. apogon, D. greenwoodi, D. longimaxilla, D.* sp. 'holochromis', *D.* sp. 'ngulube' and *Pallidochromis tokolosh*. Notably, it was distinct from *D. macrops* (similar body shape) and *D.* sp. 'limnothrissa blackdorsal' (similar male breeding dress).

Fig. 841.1: *Diplotaxodon* sp. 'bigeye blackdorsal', male, from Chilumba, 12 May 2005, not sequenced. Reprinted in Genner et al. 2007a & Konings 2016 [MJG].

Fig. 841.2: *Diplotaxodon* 'bigeye blackdorsal', D02-B03, male bought from fishermen, Nkhata Bay, 21 Feb 2016 [HS].

Fig. 841.3: *Diplotaxodon* 'bigeye blackdorsal', D02-B04, male bought from fishermen, Nkhata Bay, 21 Feb 2016 [HS].

Fig. 841.4: *Diplotaxodon* sp. 'bigeye blackdorsal', 2004-303 (BBNB15), male, purchased from traders, Nkhata Bay, 25 July 2004 [MJG].



D04-H06

D04-H09

D05-A07

D05-B05

Fig. 841.5: *Diplotaxodon* sp. 'bigeye blackdorsal', 15 specimens bought from fish traders, Chilumba, 23 Feb 2016 were sequenced: D04-H06 to H10, D05-A05 to B03, D05-B05, of which 4 representatives are shown above [HS].

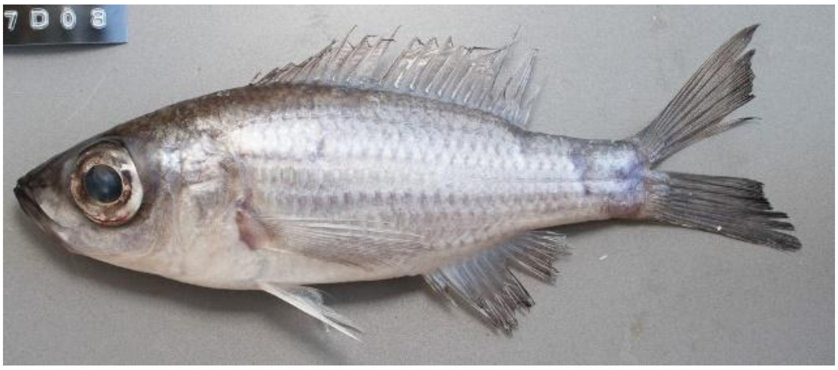


Fig. 841.6: *Diplotaxodon* sp. 'bigeye blackdorsal', D07-D08, bought from fishermen, Ngara, 25 Feb 2016 [HS].

Fig. 841.7: *Diplotaxodon* sp. ‘bigeye blackdorsal’, D10-C08, male, bought from fishermen, Chiofu Bay, 29 Feb 2016 [HS].

MC842. *Diplotaxodon* sp. 'brevimaxillaris'

Diplotaxodon sp 'brevimaxillaris' (fig. 842.1) was first mentioned by Turner (1996: fig. 842.2), based on a name on a jar of specimens collected in the 1950s, probably by T.D.Iles, who published a major taxonomic paper on the 'Utaka' (later *Copadichromis* sp.) but was reported to have been working on something similar with the *Diplotaxodon*. The species is characterized by its relatively large adult body size (at least 19cm SL) and strongly upwardly angled mouth, characteristics shared with *D. greenwoodi* (which attains larger sizes, up to 24.5cm SL). However, it differs in its larger eye, wider head and less prognathous lower jaw. Male breeding colours are not well known, but there are indications that there is a single large eggspot on the anal fin, in contrast to the multiple smaller spots seen in *D. greenwoodi*. A single male freshly collected apparently in breeding dress (whether full or partial is unclear) has been found to have a very dark dorsal and caudal fin, but a pale underside (fig. 842.3). A similar colour is shown by two preserved specimens collected in 1985 (fig. 842.4). This contrasts with the dark undersides of ripe mature males of *D. greenwoodi*. Little is known of the ecology of *D.* sp 'brevimaxillaris', it tends to be found in deep-water trawl catches (Turner 1996). A full genome sequence of this species is not yet available. The short jaws, extreme upwardly angled gape, small erect teeth and bullate premaxilla are perhaps consistent with it being a paedophage.

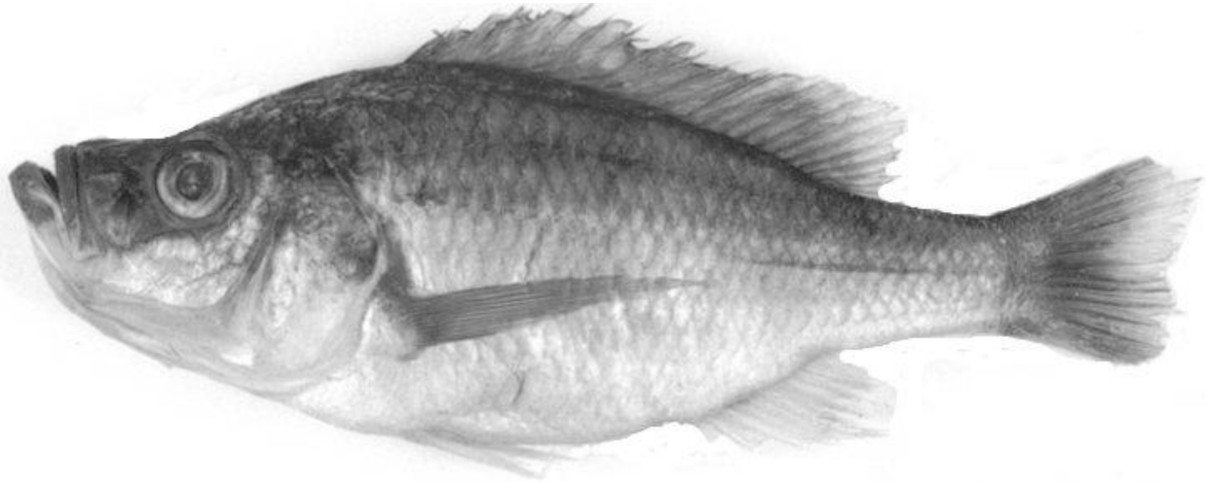


Fig. 842.1: *Diplotaxodon* sp 'brevimaxillaris, 149 mm SL, preserved, collected 1990s, from trawl at 90-100 m depth off Monkey Bay. [GFT].

Fig. 842.2: *Diplotaxodon* sp ‘brevimaxillaris, immature male (note eggspot), trawled from 84-94m, SE Arm, Off Monkey Bay, 13-Apr-92 [GFT].

Fig. 842.3: *Diplotaxodon* sp ‘brevimaxillaris, male showing some development of breeding dress (dark dorsal and caudal, also large eggspot), Cape Maclear, 15 Nov 04 [MJG].

Fig. 842.4: *Diplotaxodon* sp. ‘brevimaxillaris’: BMNH 1988.1.22:141-149, apparent adult males, 161, 182mm SL, trawl at 40 fathoms (~75m) off Monkey Bay 24 April 1985. NB dark dorsal fin and upper surface suggest breeding colour. Lower specimen shows lack of strongly prognathous jaws [GFT].

MC843. *Diplotaxodon* sp. 'ecclesi white dorsal'.

A single specimen obtained from a deep-water trawl off Cape Maclear in March 2016 could not be assigned to any known *Diplotaxodon* species, described or undescribed. It is a large adult male with large eyes, and a slender body, and was initially assigned to *D. ecclesi* (MC836). However, it is now believed not to be that species, primarily because of the male breeding colours, in particular the largely white dorsal fin (fig. 843.1), contrasting with the largely black dorsal with thin white margin shown by the type of *D. ecclesi* (fig. 836.1). The specimen has been sequenced and was resolved as the sister taxon to a large clade of species including *D. macrops* (MC840) (labelled as *D. ecclesi* in Camacho Garcia et al. 2025).

Fig. 843.1: *Diplotaxodon* sp. 'ecclesi white dorsal', D13-I09, sequenced male, trawled from Cape Maclear, 4 March 2016 [HS]; and (below) the same specimen freshly landed, showing a purplish sheen [GFT].

MC844. *Diplotaxodon* sp. 'holochromis'

This taxon was first identified in print by Turner (1996) as *Diplotaxodon* 'intermediate', recognised as being slightly more deep-bodied than individuals of *D. limnothrissa* (now regarded as a mix of species). It was mentioned that a jar of specimens collected by T.D. Iles in the 1950s was seen in the museum in the Monkey Bay Fisheries laboratory in the 1990s, containing fish of a similar body shape, but these were apparently ripe males which were uniformly dark, except for a white dorsal fin margin (Turner 1996). These were labelled as 'Diplotaxodon holochromis', but no description was published. Turner et al. (2004) considered that these were the same species, reporting them under the name *D.* sp. 'holochromis', which we continue here. Turner et al. illustrated their species account with an image of a dark male without an obvious white dorsal fin margin (Fig. 844.2) and its identification seems uncertain: it has a rather slender, more 'limnothrissa-like' body shape, and no obvious white dorsal fin margin, although this is hard to see on the white background. The status of this species has remained rather uncertain, due to the relative scarcity of males in breeding dress, lack of sequence information and the general 'average' body proportions of specimens. Specimens collected between 1996 and 2005 show clearer examples of male phenotypes with some variation in breeding dress, perhaps reflecting stages of maturity or cryptic species (fig. 844.3-5). Given the uncertainties in identification, it is difficult to report much on the morphology and ecology of the species: Turner et al. (2004) reported the species from throughout Lake Malawi, but perhaps most common around Nkhata Bay, and favouring a bottom depth of 35-160m, generally breeding on areas of steeply-shelving coasts. The maximum reported size was around 160mm SL. A full genome sequence has been obtained from a single specimen corresponding approximately to this phenotype, but lacking well-developed male breeding dress, collected from Nkhata Bay in 2016 (fig. 844.6). Phylogenetic analyses indicate that the species is related to *Diplotaxodon altus* and *D.* sp. 'ngulube'. Additional sequences are needed to help resolve this difficult group, particularly focussed on males in breeding dress.

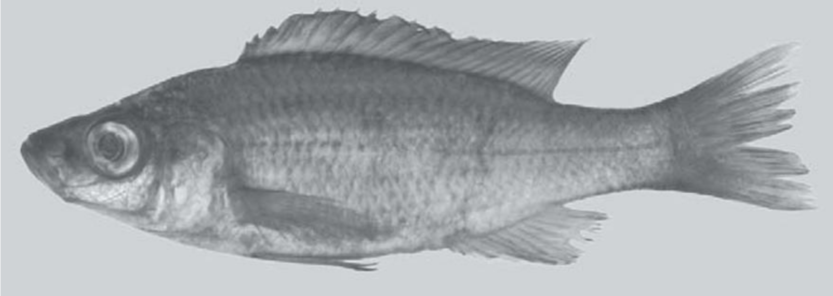


Fig. 844.1: *Diplotaxodon* sp. 'holochromis' illustrated by Turner (1996), specimen from SE Arm of Lake Malawi, 1990s [GFT].

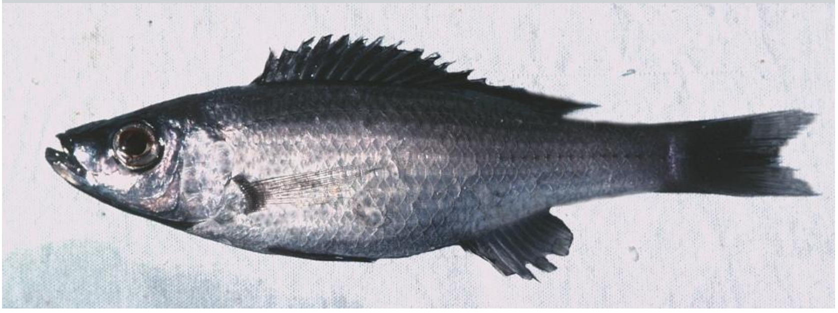


Fig. 844.2: *Diplotaxodon* cf. 'holochromis' illustrated by Turner et al. (2004). This apparent male specimen is rather slender and does not have a white dorsal fin margin. GEF 16/87/16: Senga Bay 125-128m depth, June 1997 [GEF].

Fig. 844.3: *Diplotaxodon* sp. 'holochromis' adult male 2005.249, Nkhata Bay, May 2005 not sequenced [MJG].

Fig. 844.4: *Diplotaxodon* sp. 'holochromis', #2004-136 male, Nkhata Bay, July 2004, not sequenced [MJG]

Fig. 844.5: *Diplotaxodon* sp. 'holochromis', #1996.418, non-ripe male?, Nkhata Bay, not sequenced [GFT Lab]

Fig. 844.6: D02-B05, *Diplotaxodon* cf. 'holochromis', D02-B05, bought from fishermen, Nkhata Bay, 21 Feb 2016, sequenced [HS].

MC845. *Diplotaxodon* sp. 'limnothrissa blackdorsal'

Diplotaxodon sp. 'limnothrissa blackdorsal' was reported by Genner et al. (2010), under the name *Diplotaxodon* sp. 'limnothrissa blackback', being recorded from a number of sites between Chilumba in the north and the South East Arm, and illustrated in the supplementary material to the paper. In Konings (2007, 2016), the same illustration (fig. 845.1) is labelled as 'limnothrissa black-dorsal' and as these works are more widely used, this name is retained here, although without hyphenation. Male breeding dress is rather understated, mainly consisting of a darkened upper surface and dorsal fin (fig. 845.1-2), but also in some specimens, dark pelvic and anal fins (e.g. fig. 845.1), with 1 or 2 large pale yellowish spots on the anal margin. Overall, they seem more heavily built and with larger eyes than *D. limnothrissa* sensu stricto, but are more slender with smaller eyes than those of the bigeye/macrops group, one of which has essentially identical male breeding dress (MC841). The teeth are generally smaller than those of *D. dentatus*. Full genome sequences of two specimens have been obtained (Blumer et al. 2025; Camacho Garcia et al. 2025). Both were obtained from Chilumba and were rather deep-bodied but with faint male breeding colours (fig. 845.3-4), suggesting that they were ripening, and still in good body condition. Phylogenetic analyses based on these sequences clustered the two specimens together, and placed them as the sister group to *D. limnothrissa* sensu stricto (Camacho Garcia et al. 2025).

Fig. 845.1: *Diplotaxodon* sp. 'limnothrissa blackdorsal' male, from Tukombo, just south of Nkhata Bay, not sequenced [MJG, in Konings 2016].

Fig. 845.2: *Diplotaxodon* sp. 'limnothrissa blackdorsal' male, from Kande, 5 May 2005, not sequenced [MJG].

Fig. 845.3: *Diplotaxodon* sp. 'limnothrissa blackdorsal' D05-A04, male, bought from traders, Chilumba main beach, 23 Feb 2016, sequenced [HS].

Fig. 845.4: *Diplotaxodon* sp. ‘limnothrissa blackdorsal’ D05-B04, male, bought from traders, Chilumba main beach, 23 Feb 2016, sequenced [HS].

MC846. *Diplotaxodon* sp. 'limnothrissa blackpelvic'

This species was first reported by Genner et al. (2007a), who used a suite of microsatellite loci to demonstrate that they were reproductively isolated from a number of species of the macrops phenotype as well as illustrating a mature male in colour (fig. 846.1). Genner et al. (2010) demonstrated its genetic distinctiveness from a number of other species including *D. limnothrissa* and *D.* sp. 'holochromis'. This 'reversed countershading' or 'dorsal blaze' male phenotype of limnothrissa blackpelvic also occurs in several apparently unrelated *Diplotaxodon* groups (*D. altus*, *D.* sp. 'brevimanus', *D.* sp. 'ngulube') and similar forms show up in a number of other taxa, including the *Copadichromis mloto/virginalis* complex and some *Aulonocara* species, e.g. *Aulonocara maylandi*. This species is distinguished from other *Diplotaxodon* by its combination of the male pattern and it typical '*D. limnothrissa*-type' body shape, elongated with a small head, small mouth and moderate-sized eye. When the male breeding dress is poorly developed, key colour traits to look out for include the darkened pelvic fins and the dark 'freckles' on the dorsum. Unpublished detailed morphometric and meristic studies have failed to demonstrate any means of distinguishing female or immature individuals of this species from those of *D. limnothrissa*, and so females and immature individuals can only be identified from genomic data. Genner et al. (2010) reported that adult males could be found from Ngara in the far north to Nkhata Bay, with no discernable population structure. The full genome of a single specimen was sequenced for the Blumer et al. (2025) and Camacho Garcia et al. (2025) studies. This male specimen showed very poorly developed breeding dress, and was placed in a resulting phylogenetic analysis of the genome data as basal for the entire *Diplotaxodon/Pallidochromis* clade (Camacho Garcia et al. 2025). It would be good to add additional specimens showing more developed breeding dress and also to confirm that there is not something problematic about the sequence or analysis. Four additional male specimens (fig. 846.3) have been sequenced from a collection made at Nkhata Bay in 2018, at least three of which appear to have the male breeding dress of 'black pelvic', but data from these specimens has yet to be included in a phylogenetic analysis.

Fig. 846.1: *Diplotaxodon* sp. 'black pelvic', 2005.229, male, Nkhata Bay, 8 May 2005 [MJG, reprinted in Konings 2016].

Fig. 846.2: *Diplotaxodon* 'limnothrissa black-pelvic', D04-I04, male bought from traders, Chilumba main beach, 23 Feb 2016 [HS].

D34H03 D34H04

D34H10 D34I01

Fig. 846.3: Four sequenced male specimens, probably of *Diplotaxodon* sp. 'limnothrissa black-pelvic' (D34H04 is a bit dubious) purchased from fish traders, Nkhata Bay, 20th April 2018 [Emilia Santos].

MC847. *Diplotaxodon* sp. 'limnothrissa msaka'

This taxon was first identified by Genner et al. (2010), with details given in the appendix. It has a body shape similar to *D. limnothrissa*, but male breeding dress is different, with a dark grey-black body, pelvic and anal fins, but white on the upper surface of the head and the body around the dorsal fin, much of the dorsal fin, and the upper leading edge of the caudal fin (fig. 847.1). It was only recorded from Msaka in the SW Arm in June 2005. No morphological or population genetic comparison has been made between this taxon and similar species. It is possible that it might represent a developmental stage of male breeding dress of one of the other 'limnothrissa' taxa. Tissue samples are available, but as yet no full genome sequence data are available for analysis.

Fig. 847.1: *Diplotaxodon* sp. 'limnothrissa msaka', male, Msaka, SW Arm, 20 June 2005 [MJG, edited and reprinted in Konings 2016].

MC848. *Diplotaxodon* sp. 'macrops north'

Diplotaxodon sp. 'macrops north' was sampled by Genner et al. (2010), but misattributed to *D. aeneus*: mature males have a white dorsal fin margin not known in the latter species, and the head is relatively smaller. The present nickname was adopted when illustrations were reprinted in Konings (2007, 2016). 36 adult males were collected at Nkhata Bay on 6-7 May 2005. An illustration and details of the male colour phenotype were given in the appendix to Genner et al. (2010). Populations at Nkhata Bay and Ngara were not genetically differentiated on a suite of microsatellite loci, but differed from other taxa with similar body proportions and different male breeding dress (*D. macr*ops, *D.* sp. 'offshore', *D.* sp. 'ngulube') or similar male breeding dress but different body proportions (*D.* sp. 'holochromis'). Adult males can be distinguished from those of *D. macrops* by their narrower white dorsal fin margin and generally larger body size. No detailed morphological comparison has yet been made between this taxon and similar species. Full genome data are not yet available for this species.

Fig. 848.1: *Diplotaxodon* sp. 'macrops north', male, Nkhata Bay, batch of 13 specimens coded 2005.189-191, 6 May 2005 [MJG].

MC849. *Diplotaxodon* sp. 'ngulube'

Diplotaxodon sp. 'ngulube' was first identified and illustrated by Turner et al. (2004) from a few specimens collected at Nkhata Bay (fig. 849.1). It has subsequently been referred to as *D.* sp. ‘macrops ngulube’ (Genner et al. 2007a, 2010; Konings 2007, 2016), but in the interests of succinctness, and reflecting lack of a close relationship with *D. macrops*, we have returned to the original name here. No detailed study of morphology has been undertaken to date, and the species can only be distinguished from the other ‘bigeye’ species by male breeding dress, which is generally dark but with a white/yellow upper surface and dorsal fin (fig. 849.2). Genner et al. (2010) collected mature males from Ngara and Nkhata Bay, and found no population structure among locations, but significant genetic differentiation from other *Diplotaxodon* species, including ‘bigeye’ species, such as *D. macrops, D.* sp. ‘macrops north’ (as *aeneus*), and *D.* sp. ‘offshore’. Mature adults attain relatively small sizes, ca. 13cm SL and are so far only known from the north of the lake. A full genome is available from a single specimen collected at Nkhata Bay (Blumer et al. 2025, Camacho Garcia et al. 2025). Phylogenetic analysis of these genome data indicate it is more closely related to *D. altus* and *D.* sp. ‘holochromis’, rather than to any of the other ‘bigeye’ species (Camacho Garcia et al. 2025).

Fig. 849.1: *Diplotaxodon* sp. ‘ngulube’, male, Nkhata Bay, from Turner et al. 2004 [GFT lab].

Fig. 849.2: *Diplotaxodon* sp. ‘ngulube’, from batch of 3, 2005.186, fresh male in breeding dress, Nkhata Bay, 6 May 2005, not sequenced, [MJG].

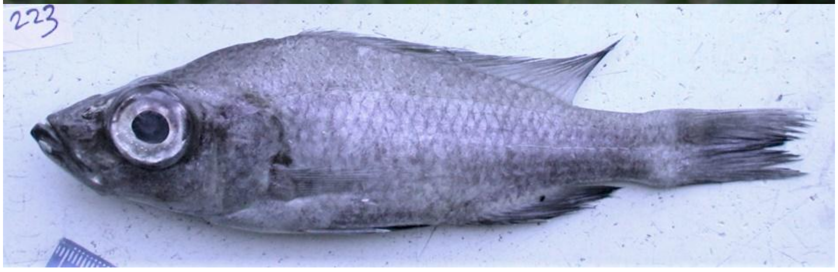


Fig. 849.3: *Diplotaxodon* sp. ‘ngulube’, #2005.223, Nkhata Bay, 7 May 2005, sequenced [MJG].

MC850. *Diplotaxodon* sp. 'offshore'

Diplotaxodon sp. 'offshore' was first identified by Turner et al. (2004), distinguished from most other 'bigeye' species on the basis of its male breeding colour, dark back, pale belly, mostly white dorsal fin, dark pelvics and anal fin. This colour pattern is shared with *D. apogon*, but that species attains a much smaller maximum size (<110mm v 133mm SL) and has a relatively shorter dorsal fin base and longer predorsal length, and also a relatively longer lower jaw. In addition to differences in male breeding colour, *D. macrops* tends to have a relatively deeper cheek and preorbital bone, while *D. aeneus* has a relatively larger head, deeper cheek and wider interobital distance. Comparisons have not been made with *D.* sp. 'macrops north' or *D.* sp. 'ngulube'. Specimens were later collected by Genner et al. (2007a) and illustrated as *D.* sp. 'macrops offshore' (fig. 850.2). These were shown to be reproductively isolated from other bigeye species such as *D.* sp. 'ngulube' and *D.* sp. 'bigeye blackdorsal'. Genner et al. (2010) collected mature males from six sites, from Ngara in the north to Kasuza (12º11'09 S; 34º01'35 E) and found significant genetic structuring. Konings (2007, 2016) reprinted Genner's photo used in the 2007a and 2010 papers (fig. 850.2 here), where it was labelled *D. ecclesi*. Turner et al. (2004) suspected that this was the most abundant big-eyed species in the offshore habitats of the lake, meaning that it could be appropriate to assign the ecological data collected on 'big-eye' species that were not further differentiated to this species. Most specimens were collected from depths of 60-184m. Allison et al. (1996) report that they mostly fed on *Chaoborus* (midge) larvae and pupae, along with some crustacean zooplankton. The species seems to be widely distributed in deeper or offshore habitats and mature males were seen in the months of May to September, but might breed all year round. Full genome data are available from two adult males (fig. 850.3) and two females collected with them (fig. 850.4), but it has yet to be analysed.

Fig. 850.1: *Diplotaxodon* sp. 'offshore', from Turner et al. (2004), SADC/GEF project 16/87/15: Senga Bay, 125-128m, June 1997 [GFT lab].

Fig. 850.2: *Diplotaxodon* sp. 'offshore', mature male from Kande Island, [MJG].

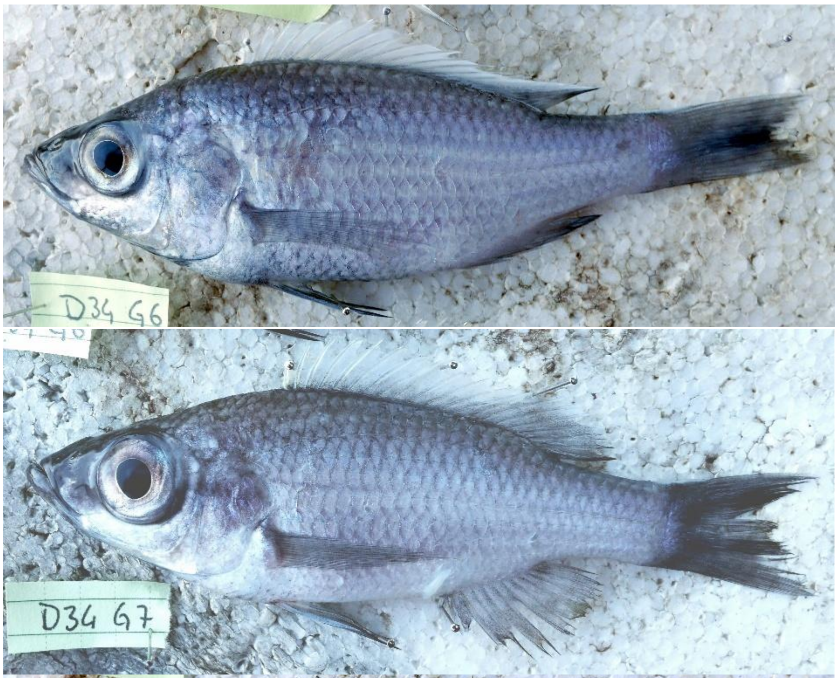


Fig. 850.3: *Diplotaxodon* sp. 'offshore', D34-G06, G07, two mature males from Nkhata Bay, 20 April 2018 [Emilia Santos].

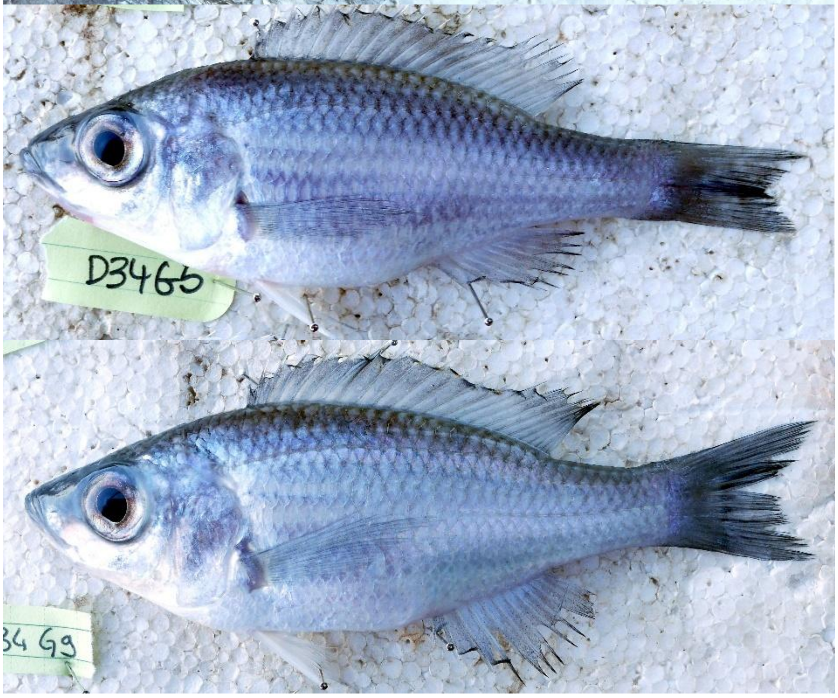


Fig. 850.4: *Diplotaxodon* sp. 'offshore', D34-G05, G09, two apparent females from Nkhata Bay, 20 April 2018 [Emilia Santos].

MC851. *Diplotaxodon* sp. 'brevimanus'

Diplotaxodon sp. 'brevimanus' was a manuscript name from the 1950s by T.D. Iles, applied to a single large specimen (209mm SL)—a presumed mature male—showing a dark body with pale dorsum and dorsal fin. It had a large rather upwardly angled mouth. The specific name 'short-hand' refers to the relatively short pectoral fins, which end anterior to the end of the pelvics. This is now regarded as conspecific to the taxon identified by Genner et al. (2010, supplement) as *D.* sp. 'similis white-back north', also appearing in Konings 2007 and 2016). Here we retain the Iles name. Genner et al. (2010) only reported the species from Chilumba and Nkhata Bay. No full genome sequences are available for this species.

Fig. 851.1: *Diplotaxodon* sp. 'brevimanus', adult male, collected by T.D. Iles in the 1950s [GFT].

Fig. 851.2: *Diplotaxodon* sp. 'brevimanus', #2005.252, adult male, from Nkhata Bay [MJG].

MC852. *Pallidochromis tokolosh* Turner 1994.

The species and monotypic genus were described by Turner (1994b), from 21 specimens from the south of the lake (fig. 852.1). The new genus was created because the species seemed intermediate between *Diplotaxodon* and *Rhamphochromis* (and also superficially quite similar to *Stigmatochromis macrorhynchos*); inclusion in *Diplotaxodon* would make that genus hard to define. The species can be identified by its overall appearance: large eyes, large mouth in a low-angled gape (24-34°, distinct from *Diplotaxodon*), strong lower jaw with large mental process, relatively small closely-packed teeth (distinct from *Rhamphochromis*) and no melanic markings beyond moderate countershading (distinct from *Stigmatochromis*). Overall, it appears much less streamlined that *Rhamphochromis* or the more elongate *Diplotaxodon* species, and specimens often have a rather flabby abdomen, probably resulting from rapid pressure changes, but more so that *Diplotaxodon* or *Rhamphochromis* from the same depth. Mature males were not known at the time of species description, but a single specimen collected in 2005 at Tukombo, just south of Nkhata Bay, shows an apparent male with a darkened upper surface and dorsal fin, which may represent full or partial development of breeding dress (fig. 852.2). The largest type was 192mm SL. The species is mainly found in deep benthic habitats, at depth of 50-125m (benthic trawlers have rarely sampled the bottom from 125-250m, so the maximum depth range is not really known). Most stomachs examined were empty but two contained remains of small benthic cichlids (Turner 1994). Genome sequence data is available for one specimen of this species (Fig. 852.3). Phylogenetic analyses indicate it is closely related to *Diplotaxodon greenwoodi*, with *D. longimaxilla* and *D. apogon* also fairly close (Camacho Garcia et al. 2025). This renders *Diplotaxodon* paraphyletic. A future revision of *Diplotaxodon* may require a new generic diagnosis to allow *P. tokolosh* to be included.

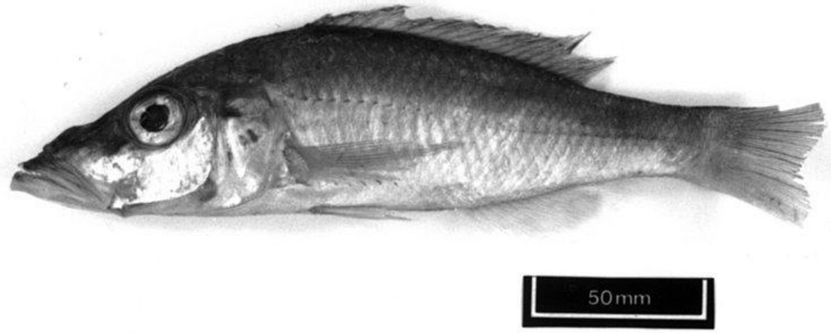


Fig. 852.1: *Pallidochromis tokolosh*, holotype [GFT lab].

Fig. 852.2: *Pallidochromis tokolosh*, #2005.181, apparent mature male, Tukombo, 6 May 2005, not sequenced [MJG].

Fig. 852.3: *Pallidochromis tokolosh*, #2004-A83SE Arm, 13 August 2004, sequenced [MJG].

Rhamphochromis Regan 1922: species MC853-867.

Family: Cichlidae; **Subfamily:** Pseudocrenilabrinae; **Tribe:** Pseudocrenilabrini; **Subtribe:** Rhamphochromina.

Type species: *Rhamphochromis longiceps* Günther 1864

Contained valid species: *Rhamphochromis esox, Rhamphochromis ferox, Rhamphochromis longiceps, Rhamphochromis lucius, Rhamphochromis macrophthalmus, Rhamphochromis woodi*

Proposed undescribed taxa: *Rhamphochromis* sp. 'chilingali', *Rhamphochromis* sp. 'grey', *Rhamphochromis* sp. 'kingiri brevis', *Rhamphochromis* sp. 'kingiri dwarf', *Rhamphochromis* sp. 'long-fin yellow', *Rhamphochromis* sp. 'longiceps yellowbelly', *Rhamphochromis* sp. 'long-snout', *Rhamphochromis* sp. 'maldeco', *Rhamphochromis* sp. 'nkhwazi'.

Taxa considered invalid: *Rhamphochromis brevis* Trewavas 1935 (=*R. woodi*), *Rhamphochromis leptosoma* Regan 1922 (=*R. esox*), *Rhamphochromis melanotus* Ahl 1926 (=*R. esox*).

Taxa of uncertain status: none.

Generic reviews & diagnoses: Regan 1922a, Trewavas 1935, Eccles & Trewavas 1989; Turner et al. 2004. No new species has been described since 1935, although we consider there are at least nine undescribed species, including the largest endemic cichlid species in Lake Malawi.

Generic diagnosis: “Slender, long-headed large mouthed predatory haplochromines endemic Lake Malawi attaining from 230 to over 350 mm SL. The premaxillaries are beak-like; the teeth are stout, unicuspid, erect but recurved at the tips and well-spaced, with the gaps between them more than the tooth diameter. The anterior teeth of the inner rows are enlarged, approaching the size of the outer ones. The melanin pattern consists of horizontal stripes or of simple counter-shading. There are 36 to 40 vertebrae, of which 17-18 are abdominal.” (Eccles & Trewavas 1989). Additionally, it should be noted that mature males of all known species show some development of yellow-orange colour, at least in the pelvic fins, but in some cases extending across the body.

Field Diagnosis: Slender, streamlined predatory-looking species with big teeth. Maybe with a faint horizontal band, or orange lower fins or underside. Generally recognised as Ncheni or Mcheni, or for bigger ones, Batala (butterfish), or Sangwe for smaller ones.

Phylogenetic comments: *Rhamphochromis* form a clear clade in all molecular analyses to date. Along with *Diplotaxodon/Pallidochromis*, they are resolved as the first endemic subradiation to have diverged from the stem *Astatotilapia*.

Ecomorphological notes: *Rhamphochromis* are typically midwater-feeding predators. Juveniles of the larger species and adults of the smaller species feed on zooplankton. Adults of some of the smaller species feed on the shoaling Lake Malawi ‘sardine’ *Engraulicypris* *sardella*. Adults of the larger species are piscivores. Species seem to vary in microhabitat preferences, some preferring rocky areas, others soft-sediment bottoms, many truly pelagic. A few species seem to have shallow water nursery areas in muddy lagoons or rocky shores. Several are satellite lake endemics. Maternal mouthbrooders, they are not known to dig in the substrate during breeding seasons. Where known, they spawn in midwater, females spinning round to catch newly released eggs in the water column.

MC 853. *Rhamphochromis esox* (Boulenger 1908)

Described as *Paratilapia esox* from three specimens (one, a skeleton), by Boulenger (1908), this was the second species to be described in what we now know as *Rhamphochromis*. It is large species with a very slender, cylindrical body and a long caudal peduncle. The lower jaw is strong, deep and smooth and the teeth are generally not visible with the mouth closed. There is some variation in the head shape, with some individuals having a relatively upwardly-angled mouth and projecting premaxillary pedicel. Others with a less upwardly-angled mouth and smoother upper head profile include the type of *Rhamphochromis leptosoma* Regan 1922 (fig. 853.6), which is considered a junior synonym by Turner et al. (2004). *Rhamphochromis melanotus* Ahl 1926 was also synonymised by Trewavas (1935), but this has not been checked subsequently. A lectotype for *R. esox* was designated by Turner et al. (2004) as BMNH 1908.10.27.62 (fig. 853.1). Small individuals are often found in shallow sandy or rocky areas, and often show a strong horizontal stripe, rarely seen in adults. Adults often have a blue sheen dorsally. Mature males have orange pelvic and anal fins. Males sometimes show 2-9 orange eggspots, but they are largely obscured when the anal fin is most vividly coloured. Turner et al. (2004) report a maximum size of 420mm SL (Yang et al. report 383.6mmSL), a lakewide distribution, and noted that ripe females were found near Nkhata Bay in June. Mature females were found as small as 187mm SL, and males from 204mm SL. Females could carry between 115 and 680 eggs, which are up to 5mm in diameter. They were found in relatively shallow waters, above lakebeds at 2-65m. The species was found to be common even in the heavily-fished southern part of the lake in trawl surveys from 2016 onwards, often mixed with *Engraulicypris sardella* and *Rhamphochromis macrophthalmus*. Dorsal fin XVIII-XXI, 11-13, Anal fin III, 9-11, Longitudinal scale rows 40-42, Lower gillrakers 14-17, teeth simple, erect, in 2 rows.

Full genome sequences are available from three specimens. One, included in analyses by Blumer et al (2025), is a large individual from Tukombo on the central Malawian coast between Nkhotakota and Nkhata Bay (2004-328). This specimen is clearly *R. esox*, based on its very elongated streamlined body, deep smooth lower jaw and long caudal peduncle (fig. 853.2). A second small juvenile (code D08-C10) from Chiofu is very likely to be the same species (fig. 853.5), and these two specimens cluster closely on a phylogenetic tree based on genome-wide data. An additional sequenced specimen, included in an analysis by Yang et al. (ms), was obtained from a batch of five adult males collected at Nkhata Bay in 2004 (fig. 853.3-4). The phylogenetic analysis based on whole genome data indicates *R. esox* is most closely related to *R. lucius* (Yang et al. ms).

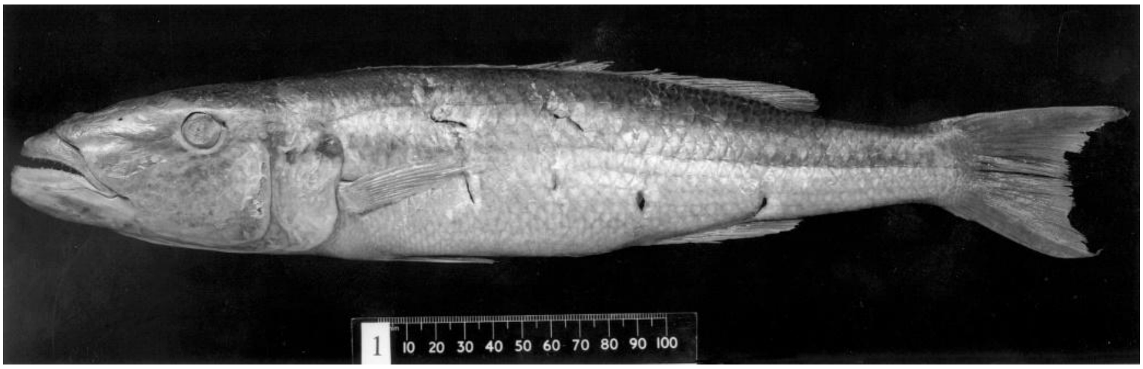


Fig. 853.1: *Rhamphochromis esox* type. BMNH 1908.10.27.62, 319mm SL.

Fig. 853.2: *Rhamphochromis esox*, 2004-328, collected from Tukombo, 27 July 2004 [MJG]

Fig. 853.3: *Rhamphochromis esox*, 2004-122a, Nkhata Bay, male with partly developed breeding dress, showing anal fin eggspots and pale orange pelvics, 27 Oct 2004 [MJG]

Fig. 853.4: *Rhamphochromis esox*, 2004-122c, Nkhata Bay, male with more developed breeding dress, showing anal fin eggspots on an orange anal fin base, and more strongly coloured orange pelvics, 27 Oct 2004 [MJG].

Fig. 853.5: *Rhamphochromis esox*, juvenile, D08-C10, SCUBA, Chiofu, 28 Feb 2016 [HS].

Fig. 853.6: *Rhamphochromis esox* BMNH 1908.10.27.63, 331mm SL. Originally a syntype of *R. esox*, this specimen was later taken as the holotype of *R. leptosoma*.

MC854. *Rhamphochromis ferox* Regan 1922.

Rhamphochromis ferox was described by Regan (1922a) from two syntypes in 1922, which had been included in *R. longiceps* (then *Champsochromis longiceps*) by Boulenger (1915). Turner et al. (2004) consider that one of them is probably *R. longiceps* after all, and designated the other as the lectotype, BMNH 1906.9.7.22 (fig. 854.1). It is a moderate-sized individual (179mm SL) with slender jaws and fairly long, widely-spaced slender teeth (compared to the smaller, more closely-packed teeth of *R. longiceps*). Turner et al. did not positively identify this species in their collections, but Genner et al. (2007b) did study a sample of *R.* cf. *ferox*, which we now identify as *R. ferox*. Mature males have bright orange pelvic and anal fins, contrasting with the translucent anal fins (with eggspots) of *R. longiceps* and *R. macrophthalmus* males (fig. 854.2). Females and immatures are hard to identify except by sequencing, although examination of the teeth and shape of the premaxillae may provide useful identifying characteristics (fig 854.5). Adults can be up to 285mm SL, which is middle-sized for a *Rhamphochromis*. Most specimens have been collected in the southern arms of the lake, although a specimen has been collected from Nkhotakota (fig. 854.3). Genome sequences for six specimens are available. Five were included in an analysis by Blumer et al. (2025). One of them was positively identified phenotypically (fig. 854.2); the others are a reasonable fit (fig. 854.4), but importantly, clustered with the more clear-cut specimen in a phylogeny based on the whole genome data. A sixth additional mature male (fig. 854.3) has been included in the analysis of Yang et al. (ms). Based on these genome-wide data, *Rhamphochromis ferox* is phylogenetically divergent from other species in the main lake, but it is closely related to satellite lake species from Lake Chilingali and Lake Kingiri.

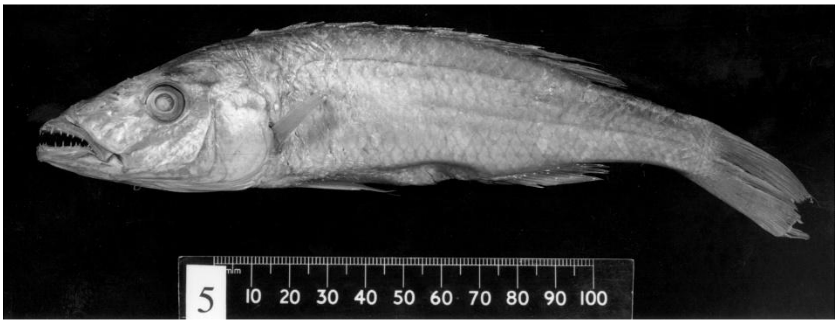


Fig. 854.1: *Rhamphochromis ferox*, Regan 1922a, lectotype, ca 179mm SL.

Fig. 854.2: *Rhamphochromis ferox*, male, D13-A02, 21cm SL, trawled from 30-40m depths off Makanjila, 2 March 2016 [HS]

Fig. 854.3: *Rhamphochromis ferox*, male, 2004.325A, purchased from fishers, Nkhotakota, 26 July 2004. Image reversed [MJG]


D12-C06


D12-C07


D12-C08


D12-D03

Figure 854.4: Specimens sequenced by Blumer et al. were all collected from trawling at 20m depths off Makanjila, 2 March 2016. All are characterised by their slender body shape, with shallower cheek and larger jaw teeth than *R. longiceps*. These are a good fit with the type of *Rhamphochromis ferox* and with the larger male D13-A02 [HS].


Rhamphochromis ferox Lectotype

Rhamphochromis longiceps Lectotype

Rhamphochromis macrophthalmus Type

Figure 854.5: Comparison of the jaws of types of the smaller *Rhamphochromis* species, showing the larger, more widely spaced teeth of *R. ferox*, particularly in comparison to *R. longiceps*. Not also that a large number of relatively large teeth are visible along the jaws in comparison to *R. macrophthalmus*, where only a few teeth can be seen on a similar degree of opening. Also, the premaxillae are more projecting rostrally, particularly noticeable on the upper profile.

MC855. *Rhamphochromis longiceps* (Günther 1864).

Rhamphochromis longiceps was the first species of the genus to be described (as *Hemichromis*, later *Champsochromis*), having been collected in the course of the early Livingstone expeditions. Günther (1864) worked with a couple of dried half-skins. Despite the poor quality of the types, the lectotype (fig. 855.1) can be identified with some certainty on the basis of its deep cheek, slender jaws and especially the relatively small, closely-packed teeth. In the works of Boulenger, a number of specimens were included in this species that were later removed to other species, so that the redescription in his 1915 volume showed a drawing of what was later to become a type of *R. woodi*. A number of specimens in later collections have correctly been identified with *R. longiceps*, from Regan (1922a), Trewavas (1935) and Eccles & Trewavas (1989). In the latter work, a drawing of a specimen from a collection made by Cuthbert Christy (collected 1925-26, registered 1935) was used to represent the species (see photo in figure 855.2). Interestingly, Günther's original description recorded that the upper parts of the specimens were dark green, which is true of females and juveniles of this species, and distinctive among *Rhamphochromis*, so far as is known. However, mature males have dark blue iridescence. Mature males also have bright orange pelvic fins, and are darker dorsally, including the dorsal fin, and also on the pectoral and caudal fins (fig. 855.3). Full genome sequences are available for five individuals. A single probable female included in analyses by Blumer et al. (2025) has small teeth and a deep cheek (Fig. 855.4). An additional four mature males in breeding dress (figs 855.4-5) were included in a phylogenetic analysis by Yang et al. (ms): these all cluster together.

Field surveys focussed on Lake Malawi fisheries have not distinguished this species from *R. macrophthalmus*, but that species has rather larger, more widely-spaced teeth, bigger eyes and a shallower cheek. Male breeding colours seem to be almost identical, and both mature at around the same size. Laboratory work by Turner et al. (2004) differentiated this species from *R. macrophthalmus* (under the name *R.* 'slender') but only after completion of fieldwork. Thus, ecological information in this and previous studies is therefore probably a composite these two species (e.g. Turner 1996, Allison et al. 1996, Turner et al. 2004). Both *R. longiceps* and *R. macrophthalmus* are found throughout the lake, including the open waters above the anoxic zone, feeding on crustacean zooplankton when small, when larger transitioning to larvae and juveniles of usipa, the pelagic danionid *Engraulicypris sardella*. Sexual maturity is attained at 109 (M) - 130 (F) mm SL. The maximum size is 204.7mm SL (Yang et al. ms). Ripe females contained 52-76 eggs of about 4mm diameter, and were reported throughout the year and all around the lake (Turner et al. 2004). Work by Genner et al. (2007b, 2008) did distinguish the species from *R. macrophthalmus* (with that species going under the name *R.* 'longiceps grey back'), and reported that *R. longiceps* is unusual in that mouthbrooding females congregate in shallow lagoons or river mouths to release their fry (Genner et al. 2008). This led to the suggestion that this species was the likely the closest relative of the satellite lake taxa (Genner et al. 2007b). This idea has not been supported by molecular phylogenetic analyses of the genome-wide data, which instead shows *R. ferox* to be the sister group to the Lake Chilingali and Kingiri populations (Yang et al. ms). Genomic data indicates that *R. longiceps* lies basally within the *Rhamphochromis* clade and is not closely related to *R. macrophthalmus* (Yang et al. ms).

Fig. 855.1: Type of *Hemichromis longiceps* Günther 1864. BMNH 1863.12.21.5.

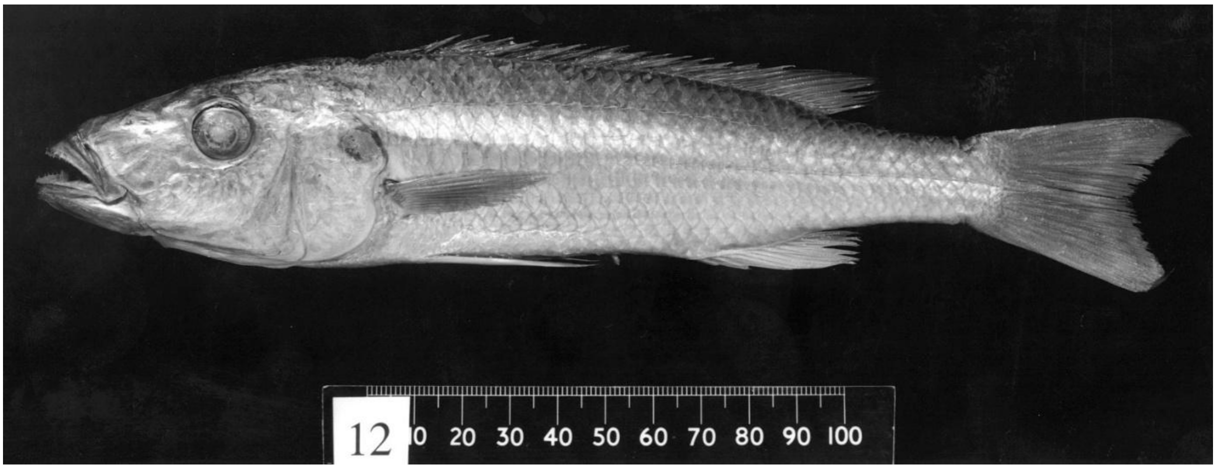


Fig. 855.2: *Rhamphochromis longiceps,* non-type specimen BMNH 1935.6.14.2177, 195mm SL. A drawing of this specimen was used to illustrate the redescription by Eccles & Trewavas (1989), here photographed in the 1990s.

Fig. 855.3: *Rhamphochromis longiceps,* freshly collected mature male 2005.19a, showing typical orange pelvic fins and orange eggspots on the anal fin. Collected at Salima, 27 Aug 2005 [MJG].

Fig. 855.4: *Rhamphochromis longiceps,* D13-A06, 17cm SL, trawled from 30-40m, off Makanjila, 2 March 2016, sequenced by Blumer et al. (2025) [HS]

Fig. 855.5: *Rhamphochromis longiceps,* 2004.A62, mature male, SE Arm, Nkhudzi, 13 Aug. 2004, sequenced by Yang et al. [MJG]

Fig. 855.6: *Rhamphochromis longiceps*, 2004.346a-c, SW Arm, Chipoka, 28 July 2004: all three sequenced by Yang et al [MJG]

MC856. *Rhamphochromis lucius* Ahl 1926.

The species was described by Ahl (1926) from two specimens from Langenburg in Tanzania (fig. 856.1) and has since remained unrecognised in the field, suggested as a possible junior synonym of *R. woodi* by Turner et al. (2004) and of *R. esox* by Konings (2016), the latter accepted by Fricke et al. (2025) at time of writing. In addition, a number of specimens in the London Natural History Museum are erroneously labelled as *R. lucius*, so identification via the collections or published works such as Trewavas (1935) or Eccles & Trewavas (1989) are unreliable. We have examined the type from Berlin, and identified *R. lucius* with a taxon previously reported as *R.* sp. 'stripe', which was previously tentatively suggested by Turner et al. (2004). This form has been present in subsequent field collections as a consistent phenotype often collected in steeply-shelving rocky areas (fig. 856.2-5).

Rhamphochromis lucius is characterized by its extremely long, head and snout, but with generally smooth contours around the snout and jaws, in contrast to the jutting premaxillary pedicel and lower jaw angles of *R. woodi* and *R.* sp. 'nkhwazi'. The jaws are large and robust, and the lips thick and slightly fleshy. In contrast, the lips of *R. woodi* and *R.* sp. 'longfin' are bonier, and the roots of the teeth often tend to show through the jaw surface, particularly rostrally. The snout profile of *R. lucius* is generally more horizontal than in *R.* sp. 'longsnout', where it tends to be deflected downwards. It is generally stockier than *R. esox*, with a deeper caudal peduncle. *Rhamphochromis lucius* also has a more contoured lower jaw, as opposed to the deep, smooth lower jaw of *R. esox* and *R.* sp. 'maldeco'. Among large *Rhamphochromis*, it is unusual in persistently exhibiting a dark midlateral stripe (noted by Ahl in the original description), although this is also often shown by smaller specimens of *R. esox*. Larger specimens are often very dark overall (fig. 856.4). Mature males have orange pelvic and anal fins (fig. 856.3).

Genome wide data are available for a single specimen, and included in the analysis by Yang et al. (ms). This fish was collected from a trawl near Chinyamwezi Island (fig. 856.5), and is a large-heavily-built ripe female, exhibiting a strong mid-lateral stripe. Phylogenetic analyses based on the genome-wide data indicates that *R. lucius* is the sister species to *R. esox*.

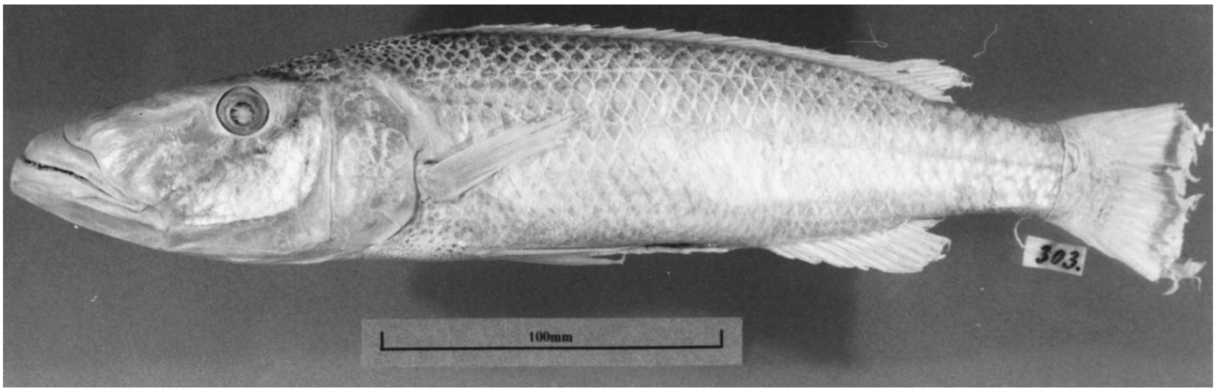


Fig. 856.1: *Rhamphochromis lucius* lectotype ZMB 303, 307mm SL.

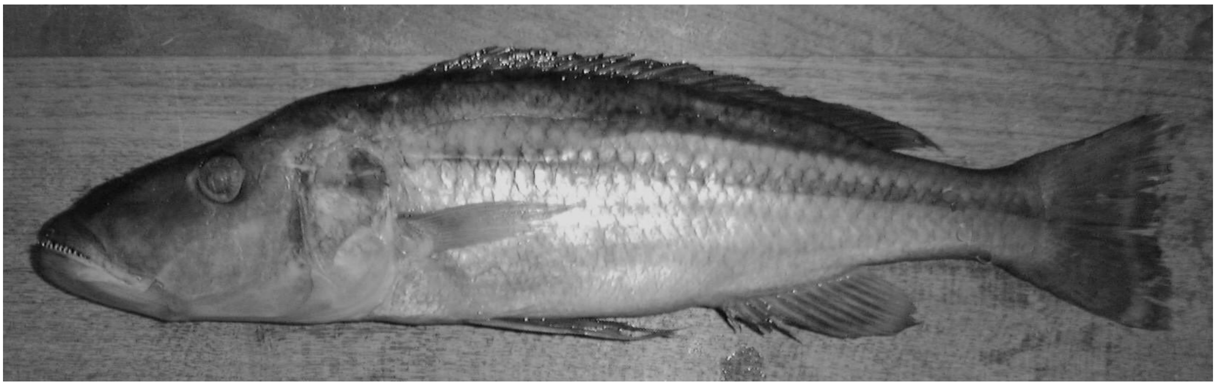


Fig. 856.2: *Rhamphochromis lucius* #2444, Likoma Island 1977, 322mm SL [GFT].

Fig. 856.3: *Rhamphochromis lucius* male, 2005.449, trawled from SE Arm, 2 June 2005 [MJG]

Fig. 856.4: *Rhamphochromis lucius* purchased from fish traders at Nkhata Bay, October 2023 [GFT].

Fig. 856.5: *Rhamphochromis lucius*, 2004.449, ripe female, trawled from 80-90m depth, SE Arm, near Chinyamwezi Island, 16 Nov 2004, sequenced by Yang et al ms. [MJG]

MC857. *Rhamphochromis macrophthalmus* Regan 1922.

Rhamphochromis macrophthalmus was described by Regan (1922a) from three specimens ranging from 167-197mm SL. They were distinguished from most other species by their relatively larger eyes, and from *R. esox* by their less elongated body shape and from *R. longiceps* by their larger, more widely spaced teeth. This species proved problematic to identify in the field. For a while it was imported as an aquarium fish and correctly identified, but Eccles & Trewavas (1989) mistakenly identified it as a larger species which often had a brownish cast and was common in deep-water trawl catches, and this was carried on by Turner et al. (2004). We now identify the 'benthic brown' species as the undescribed *Rhamphochromis* sp. 'longsnout'. A key observation is that Regan noted that the type specimens of *R. macrophthalmus* had orange pelvic and anal fins (no longer visible), indicating them as mature males, suggesting they were unlikely to grow much larger. So, it is a small species. Konings (2016) stated it as a junior synonym of *R. longiceps*, and this is accepted by Fricke et al. (2025) at time of writing. We consider it to be distinct species, formerly identified as *Rhamphochromis* sp. 'slender' by Turner et al. (2004) and as *R.* 'longiceps grey back' by Genner et al. (2007b). *R. longiceps* and *R. macrophthalmus* have similar male breeding colours and sizes at maturity, but *R. macrophthalmus* has larger, more widely-spaced teeth (see fig. 857.5), a larger eye and shallower cheek (fig 857.1). *R. macrophthalmus* is probably the most abundant *Rhamphochromis* species in Lake Malawi, but ecological information has been confused with *R. longiceps*, although some differentiation has been possible in the *post-hoc* reanalysis of data by Turner et al. (2004). Based on that reanalysis, it seems that *R. macrophthalmus* is more common than *R. longiceps* in open water habitats. *R. macrophthalmus* is also not known to use lagoons and river mouths as nursery areas. Turner et al. (2004) report mature males as small as 138mm SL and females to 143mm SL, slightly larger than *R. longiceps*. Genner et al. (2007b) report a maximum size of 214mm SL. Ovaries of ripe females contained 27-68 eggs. Ripe individuals were collected throughout the year, and it was found all round the lake.

Genome data are available from 12 specimens from throughout the lake - Chilumba, Nkhata Bay, Chiofu, SW Arm and the SE Arm off Monkey Bay (fig. 857.2-3). Those data were analysed by Blumer et al. (2025), and were included in the phylogenetic analyses by Yang et al. (ms), where they formed a clade only distantly related to *R. longiceps*.

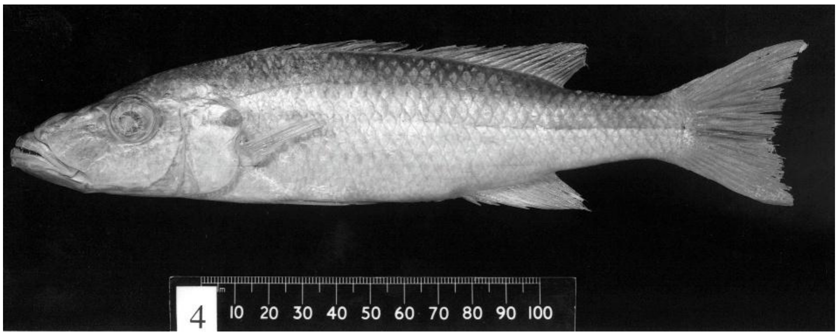


Fig. 857.1: Syntype of *Rhamphochromis macrophthalmus*, BMNH 1921.9.6.217 [NHM].

Fig. 857.2: *Rhamphochromis macrophthalmus,* D02-C03, male, 17cm SL, bought from fishermen, Nkhata Bay, 21 Feb 2016 [HS].

D02-I10, male, 16.5cm SL, bought from fishermen, Nkhata Bay, 21 Feb 2016.

D02-J01, male 17cm SL, bought from fishermen, Nkhata Bay, 21 Feb 2016

D02-J02, male 17.5cm SL, bought from fishermen, Nkhata Bay, 21 Feb 2016

D03-D05, male 17.5cm SL, bought from fishermen, Nkhata Bay, 21 Feb 2016

Fig. 857.3: Four *Rhamphochromis macrophthalmus* mature males collected from Nkhata Bay, showing orange pelvic fins, and a translucent anal fin with conspicuous orange eggspots, surrounded by a white margin. A sixth specimen, D01-A05 looks similar. Sequenced by Blumer et al. (2025), [HS].

D10-D01, female 18cm SL, bought from fishermen, Chiofu, 29 Feb 2016

D11-D08, *Rhamphochromis macrophthalmus*, male 16cm SL, trawled from 85-95m off Monkey Bay, 4 March 2016

D12-B10, *Rhamphochromis macrophthalmus*, male 17cm SL, trawled from 85-95m off Monkey Bay, 4 March 2016

D14-E09, *Rhamphochromis macrophthalmus*, 16.5cm SL, trawled from 40-48m in SW Arm, 4 March 2016

Fig. 857.3: Photographs are available for an additional four additional sequenced specimens of *Rhamphochromis macrophthalmus,* from Chiofu, Monkey Bay and SW Arm, representing both sexes. No photographs are available for the two Chilumba specimens (D04-H05, D04-I08), but they cluster with the others [HS].

MC858. *Rhamphochromis* sp. 'chilingali'.

In 2004, an undescribed small-bodied *Rhamphochromis* was discovered in satellite Lake Chilingali, near Nkhotakota, on the Kaombe River a few kilometres to the West of the shoreline of the central part of Lake Malawi (Genner et al. 2007b; Turner et al. 2019; Yang et al. ms.). It has relatively large widely-spaced teeth on small delicate jaws. Mature males have orange pelvic and anal fins (fig. 858.1): when actively courting, they lose their countershading and become more uniformly mid-grey, while the orange ventral colour can extend to the lower part of the trunk, caudal peduncle and caudal fin, as well as the throat membrane. The pelvic and anal fins can become darker distally. Sometime dark vertical bars can be seen. The species mainly feeds on planktonic invertebrates, particularly chaoborid larvae and pupae. Adult males ranged from 76-106mm SL (Genner et al. 2007b), although they will reach 15cm SL in captivity (fig. 858.2). Females spawn in midwater and catch the eggs as they drop. There are no records of females defending free-swimming fry. The species has not been collected scientifically in the wild since samples obtained from fishers catches on 12 January 2011 (by MJG, Turner et al. 2023). After this, the dam built to expand the lake collapsed, between June and September 2014 (Turner et al. 2019; 2023). It is not known from any other location. Genome sequence data are available from 11 specimens. Data from eight were included in the study of Blumer et al. (2025), 7 collected from the wild and one from an aquarium strain. Data from a further three specimens were analysed by Yang et al. (ms). In these cases, tissue samples were collected in batches and illustrations of individuals are not available. All specimens clustered together in a single clade and showed close affinities with the satellite lake population from Lake Kingiri, along with *Rhamphochromis ferox*- notably all are species with delicate jaws with large, widely spaced teeth and males with uniformly orange anal fins.

Fig. 858.1: *Rhamphochromis* sp. ‘chilingali’, male, Lake Chilingali, June-July 2009.

Fig. 858.2: *Rhamphochromis* sp. ‘chilingali’, aquarium strain, showing larger size attained in captivity [GFT].

MC859. *Rhamphochromis* sp. 'grey'.

This undescribed species was first reported by Turner et al. (2004). It is a medium-sized deep-bodied species (up to 322mm SL) with a small mouth, rather delicate jaws and a laterally compressed, straight snout. It tends to be dark overall, and less countershaded than other *Rhamphochromis*. The species is most commonly found at Nkhata Bay, so it may prefer rocky habitats. Adults are metallic silver, most strikingly on the head, with darker fins (fig. 859.1-2). Mature males are darker overall with the dorsal, pelvic and anal fins suffused with orange (fig. 8592.3-4). Genome data are available for four specimens. One very silvery specimen collected at Nkhata Bay in 2016 (fig. 859.2) was included in an analysis by Blumer et al. (2025). Three additional specimens were included in the analysis by Yang et al. (ms), sampled from a batch of seven mature males, of which two examples are illustrated (fig. 859.3-4). Phylogenetic analyses of these genome-wide data suggests *R.* sp. 'grey' is a sister species to the much larger, big mouthed *R. woodi*.

Fig. 859.1: *Rhamphochromis* sp 'grey', Mature male, freshly collected from Nkhata Bay, 2016 [GFT].

Fig. 859.2: *Rhamphochromis* sp. 'grey' 25cm SL, D03-D04, bought from fish traders, Nkhata Bay, 21 Feb 2016 [HS].

Fig. 859.3: *Rhamphochromis* sp 'grey', #2004. 121, mature male, collected from Nkhata Bay, 27 Oct 2004 [MJG].

Fig. 859.4: *Rhamphochromis* sp 'grey', #2004. 121, mature male, collected from Nkhata Bay, 27 Oct 2004 [MJG].

MC860. *Rhamphochromis* sp. 'kingiri large'.

Rhamphochromis sp. 'kingiri large' (recorded as 'kingiri brevis' in early records) was collected in 2011, from crater Lake Kingiri to the north of Lake Malawi (in Tanzania), where it co-occurs with a much smaller and more abundant species within this tiny lake (Turner et al. 2019; Yang et al. ms). It is easily distinguished by its size and location. A sample of eight adults ranged from 153-205mm SL, well above the maximum size of 69mm SL reported for *R*. sp. 'kingiri dwarf' found in the same lake. Genome data are available for nine individuals. One specimen (fig. 860.1) was included in an analysis by Blumer et al. (2025). This fish was taken from a batch of five adult males obtained from gillnets in July 2011. The remaining four specimens were included in the analysis by Yang et al. (ms), along with an adult female and a juvenile (not photographed) from the same time and place, and an additional two adult males from November 2011 (fig. 860.2). The species has not been reported since 2011. Phylogenetic analyses of these data show individuals cluster in a clade, and are differentiated from *R*. sp. 'kingiri dwarf' (Yang et al. ms).

Figure 860.1: *Rhamphochromis* sp. 'kingiri large', 5 adult males were collected together, one of which was sequenced by Blumer et al. (2025); 4 by Yang et al ms, Lake Kingiri, 15 July 2011 [MJG].

Figure 860.2: *Rhamphochromis* sp. 'kingiri large', adult male 3C2, sequenced by Yang et al. ms, collected 26 Nov 2011 [MJG].

MC861. *Rhamphochromis* sp. 'kingiri dwarf'.

Rhamphochromis sp. ‘kingiri dwarf’ was collected in 2011, from crater Lake Kingiri to the north of Lake Malawi (in Tanzania), where it co-occurs with a much larger and scarcer species *R*. sp. ‘kingiri large’ within this tiny lake, which is about 600m in diameter and 34m deep (Turner et al. 2019; Yang et al. ms). Mature males are easily distinguished by their bright orange pelvic and anal fins, shown at sizes of 57-69mm SL. Large numbers of courting adult males were seen chasing after females (many mouthbrooding), around a sunken tree at a depth of about 5m in March 2015. Underwater photographs show that mature males may show faint vertical bars and brooding females horizontal melanic elements (figs. 861.3-4). Otherwise, little is known of their ecology.

Full genome data are available for eight specimens. Data from one specimen (fig. 861.1) were analysed by Blumer et al. (2025), taken from a batch of two adult males collected in July 2011. Data from an additional seven specimens from collections also made in 2011 (figs. 861.2-3) were analysed by Yang et al. (ms). Phylogenetic analyses of these genome-wide data indicate indicate the species is very closely related to *R*. sp. ‘kingiri large’, and its nearest relatives from elsewhere are *Rhamphochromis* sp. ‘chilingali’- another dwarf satellite lake species, and the larger *R. ferox* from the main body of Lake Malawi.

Fig. 861.1: *Rhamphochromis* sp. ‘kingiri dwarf’, males, one of batch 2011.384 was sequenced, Lake Kingiri, 21 July 2011 [MJG]

Fig. 861.2: *Rhamphochromis* sp. ‘kingiri dwarf’, 2011.1 sequenced, Lake Kingiri, 14 July 2011 [MJG]

Fig. 861.3: *Rhamphochromis* sp. ‘kingiri dwarf’, two of 2011.89A-C sequenced, Lake Kingiri, 15 July 2011 [MJG]

Fig. 861.4: *Rhamphochromis* sp. ‘kingiri dwarf’, adult male photographed underwater, 2016 [AK]

Fig. 861.5: *Rhamphochromis* sp. ‘kingiri dwarf’, mouthbrooding female, showing considerable development of horizontal melanic elements, 2016 [AK]

MC862. *Rhamphochromis* sp. 'longfin yellow'.

Rhamphochromis sp. ‘longfin yellow’ (or sometimes just ‘longfin’) was first reported by Turner (1996) from the SE Arm of Lake Malawi (fig. 862.1). Mature males are conspicuous by their long pelvic fins and their extensive bright yellow-orange colour which can cover all of the lower half of the body and fins, sometimes even more. Females and immatures are generally harder to identify, but have short bodies, large eyes, large upwardly-angled mouths with long, slender, widely-spaced teeth and the head profile is generally disrupted by a prominent premaxillary pedicel and posterior lower jaw angle. The lower jaw juts out beyond the upper jaw. Mature adults are reported to range from 160 to 247mm SL (Yang et al. ms). It is found throughout the coastal areas of the lake, often in deep water, in bottom trawl catches, but occasionally can be caught in quite shallow waters. Genome data are available for three specimens. One single specimen, included in analyses by Blumer et al. (2025) had weakly developed fins and breeding dress, but characteristic body proportions, jaws and teeth (fig. 862.2). Data from two additional specimens were included in analyses by Yang et al. (ms) included one specimen with well-developed breeding dress (figs. 862.3-4). Phylogenetic analyses of these genome-wide data indicate the species is most closely related to *R.* sp. ‘longsnout’, *R.* sp. ‘nkhwazi’ and *R.* sp. ‘maldeco’.

Fig. 862.1: *Rhamphochromis* sp. ‘longfin’ male, trawled from 24-28m, SE Arm, Palm Beach to Maldeco, 21-Oct-91 [GFT].

Fig. 862.2: *Rhamphochromis* sp. ‘longfin’, D13-J06, male, 18cm SL, trawled from Cape Maclear, 4 March 2016 [HS]

Fig. 862.3: *Rhamphochromis* sp. ‘longfin’, 2005.119, male, Nkhata Bay 6 Feb 05 [MJG]

Fig. 862.4: *Rhamphochromis* sp. ‘longfin’, 2005.426, male, S Arm 1 June 05 [MJG]

MC863. *Rhamphochromis* sp. 'longiceps yellowbelly'

This species was first reported by Genner et al. (2007b). It is a small slender species, with mature males ranging from 151-206mm SL. Males can be differentiated from those of *R. longiceps* and *R. macrophthalmus* by the solid orange anal fin, as opposed to translucent fins with eggspots (figs 863.1-3). In full breeding dress (fig. 863.1), the dorsal fin and lower half of the caudal are also orange, and the underside of the throat, trunk and caudal peduncle too. The edges of the upper part of the caudal, the pelvics and the margins of other fins, along with the snout and chin are darkened. Full genome data from single specimen with orange pelvic and anal fins was included in analysis Blumer et al. (2025), and may possibly be a non-breeding male of this species (fig. 863.4). However, this specimen lacks the characteristic yellow-orange coloration of the dorsal fin and lower half of the anal fin, seen in males of this species. Phylogenetically, this specimen seems to be distinct from other *Rhamphochromis* and possibly basal, assuming this is not a sequencing artifact.

Fig. 863.1: *Rhamphochromis* sp. 'longiceps yellow belly' male, 2005-382ii, Nkhata Bay, 13 May 05, [MJG]

Fig. 863.2: *Rhamphochromis* sp. 'longiceps yellow belly' male, 2005-391iii, Nkhata Bay, 15 May 05, [MJG]

Fig. 863.3: *Rhamphochromis* sp. 'longiceps yellow belly' male, 2005-391i, Nkhata Bay, 15 May 05, [MJG]

Fig. 863.4: *Rhamphochromis* cf. 'longiceps yellow belly' D13-B01, 19cm SL, trawled from 30-40m, off Makanjila, 2 March 2016 [HS].

MC864. *Rhamphochromis* sp. 'long-snout'.

Rhamphochromis sp. ‘longsnout’ was first identified as a new species by Turner (1996) who noted it as common in deep-water trawl catches, generally over bottom depths of 40-100m in the southern arms. The generally brownish colour of non-breeding individuals, and rather flaccid belly and non-streamlined shape, combined with relatively large eye and long often downwardly-angled snout were distinctive features (fig. 864.1), and possibly suggested a slower-moving benthic feeding habit than is usual for *Rhamphochromis*. The mouth is moderate-sized without a very prominent premaxillary pedicel. The lower jaw is fairly strong and deep, with a rather contoured appearance, in contrast to the smooth-jawed *R. esox* and *R.* sp. ‘maldeco’. Mature adults ranged from 231-321mm SL. Subsequently Turner et al. (2004) discussed the same species under the name *R. macrophthalmus*, but Genner et al. (2007b) returned to *R.* sp. ‘longsnout’, although referring to *R.* sp. ‘longsnout south’. Mature males are darker on the upper surface and have orange pelvic and anal fins (fig. 864.2). Genome-wide sequence data are available for eight specimens. Three specimens were included in analyses by Blumer et al. (2025)—one mature male from Nkhata Bay (fig. 864.2) and two specimens from the south (fig. 864.3-4). An additional five specimens were included in analyses by Yang et al. (ms), two from the northern region of Malawi, and three males from the south (figs. 864.5-6). In each case, northern and southern specimens cluster together, but as sister clades. The full set of eight individuals have not yet been analysed collectively. In phylogenetic analyses of the genome-wide data from both studies, the sister group is *R.* sp. ‘longfin’, while *R.* sp. ‘nkhwazi’ and *R.* sp. ‘maldeco’ are close relatives.

Fig. 864.1: *Rhamphochromis* sp. ‘longsnout’ (left) SE Arm, Chirombo-Nkhudzi 29 Feb 1991 [GFT]; (right) #900, SE Arm, north of Boadzulu Is. 1996-98 [RL Robinson].

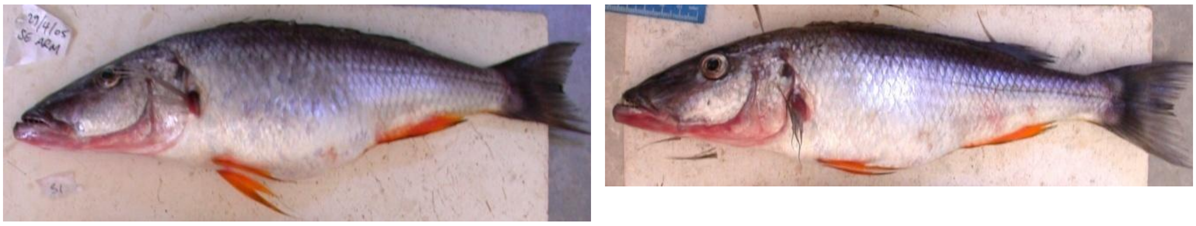
Fig. 864.2: *Rhamphochromis sp.* ‘longsnout’, D02-C02, male, 21cm SL, bought from fish traders, Nkhata Bay, 21 Feb 2016 [HS].

Fig. 864.3: *Rhamphochromis* sp. 'longsnout', D11-C02, 21cm SL, trawled from 85-95m off Monkey Bay, 2 March 2016 [HS]

Fig. 864.4: *Rhamphochromis* sp. 'longsnout', D13-J04, 26cm SL, trawled off Cape Maclear, 4 March 2016 [HS].

2005-83 2005-84

Fig. 864.5: *Rhamphochromis* sp. 'longsnout', Nkhata Bay, 4 Feb 2005 [MJG]



2005-31a-d 2005-31-a-d

Fig. 864.6: *Rhamphochromis* sp. 'longsnout', SE Arm, 29 Apr 2005- 3 specimens from a batch of 4 were sequenced [MJG]

MC865. *Rhamphochromis* sp. 'maldeco'

The species was first identified by Turner et al. (2004) and reported as *R.* sp. ‘maldeco yellow’ by Genner et al. (2007b). Overall, they are deep bodied, but rather streamlined with smooth head contours. No trace of a horizontal stripe is apparent. The cheek depth is greater than in *R.* sp. ‘grey’, and individuals have smaller mouths than those of *R. woodi* and *R.* sp. ‘longsnout’, wider interorbital distances than *R.* sp. ‘longsnout’, and a deeper body and longer pelvic fins than *R. esox*. Mature males have a bright yellow-orange colour extending to the dorsal fin and over most of the lower part of the body and fins (fig. 865.1, 6). Some (or perhaps all) mature females also have yellow pelvic and anal fins. Mature adults range from 202-316mm SL. The species is largely known from the south of the lake, but occasional specimens are recorded from Nkhata Bay. Genome-wide sequence data are available for four specimens. A single mature male (fig. 865.2) was included in an analysis by Blumer et al. (2025). Three more were included in the analyses of Yang et al. (ms), including one from Nkhata Bay (fig. 865.3-5). Phylogenetic analyses of the genome-wide data indicate the species is sister to a group including *R.* sp. ‘longfin’, *R.* sp. ‘longsnout’ and *R.* sp. ‘nkhwazi’.

Fig. 865.1: *Rhamphochromis* sp. ‘maldeco’, #355, trawled from 80m depth off Monkey Bay, 23 Feb 96 [RL Robinson].

Fig. 865.2: *Rhamphochromis* sp. ‘maldeco’, D13-H03 male, 23cm SL, trawled from 45-50m depths in SE Arm, 3 March 2016 [HS].

Fig. 865.3: *Rhamphochromis* sp. ‘maldeco’, 2004-331, male, Nkhata Bay, 27 July 2004 [MJG].

Fig. 865.4: *Rhamphochromis* sp. 'maldeco', 2005-242, male, SE Arm, Maldeco, 13 Feb 2005 [MJG].

Fig. 865.5: *Rhamphochromis* sp. 'maldeco', 2005-56, male, SE Arm, Maldeco, 30 Apr 2005 [MJG].

Fig. 865.6: *Rhamphochromis* sp. 'maldeco', 12B06, male, trawled form 85-95m off Monkey Bay, SE Arm, 2 March 2016 [HS].

MC866. *Rhamphochromis* sp. 'nkhwazi'.

Remarkably, the largest endemic cichlid in Lake Malawi appears to be undescribed and indeed has only just been properly distinguished. As an adult, it is a huge heavily-built species with heavy jaws, a projecting lower jaw, and large stout teeth. It has a very distinctive 'aquiline' snout profile, more obvious in larger fish, caused by its short jutting premaxillary pedicel (as opposed to the long straight pedicel in *R. woodi,* the other really large heavily-built species). Mature males are silvery grey with orange pelvic and anal fins, but without the orange throat membrane shown by *R. woodi*. Turner et al. (2004) showed a large hump-backed specimen as *R. woodi*. Genner et al. (2007b) showed the species as *R.* cf. *woodi*. It is now realised that it represents a distinct undescribed species, here named *Rhamphochromis* sp. 'nkhwazi' (fish eagle), that is mature at sizes of 235-401mm SL. Genome-wide data are available for six specimens. A single specimen from Nkhata Bay (fig. 866.1) was included in an analysis by Blumer et al. (2025). Five additional specimens were included in analyses by Yang et al. (ms), from Nkhata Bay and Chipoka (figs. 866.2-5). Phylogenetic analyses of these genome-wide data indicate *R.* sp. 'nkhwazi' is most closely related to *R.* sp. 'longfin', *R.* sp. 'longsnout' and *R.* sp. 'maldeco', and not to *R. woodi*.

Fig. 866.1: *Rhamphochromis* sp. 'nkhwazi'. 2004-397b, male, ~31cm SL, Nkhata Bay, 6 Nov 2004 [MJG].

Fig. 866.2: *Rhamphochromis* sp. 'nkhwazi'. 2004-396b (MS151), male, Nkhata Bay, 6 Nov 2004 [MJG].

Fig. 866.3: *Rhamphochromis* sp. ‘nkhwazi’. 2004-314a,b (2 from a batch of 4 sequenced), Nkhata Bay, 27 July 2004 [MJG].

Fig. 866.4: *Rhamphochromis* sp. ‘nkhwazi’. 2004-376a,b (batch of 2 sequenced), Chipoka, 29 July 2004 [MJG].

MC867. *Rhamphochromis woodi* Regan 1922.

The species was described by Regan (1922a), from four specimens, the largest of which (a 284mm SL specimen collected by Rhoades) had been used in Boulenger (1915) to illustrate *Rhamphochromis longiceps*. The three smaller specimens were collected by Wood. One of these (182mm SL, fig. 867.1) was chosen as the lectotype by Eccles & Trewavas (1989), who seemed to have missed the Rhoades specimen entirely from their list of types. This is a pity, as the Rhoades specimen shows the characteristic features of the species much more clearly than the lectotype, such as the long straight premaxillary pedicel, large mouth, deep cheek and small eyes (fig. 867.2-3). However, we are confident that they are conspecific. The choice of lectotype, lack of good illustration and minimal description may have led to the difficulties experienced by fieldworkers in identifying this large, abundant, widely-exploited food fish. Another problem was the description of *Rhamphochromis brevis* Trewavas 1935, based on four specimens (fig. 867.4-5). No actual description is given beyond the size and number of the specimens. In the key of Trewavas (1935), *R. brevis* is distinguished from *R. woodi* based on an overlapping measure of eye diameter in relation to head length (more or less the same key appears in Eccles & Trewavas 1989). This seems to be of no value in distinguishing them: for the types of *R. brevis*, we record Eye Diameter as 15.8-18.6% Head Length, compared to 15.9-17.9% in the Wood specimens of *R. woodi*. As with *R. woodi*, the largest specimen shows the characteristic features of the species most clearly (fig. 867.5), but again, it was not selected as the lectotype. From examination of a range of features of the types, many specimens in museum collections and numerous examined in the field, we cannot establish *R. brevis* as a distinct phenotype and therefore consider it to be a junior synonym of *R. woodi*.

Turner (1996) was unable to adequately identify *R. woodi* in the field and reported some information on the species under the name *R.* 'bigmouth'. Turner et al. (2004) did identify *R. woodi* with this form, but also still confused specimens of *R.* sp. 'nkhwazi'. Genner et al. (2007b) consistently distinguished the *R. woodi* from *R.* sp. 'nkhwazi', but identified what we now call *R. woodi* as *R.* cf. *brevis*, while their *R.* cf. *woodi* we now identify as *R.* sp. 'nkhwazi'. *Rhamphochromis woodi* can be identified by its large maximum size (mature adults 210-388mm SL: Yang et al. ms), laterally compressed snout, huge mouth, large stout, widely spaced teeth with roots often visible in the jaws, heavy contoured lower jaw projecting beyond the upper, small eye and deep cheek, long, generally straight premaxillary pedicel and male breeding dress with orange throat membrane as well as pelvic and anal fins, sometimes more orange on the ventral body surface. Genome data are available for eight *R. woodi* specimens. Three were included in analyses by Blumer et al. (2005): two large ones are unmistakeably *R. woodi* (figs. 867.6-7), while the third, smaller specimen is a reasonable phenotypic fit (fig. 867.8) and clusters with the larger fish on phylogenetic trees based on the genome-wide sequence data. Yang et al. (ms) analysed genome data from an additional five specimens from the SE Arm and Nkhata Bay: photographs give a good overview of the range of shapes of large adults of the species, and colours of adult males (fig 867:9-13). Specimens 2004-398c,d and 446a,c were sequenced individually, but were collected in batches of fin clips of 3 and 4 specimens respectively stored in the same vial, and cannot be assigned to individual photographs. The species appears to be a large open-water piscivore. In phylogenetic analyses of the genome data, *R. woodi* consistently clusters with *R.* sp 'grey'.

Fig. 867.1: *Rhamphochromis woodi* Regan 1922 Lectotype, 182mm SL, collected by Wood [NHM].

Fig. 867.2: *Rhamphochromis woodi* Regan 1922. Paralectotype, coll. Rhoades, 284mm SL [GFT].

Fig. 867.3: *Rhamphochromis woodi* Regan 1922. Paralectotype: head close-up, showing long snout & long, straight premaxillary pedicel, large jaws and teeth, small eye and deep cheek [GFT].

Fig. 867.4: *Rhamphochromis woodi.* Three of the types of *Rhamphochromis brevis*: the lectotype is the smallest specimen [GFT].

Fig. 867.5: *Rhamphochromis woodi.* The largest type of *Rhamphochromis brevis* [GFT]

Fig. 867.6: *Rhamphochromis woodi,* D03-A01, male, ~30cm SL, bought from fish traders, Nkhata Bay, 21 Feb 2016 [HS]

Fig. 867.7: *Rhamphochromis woodi* D14-F02, male, ~28cm SL, trawled from 40-48m, SW Arm, 4 March 2016 [HS]

Fig. 867.8: *Rhamphochromis woodi*, D12-C10, 12.5cm SL, trawled from 20m depths off Makanjila, 2 March 2016 [HS]

Fig. 867.9: *Rhamphochromis woodi*, 2004-398-MS156, adult male, Nkhata Bay, 6 Nov 2004 [MJG]

Fig. 867.10: *Rhamphochromis woodi*, 2004-398-MS157, adult male, Nkhata Bay, 6 Nov 2004 [MJG]

Fig. 867.11: *Rhamphochromis woodi*, 2005-252, adult male, SE Arm, 12 Feb 05 [MJG]

Fig. 867.12: *Rhamphochromis woodi*, 2005-446ii, adult male, SE Arm, 1 June 06 [MJG]

Fig. 867.13: *Rhamphochromis woodi*, 2005-446iii, adult male, SE Arm, 1 June 06 [MJG]

Astatotilapia Pellegrin 1904, MC868-875.

Family: Cichlidae; **Subfamily:** Pseudocrenilabrinae; **Tribe:** Pseudocrenilabrini; **Subtribe:** none allocated.

Type species: *Astatotilapia desfontainii* (Lacépède 1802) – in older publications, often written as '*desfontainesii*' or '*desfontainesi*'.

Contained valid species within the Lake Malawi catchment: *A. calliptera, A. gigliolii.*

Proposed undescribed taxa in the catchment: *A.* sp. 'calliptera chizumulu'; *A.* sp. 'itamba dark'; *A.* sp. 'ikapu dark'; *A.* sp. 'ilamba black'; *A.* sp. 'kingiri black'; *A.* sp. 'masoko benthic'.

Taxa considered invalid (relating to taxa in the catchment): *Haplochromis centropristoides, Neochromis simotes nyassae, Tilapia swynnertoni***,** (junior synonyms of *A. calliptera*), *Astatotilapia tweddlei, Paratilapia vollmeringi* (junior synonyms of *A.gigliolii*)

Taxa of uncertain status: *A.* sp. 'itende'; *A.* sp. 'masoko littoral' (cited by Morgenstern et al. 2025), but here considered populations of *A. calliptera*.

Generic reviews & diagnoses: Regan 1922, Greenwood 1979, Turner et al. (2021).

Generic diagnosis: (i) the size of the scales on the flank grade in size gradually to the smaller chest scales; (ii) the anal fin of the males is marked by 3-9 yellow-orange spots which are 'ocellated' (surrounded by a contrasting dark or translucent area); (iii) the anal fin has 3 spines and the dorsal fin rarely more than 16 spines; (iv) the teeth in the outer row of the oral jaws are either unicuspid or unequally bicuspid with the tip lying within the major axis of the tooth (in other words, not too bent). (Turner et al. 2021, largely abridged from Greenwood 1979).

Field Diagnosis: Moderately slender sandy coloured haplochromines generally with pointed snouts and short pectoral fins; mature males conspicuously-coloured with bright yellow-orange eggspots surrounded by a contrasting margin.

Phylogenetic comments: *Astatotilapia* is not monophyletic and occupies the position as ancestral to many haplochromine lake radiations including those of Lake Malawi and Victoria.

Ecomorphological notes: The species are generally small to medium-sized fish living in shallow weedy habitats (an exception being the deep-water habitats in Lakes Masoko and Kingiri), around the margins of lakes and rivers. They seem to have broad diets including fish, invertebrates (including molluscs), algae and other plant material and detritus. Although their diets are broad, their habitat preference is generally quite strict and they avoid the faster-flowing parts of rivers and streams (although presumably using them as migration corridors), as well the deep-waters in rivers or lakes. They are seldom seen in open areas in Lake Malawi, tending to stick to reedbeds in water of less than 1m deep. Even beds of other macrophytes such as *Ceratophyllum* and *Potamogeton* are generally avoided. In Lake Kingiri, they were found to live among rocks or sunken wood, down to depths of 20m, with adult males excavating burrows. In Lake Masoko, the benthic morph lives down to at least 38m, venturing out over the open silt plain, and juveniles feed in schools well off the bottom, which has never been observed elsewhere in any *Astatotilapia* (Turner et al. 2019).

The genus *Astatotilapia* is controversial. It is no defining synapomorphies (unique derived traits) and is not resolved as monophyletic by any molecular analysis: indeed as generally currently used, it is ancestral to the entire endemic haplochromine radiations of Lake Malawi and Lake Victoria, a number of other lake radiations in the Lake Victoria region, as well as the crater lake endemics in the Malawi catchment in Tanzania. The genus was originally proposed to include three species: *A. desfontainii* (Lacépède 1802), *A. livingstonii* (Günther 1894) and *A. johnstoni* (Günther 1894). The former is (or perhaps was, as it may be extinct) found in a few small springs in Tunisia, while the latter two are Lake Malawi endemics, now regarded as *Nimbochromis livingstonii* and *Placidochromis johnstoni*. The name fell out of use, and the species moved to the genus *Haplochromis* (type species *H. obliquidens*, a Lake Victoria endemic), before being briefly re-used by Regan (1922) who included 7 species from a variety of locations around Africa and fixed the type species as *A. desfontainii*. However, Regan later moved the included species (in many cases back) into *Haplochromis*. *Astatotilapia* was revived by Greenwood (1979) who attempted to restrict *Haplochromis* to a number of Lake Victoria region endemics with a characteristic tooth form, along with reviving or creating a number of other genera for both Lake Victoria region and riverine haplochromine cichlids. However, many researchers working on the Lake Victoria region did not find these genera practical work with (e.g. Hoogerhoud 1984). As a kind of compromise, it was suggested that perhaps *Haplochromis* could be used to cover all the Lake Victoria endemics, leaving other genera for use for the riverine populations (van Oijen 1996). This would allow *Astatotilapia* and other genera as defined by Greenwood (1979) available for non-Victorian taxa. However, a number of publications have persisted in using *Haplochromis* for taxa outside the Victoria basin (e.g. Schedel et al. 2014; 2018; Vranken et al. 2019). In some studies, riverine populations are allocated to *Astatotilapia, Haplochromis* or the nomenclaturally invalid construct 'Haplochromis' (e.g. Meyer et al. 2015; Meier et al. 2017). This is generally not related to any morphological or genetic traits and seems basically random, perhaps influenced by the terms used in other papers. A consequence of the Greenwood revision was also that the Lake Malawi endemics formerly included in *Haplochromis* were transferred to *Cyrtocara* (e.g. Ribbink et al. 1983, Lewis et al. 1986) and later split into a variety of endemic genera (Eccles & Trewavas 1989). Malawi cichlid researchers have been essentially unanimous in their adoption of *Astatotilapia* for riverine non-endemic haplochromine cichlids from the region, excluding those lying within the current definitions of *Pseudocrenilabrus* and *Serranochromis*. The situation is then sightly complicated by the fact that a number of endemic populations (MC869-874) within the catchment showing striking differences in male breeding dress are clearly morphologically very similar to *A. calliptera* (MC868); analysis of genome sequences confirms that these are indeed recently derived from that widespread species. The distantly related *A. gigliolii* (under the name *A. tweddlei*) was known from Lakes Chilwa and Chiuta, which are not presently connected to the Lake Malawi catchment, but are more associated with the upper tributaries of the Ruvuma River system, in which the species is also widespread. However, the species has been recorded in and around a fish farm which lies on a Lake Malawi catchment tributary in the town of Songea in Tanzania (Turner et al. 2021). The Ruvuma catchment is very close by, but it is not clear whether *A. gigliolii* has crossed between the catchments by natural means, such as tributary capture, or whether it was transplanted, perhaps inadvertently by fish farmers stocking ponds with *Oreochromis*. To date, it is not certain if the species is established.

MC868. ***Astatotilapia calliptera*** **(Günther 1894).**

Astatotilapia calliptera was first described as *Chromis callipterus* by Günther in 1894. It was then moved into *Haplochromis* and then into *Astatotilapia* by Greenwood in 1979. Not all researchers working on Lake Victoria or riverine haplochromines have accepted Greenwood's splitting of *Haplochromis*, but all Lake Malawi researchers have done so, and *A. calliptera* seems to be consistently used. It is also used in Skelton's authoritative work on southern African fishes (Skelton 2024) and recognised in Eschmeyer's online catalogue (Fricke et al. 2025). The species has been re-described at least three times, as *Tilapia swynnertoni* Boulenger 1907, *Haplochromis centropristoides* Nichols and LaMonte 1931, *Neochromis simotes nyassae* Borodin 1936.

Female and immature males can be distinguished from Lake Malawi cichlids of other genera by their overall body shape, and they often show irregular longitudinal markings, sometimes with faint vertical dark markings; the caudal and soft dorsal fins are generally covered in brownish spots, and the pelvic, anal and lower part of the caudal fin can be yellow-orange. They have a short pectoral fin, a trait shared with mbuna (Pseudotropheina), but differ in the gradual diminution of scales from the flanks to the chest, as opposed to the abrupt transition seen in the mbuna. Mature males have a distinctive largely yellow breeding dress and large eggspots with a clear surrounding ring, generally extending on to the anterior part of the anal fin in a single row. Related taxa in Lakes Masoko (deepwater ecotype), Ilamba, Itamba, Kingiri and Ikapu, as well as Chizumulu Island in Lake Malawi (MC870-874) have indistinguishable females and juveniles, but different male breeding dress. The distribution of 'classic' yellow morph includes the shallow waters of Lake Malawi (apart from Chizumulu Island), rivers, streams and smaller lakes in the catchment, but also Lakes Chilwa and Chiuta, the Ruvuma River system, the Lower Shire River, the Zambezi and a number of East-flowing rivers in Mozambique, including the Pungwe, Buzi and the lower Save. Among the catchment lakes, Lake Chilingali, Lake Itende and the shallow waters of Lake Masoko have largely yellow morph males that are not readily distinguished from the widespread Lake Malawi/riverine phenotypes. Many individuals have had their full genomes sequenced. Analyses of those data show that *A. calliptera* is paraphyletic relative to other taxa listed here blue/grey/black breeding males (MC869-MC894), which are very closely related to *A. calliptera*, or derived from it. Herein we refer to these taxa as the *A. calliptera* complex. Collectively, the species is resolved as part of the Lake Malawi radiation, and not as the sister taxon: this is likely due to the persistence of the ancestral population with occasional gene flow throughout its range, while successively budding off the three main lineages of the radiation (Malinsky et al. 2018).

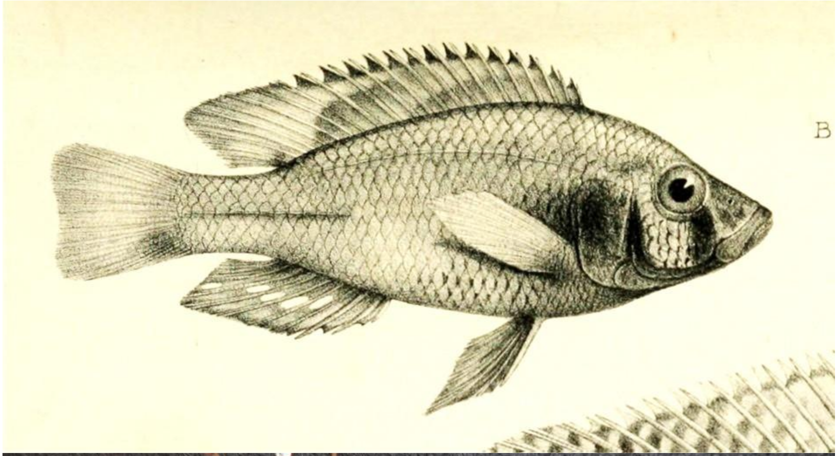


Fig. 868.1: *Astatotilapia calliptera*, male, paralectotype, illustration from original description.

Fig. 868.2: *Astatotilapia calliptera*, lectotype, male [GFT].

Fig. 868.3: *Astatotilapia calliptera*, female collected in Mbaka River, Lake Malawi catchment, Tanzania, 17 July 2011 [GFT/ MJG lab]

Fig. 868.4: *Astatotilapia calliptera*, mouthbrooding female collected in Mgwisi River near Lake Ilamba, Tanzania, 16 July 2011 [GFT/ MJG lab]

Fig. 868.5: *Astatotilapia calliptera*, male collected from the Kamuzu Dam, Malawi, 16 July 2011 [GFT lab]

Fig. 868.6: *Astatotilapia calliptera*, male from Senga Bay, photographed in Bangor University research aquarium [GFT]

Fig. 868.7: *Astatotilapia calliptera*, male photographed underwater in Lake Masoko- littoral (shallow) ecotype [AK]

MC869. *Astatotilapia* sp. 'calliptera chizumulu'

This taxon was first ilustrated by Konings (2001), distinguished by its distinctive male breeding dress of blue-grey (fig. 869.1), as opposed to the mainly yellow colour shown by males of the majority of populations of *A. calliptera*, both within Lake Malawi and in riverine systems in SE Africa. Konings (2001, 2016) suggests it may warrant being regarded as a distinct species. Malinsky et al. (2018) included a full genome sequence from an individual sourced from Bangor University aquarium stocks sourced from Chizumulu (fig. 869.2). Phylogenetic analyses placed the taxon basally within the *A. calliptera* clade, which may indicate longstanding genetic isolation of this population, although it is not clear if this position will be maintained when additional populations are added. Laboratory mate choice experiments by Tyers & Turner (2013) showed significant but incomplete assortative mating between *A.* sp. 'calliptera chizumulu' and *A. calliptera* populations from the Salima area (Mphatsanjoka Dambo, a swamp near Lake Malawi) and Lake Chilingali (a small lake on the Kaombe river near Nkhotakota). Konings (2016) reports that pharyngeal dentition is less strongly molariform than that of many other populations. Females are essentially indistinguishable from other taxa in the *A. calliptera* complex.

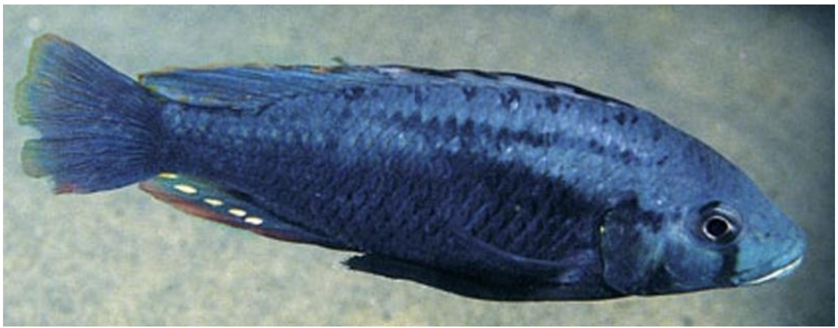


Fig. 869.1: *Astatotilapia* sp. 'calliptera chizumulu', male, taken underwater [AK].

Fig. 869.2: *Astatotilapia* sp. 'calliptera chizumulu', male, Bangor University aquarium strain [GFTlab].

Fig. 869.3: *Astatotilapia* sp. 'calliptera chizumulu', male, Bangor University aquarium strain [GFTlab].

MC870. *Astatotilapia* sp. 'ikapu dark'

The *Astatotilapia* population of Lake Ikapu was reported by Malinsky et al. (2015) as *Astatotilapia* sp. 'ikapu dark'. Lake Ikapu is a difficult place to collect fish. They can be caught gillnetting alongside *Oreochromis* sp. and *Tilapia sparrmanii*, but seine netting is largely prevented by the heavy coverage of macrophytes across the entire known lake bottom (Turner et al. 2019). SCUBA and snorkelling visits have not been successful in observing territorial males: but generally pale-coloured fish in loose feeding groups were observed. A few individuals caught by angling showed a generally dark brown male breeding dress (fig. 870.1) with hints of blue-green on the head. It is not clear if this represents the full breeding dress: it is quite possible they could even turn bright yellow like typical riverine/Lake Malawi *A. calliptera*. Genome sequences are available from two individuals collected from 2017. Analyses of these data show close affinities with the lacustrine populations in nearby Lakes Ilamba and Itamba as well as riverine populations in the proximate Mguwisi River.

8

Fig. 870.1: *Astatotilapia* sp. 'ikapu dark', male, collected June 2017, one of a batch sequenced [GFT].

MC871. *Astatotilapia* sp. 'ilamba black'

Under the name *Astatotilapia* sp. 'ilamba black', this population was mentioned by Malinsky et al. (2015). It was later illustrated and discussed by Turner et al. (2019) (fig. 871.1). Mature males are quite deep-bodied, very dark grey to black, with a red margin to the anal fin and dark orange eggspots. Full genome sequences are available from four individuals. Analyses of those data indicate that the population is closely related to those of Lakes Itamba and Ikapu as well as the neighbouring Mguwisi River (fig. 871.2).

Fig. 871.1: *Astatotilapia* sp. 'ilamba black' adult male, July 2011 [MJG lab].

MG1020

MG1025

MG1023

MG1028

Fig. 871.2: *Astatotilapia* sp. 'ilamba black' adult males, collected 20 September 2019, sequenced [MJG].

MC872. *Astatotilapia* sp. 'itamba dark'

Under the name *Astatotilapia* sp. 'itamba dark', this population was mentioned by Malinsky et al. (2015). It was later illustrated and discussed by Turner et al. (2019) (fig. 872.1-4). It was first collected in 2011. Mature males are generally slender, and colour varies from yellowish to dark grey, almost black, although some specimens were rather pinkish overall. Most specimens showed a narrow red dorsal fin margin and a wider red margin to the anal fin and dark orange eggspots. Wild male specimens brought back to Bangor University initially varied in general background colour, either being predominantly greyish or olive brownish, but offspring reared in captivity have tended to be dark grey. Females were a generally sandy colour, countershaded, much like those of other populations of the *A. calliptera* complex. Genome sequences of 30 wild-caught specimens representing a range of male colours were analysed by Malinsky et al. (2015), revealing no significant genetic structuring among individuals in the population, suggesting that all colour forms were exhibited by members of a single gene pool. Phylogenetic analysis of these sequences indicate that the population is closely related to those of Lakes Ilamba and Ikapu as well, as the neighbouring Mguwisi River.

Fig. 872.1: *Astatotilapia* sp. 'itamba dark' adult male, dark phase, 19th July 2011 [GFT/MJG lab].

Fig. 872.2: *Astatotilapia* sp. 'itamba dark' adult male, yellow phase, 19th July 2011 [GFT/MJG lab].

Fig. 872.3: *Astatotilapia* sp. 'itamba dark' adult male, pink phase, 19th July 2011 [GFT/MJG lab].

Fig. 872.4: *Astatotilapia* sp. ‘itamba dark’ adult male, in Bangor University aquarium [GFT].

MC 873. *Astatotilapia* sp. 'kingiri black'.

A single dark-coloured male specimen collected with a hand net on 14th July 2011 was the first indication that *Astatotilapia* populations in the Tanzanian crater lakes included individual males with very different colours to the typical Lake Malawi/riverine yellow phenotype. Under the name *Astatotilapia* sp. 'kingiri black', this population was mentioned by Malinsky et al. (2015). It was later illustrated and discussed by Turner et al. (2019) (fig. 873.1). Mature males are generally slender, and dark-grey to black. Most specimens showed a narrow red dorsal fin margin and a wider red margin to the anal fin and dark orange eggspots (figs. 873.4-5). Females and immature males are generally a sandy colour, countershaded, much like those of other populations of the *A. calliptera* complex (figs. 873.2-4). Genome-wide RAD sequencing indicated that the population is closely related to those of the Mguwisi River, as well as lakes Ilamba, Itamba and Ikapu. Subsequent analysis of full sequences (14 specimens from less than 5m deep, 6 specimens from deeper than 10m, collected 7th May 2016) failed to indicate any genetic structuring by depth within the lake.

Fig. 873.1. *Astatotilapia* sp. 'kingiri black', mature male, freshly collected, 15th July 2011 [GFT/MJG lab].

Fig. 873.2. *Astatotilapia* sp. 'kingiri black', young male, freshly collected, 15th July 2011 [GFT/MJG lab].

Fig. 873.3. *Astatotilapia* sp. 'kingiri black', female, freshly collected, 15th July 2011 [GFT/MJG lab].

Fig. 873.4. *Astatotilapia* sp. ‘kingiri black’, adult and immature males in the research aquarium at Bangor University [GFT].

Fig. 873.5. *Astatotilapia* sp. ‘kingiri black’, mature male, freshly collected, 25th June 2017 [GFTlab].

MC874. *Astatotilapia* sp. 'masoko benthic'

On 17th July 2011, a survey team on Lake Masoko (also known as Kisiba) collected a large number of female, immature and yellow-brownish males broadly looking like a collection of non-breeding *Astatotilapia calliptera* of the widespread river/Lake Malawi phenotype. However, a few smaller males were unusually dark, and single larger male seemed rather slender and dark, almost bluish. A gillnet set in deepwater on the far side of the lake from the landing beach, by staff of the Tanzanian Fisheries Research Institute (TAFIRI) yielded two relatively large males that showed a clear blue phenotype, indicating that there might be two different species or ecotypes within the lake (fig. 874.1). These two forms have since been studied in-depth as a model of sympatric speciation (Malinsky et al. 2015, Carruthers et al. 2022, Vernaz et al. 2022). The shallow-water 'littoral' form is ecologically and morphologically little changed from the riverine ancestor (although it turns out there are some big changes in patterns of gene expression and DNA modification (methylation: Vernaz et al. 2022) from that riverine ancestor. Consequently, we consider the 'littoral' form is best considered as a population of *A. calliptera*. However, the deep-water 'benthic' form is very different: the blue male breeding colour is the most obvious difference, but they tend to have a more slender body shape, lighter pharyngeal dentition and exhibit considerable physiological differences.

Molecular analysis of genome-wide data suggest that the founding population is from nearby tributaries of the Mbaka River, and first adopted the littoral niche (Malinsky et al. 2015; Vernaz et al. 2022). The well-lit, vegetated habitat, with warmer, more oxygenated water and a wide range of potential dietary items would not be very different from life at the margins of a river or in the floodplain pools where this species is often very abundant. The deep-water 'benthic' population seems to have evolved from a subset of the littorals. Individuals of this benthic ecotype largely live out on the open mud-plain, which starts from around 15-20m depth. Large males seem to hold territories year-round at a depth where only a little green light penetrates (fig. 874.2-3). Smaller males seem to swim in schools with the females and young, sometimes coming into quite shallow water.

DNA analysis of gut contents (Pillay et al. 2025) suggests that both ecotypes consume a lot of copepods and dipterans, but while the littoral ecotype has a broad diet, the benthic ecotype otherwise eat mostly diatoms and annelids. Given the dramatic differences in ambient light spectrum at different depth, it is not surprising that the visual systems of the two ecotypes are quite distinct: this is achieved via differences in cone pigment expression levels rather than differences in coding sequences (Carruthers et al. 2025). Genomic analysis of a large number of specimens indicates that there are some genetically intermediate forms, so the two ecotypes are not completely reproductively isolated. Indeed, laboratory mate choice experiments indicate that females of the benthic ecotype have no strong preference for benthic males, (littorals seem to have a significant preference) so assortative mating is likely due to microhabitat preference (Malinsky et al. 2015). However, the substantial ecological and phenotypic differences are consistent with them being best regarded as distinct species.

Fig. 874.1: *Astatotilapia* sp. ‘masoko benthic’ adult male #223- the first to be clearly identified- freshly collected on 17 July 2011 [GFT/MJG lab].

Fig. 874.2: *Astatotilapia* sp. ‘masoko benthic’ adult male photographed underwater [AK].

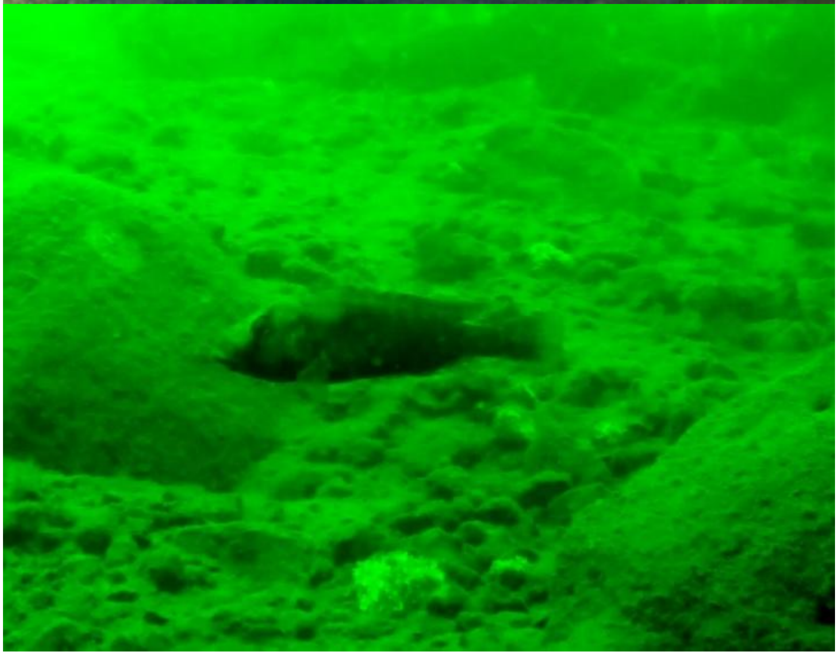


Fig. 874.3: *Astatotilapia* sp. ‘masoko benthic’ adult male photographed underwater on his territory at the base of the crater wall, at about 15-17m depth, without artificial light. This gives an impression of the actual spectrum of light available, as detected by a sensitive camera or spectrometer. To a human diver, it will appear in shades of grey, as it is generally so dim that we would be using rods [GFT].

MC875. *Astatotilapia gigliolii* (Pfeffer 1896)

This species was originally described as *Hemichromis gigliolii* by Pfeffer in 1896 from a single specimen collected in the Kingani River (now part of the Southern Ruvu River) in Tanzania in a German-language publication. The species was discussed by Boulenger (1898), who mistakenly synonymised it with *A. bloyeti* (then *Paratilapia bloyeti*). Regan (1922b) corrected this and correctly regarded *A. vollmeringi* (from the Great Ruaha River on the Rufiji catchment) as a synonym. Apart from a brief mention in a catalogue (van Oijen et al. 1991), the species disappeared from the literature for almost a century until Turner et al. (2021). It was never mentioned by researchers working on Malawi fishes, nor was it considered for inclusion in *Astatotilapia* or any other genus by Greenwood (1979). Turner et al. (2021) found only a single haplochromine cichlid from extensive collections in the Ruvu, and it corresponded well to the types of *A. gigliolii* and *A. vollmeringi*. It was also one of many species found in the Rufiji system (all the others being undescribed: Turner et al. 2021). The occurrence of the species in the Ruvuma system was not reported until Turner et al. (2021).

In the meantime, a population from Lakes Chilwa and Chiuta was described as *Astatotilapia tweddlei* Jackson 1985. The holotype in South Africa (SAIAB) is in very poor condition (apparently partly decomposed) and the paratype in the London collection is very bent, but some of the paratypes in South Africa are in reasonable condition and were examined by one of us (GFT: fig 875.3) and, along with the description, and fresh material collected from the location, felt to be consistent with the phenotype of *A. gigliolii* (Turner et al. 2021). These lakes lie on (Chiuta) or near (Chilwa) a tributary of the Ruvuma and share many species with that system. Presence of the species in the Lake Malawi catchment was established in collections made in 2013 from the upper tributaries of the Ruhuhu in the vicinity of Songea in Tanzania (figs. 875.5-7) and reported by Turner et al. (2021). Some of the specimens were collected within the Ruhila fish farm, which housed a variety of tilapia species both native and non-native to the catchment (and hybrids among them). These were being cultured in ponds that were not isolated from the local rivers, with a natural stream channelled to flow through the ponds, which drained then back into the river system. Numerous individuals of the species were also caught downstream in natural waters from the farm, along with the non-native *Oreochromis leucostictus* (MC882), another species bred in the farm ponds. *Astatotilapia gigliolii* was also found to be abundant in the tributaries of the Ruvuma River which also flow in the vicinity of Songea (Turner et al. 2021) and it is not clear whether its presence in the Ruhuhu in this area is natural or anthropogenic (likely via the Ruhila fish farm). At the time of writing, the species has not been recorded from lower down on the Ruhuhu system nor anywhere else in the Lake Malawi catchment.

Astatotilapia gigliolii females and young are hard to distinguish from those of *A. calliptera*. Adult males, particularly large ones have a more slender body, larger mouth and different male breeding dress: also yellowish, but with dark brown to dark red spots on each flank scale as well as across most of the dorsal and caudal fins. Males lack the bright blue lips, greenish-blue snout and cheeks and the reddish nape of mature *A. calliptera*. They also lack the dark submarginal band in the anterior of the dorsal fin of large dominant *A. calliptera* males.

Fig. 875.1: Type of *Astatotilapia gigliolii*, adult male, from the Ruvu River in Tanzania, first illustrated by Turner et al. 2021 [ZMB].

Fig. 875.2: *Astatotilapia gigliolii* non-breeding male from lower reaches of the 'southern' Ruvu River (-6.698, 38.703), 2 Dec 2011, ~28km from the type locality [GFT/MJG].

Fig. 875.3: *Astatotilapia gigliolii,* paratype of *A. tweddlei* from SAIAB collection, collected from Lake Chiuta, showing the pointed head and strong eye-bar characteristic of a mature male [GFT].

Fig. 875.4: *Astatotilapia gigliolii,* male from Lake Chilwa, 15 Feb 2005 [MJG].

Figure 875.5: *Astatotilapia gigliolii* large male, 10th Sept. 2013 from the Ruhila Fish Farm (-10.623, 36.636), on a tributary of the Ruhuhu near Songea. NB pointed snout & concave upper head profile [GFT].

Fig. 875.6: *Astatotilapia gigliolii* male collected on 9th September 2013 from the Lumecha River (-10.502, 35.671), a tributary of the Ruhuhu near Songea. NB short snout & rounded head [GFT/MJG lab].

Figure 875.7: *Astatotilapia gigliolii* female, 10th Sept. 2013 from the Ruhila Fish Farm (-10.623, 36.636), on a tributary of the Ruhuhu near Songea [GFT].

Pseudocrenilabrus Fowler 1934. MC 876.

Family: Cichlidae; **Subfamily:** Pseudocrenilabrinae; **Tribe:** Pseudocrenilabrini; **Subtribe:** Pseudocrenilabrina.

Type species: *Pseudocrenilabrus natalensis* Fowler 1934 (NB this is currently regarded as a junior synonym of *P. philander*, but this does not matter!).

Contained valid species within the Lake Malawi catchment: *P. philander.*

Proposed undescribed taxa in the catchment: none.

Taxa considered invalid (relating to taxa in the catchment): There are several invalid taxa associated with the genus, but none of these were described from the Malawi catchment.

Taxa of uncertain status: The Malawi catchment population of *P. philander* may ultimately be reclassified.

Generic reviews & diagnoses: Trewavas 1973, Greenwood 1984, 1989, Schedel et al. 2020, Skelton 2024.

Generic diagnosis: maternal mouthbrooders in which the male presents the female with a folded anal fin with a single egg-dummy at the tip, caudal fin rounded, lachrymal with 4 pores. In fact, not all of these traits have been documented in all species, and *P. pyrrhocaudalis* has a truncate caudal, and several populations of *P. philander* lack the anal spot and some have 5 lachrymal pores.

Field Diagnosis (Malawi catchment): Small moderately slender sandy coloured haplochromines generally with rounded snouts and short pectoral fins; mature males conspicuously-coloured with a single red-orange eggspot at the tip of the anal fin.

Phylogenetic comments: *Pseudocrenilabrus* may not be monophyletic. It certainly not closely related to the endemic radiation of haplochromines in Lake Malawi, although there are indications that ancient hybridization may have led to some of its DNA getting into part of the shallow benthic lineage (Cyrtocarina: Blumer et al. 2025).

Ecomorphological notes: The species are generally small fish living in shallow weedy habitats, around the margins of lakes and rivers. They seem to have broad diets including fish, invertebrates, algae and other plant material and detritus. Although their diets are broad, their habitat preference is generally quite strict and they avoid the faster-flowing parts of rivers and streams (although presumably using them as migration corridors), as well the deep-waters in rivers or lakes. They have never been recorded in Lake Malawi *per se,* but are present in the catchment in the vicinity of Nkhotakota in the Central West and Kyela in the north, where they can be found in pools very close to the main body of Lake Malawi.

Discussion: The genus was created for *P. natalensis* but fell into disuse - it wasn't even thought to be a cichlid, but had been placed in the subfamily Pseudocrenilabrinae of the family Pseudochromidae - marine 'dottybacks'. Wickler (1963) created the genus *Hemihaplochromis* for what was then *Haplochromis multicolor* and *H. philander*, based on the single egg-dummy which was displayed on a half-closed anal fin by the courting male (in *H. multicolor*). However, Trewavas (1973) discovered that *P. natalensis* was a junior synonym of *H. philander* which meant that *Pseudocrenilabrus* was a senior synonym of *Hemihaplochromis*.

MC876. *Pseudocrenilabrus philand*er (Weber 1897)

This species was described as *Chromis philander* from specimens collected in KwaZuluNatal in South Africa. The species was moved into *Haplochromis*, then *Hemihaplochromis* and later *Pseudocrenilabrus.* It is widespread over southern Africa and local populations often have strikingly different male breeding colours (Twentyman-Jones et al. 1997, e.g. fig. 876.1). The Lake Malawi catchment population males are generally yellowish, with some blue sheen on the upper flanks, orange and blue spots on the unpaired fins, a thin dark dorsal margin, with paler lappets, a very clear blue streak along the lower jaw extending posteriorly along the cheek, and a large bright red anal fin spot (fig. 876.2-5). Females are sandy, countershaded, sometimes with faint dark vertical bars on the flanks and yellow-orange cast on the pelvic, anal and lower caudal fins (fig. 876.6). Skelton reports max size of 13cm TL, or ~10.5cm SL: in the Lake Malawi catchment, it would be unusual for an adult male to be as large as 7cm SL. They are generally found in shallow weedy areas: Skelton (2024) reports a diet of small fish, insects and shrimp. Their distribution in the Lake Malawi catchment is peculiar: they are abundant in the small lakes and river margins around Nkhotakota and in the rivers at the northern end of Lake Nyasa around Kyela for example in the Mguwisi and Mbaka Rivers (Turner et al. 2019), but they have not been recorded anywhere in the catchment in between those two areas, have never been reported from Lake Malawi at all, and appear to be absent from all the Tanzanian crater lakes in the Nyasa catchment. Males are readily identified by having a single red spot at the tip of their anal fin, females and immatures can be distinguished from *A. calliptera* by their more rounded caudal fins and less pointed snouts. The specimens from the Malawi catchment have not yet been sequenced and the relationships between the two catchment populations and those in the wider range of the species are unknown. *Pseudocrenilabrus* species are also known from the Lower Shire (Tweddle & Willoughby 1979), Lakes Chilwa and Chiuta, the Zambezi and Saisi River in the Rukwa catchment (Seegers 1996) as well as the Ruaha in the Rufiji catchment in Tanzania, but little is known of these. Given the location of the type locality, it would not be surprising if the Lake Malawi catchment populations were to end up being reclassified into a new species.

Fig. 876.1: *Pseudocrenilabrus philander* male from Lake Sibaya in KwaZuluNatal, not far from the type locality of P. philander [from Twentyman-Jones et al. 1997].

Fig. 876.2: *Pseudocrenilabrus philander* male from Lake Chilingali, near Nkhotakota, 2016, showing well-developed breeding dress, including eyebar and blue lower jaw [GFT].

Fig. 876.3: *Pseudocrenilabrus philander* male from Lake Chilingali, near Nkhotakota, 2nd Sept 2024, showing red anal fin spot [GFT].

Fig. 876.4: *Pseudocrenilabrus philander* male from Lake Tabitabi, near Nkhotakota, 4th Sept 2024, showing red anal fin spot and blue lower jaw [GFT].

Fig. 876.5: *Pseudocrenilabrus philander* male from the mouth of the Mguwisi River, Lake Nyasa catchment, Tanzania, 2019 [MJG].

Fig. 876.6: *Pseudocrenilabrus philander* female/immature from Lake Mdila, near Nkhotakota, 8th Sept 2024 [GFT].

Serranochromis Regan 1920. MC877.

Family: Cichlidae; **Subfamily:** Pseudocrenilabrinae; **Tribe:** Pseudocrenilabrini; **Subtribe:** none allocated.

Type species: *Chromys thumbergi* Castelnau 1861

Contained valid species within the Lake Malawi catchment: *S. robustus.*

Proposed undescribed taxa in the catchment: none.

Taxa considered invalid (relating to taxa in the catchment): There are several invalid taxa associated with the genus, but none of these were described from the Malawi catchment.

Taxa of uncertain status: None.

Generic reviews & diagnoses: Regan 1920, Trewavas 1964, Greenwood 1979, Schwarzer et al. 2012, Stauffer et al. 2021, Skelton 2024.

Generic diagnosis: maternal mouthbrooders with large number of small anal fin spots, numerous rows of cheek scales (5-9), numerous dorsal rays (12-16) and lower gill rakers (10-15) and vertebrae (29-36), with general predatory facies (large maximum size, large mouth, strong simple teeth, non-molariform pharyngeal dentition).

Field Diagnosis (Malawi catchment): Large mouth, deep cheek and relatively small eyes, females and immatures with irregular dark brown horizontal markings; males with numerous eggspots.

Phylogenetic comments: Oliver (2024) did not propose a subtribe for the *Serranochromis* group (Eccles and Trewavas 1989, Greenwood 1993) (that is comprised of *Chetia* Trewavas 1961; *Sargochromis* Regan 1920; *Serranochromis* Regan 1920; and *Pharyngochromis* Greenwood 1979) as he stated that no synapomorphies had been identified for the group. Skelton refers to the group informally as 'serranochromines' and also includes some southern African species currently placed in *Thoracochromis*.

Ecomorphological notes: A piscivore found mainly in swampy areas in Lake Malawi, as well as rivers and smaller lakes in the catchment.

Discussion: The genus was created for *S. thumbergi* in a footnote in Regan's paper on Lake Tanganyika cichlids in 1920. The generic description was simply 'as *Haplochromis* but inferior apophyses on 4th vertebra very small'. A substantial revision by Trewavas in 1964 (not seen by the authors) recognised eight species, three of which were new, inhabiting mostly southern Africa. *Serranochromis* has not recorded from Lake Tanganyika (although populations are recorded both upstream in the Malagarasi and downstream in the Congo). *S. robustus robustus* reported from Lake Malawi and the Upper Shire has previously been regarded as conspecific with *S. robustus jallae* (widely distributed in north-central southern Africa, including the Okavango, Upper Zambezi and Kafue). Greenwood (1979) regarded the molluscivorous *Sargochromis* as a subgenus of *Serranochromis*, but since then additional species have been described, *Sargochromis* has been split off again, and the generic traits revised (for example, it had been stated that males had non-ocellated anal fin spots, which was not correct). *Serranochromis robustus* and *S. jallae* were recognised as distinct species by Stauffer et al. (2020).

MC877. *Serranochromis robustus* (Günther 1864)

Described by Günther from a half skin in 1864, it was one of the first batch of Lake Malawi cichlids to be collected by Dr John Kirk on Livingstone's expedition in 1861 (fig. 877.1). It is a very distinctive species, with its huge head and mouth, small eye, deep cheek and horizontal brownish blotchy stripes (fig. 877.2-5). It is not clear whether or not this is a Lake Malawi endemic: populations in southern Africa formerly regarded as conspecific (a subspecies) are now assigned to *Serranochromis jalla*e, but it is possible that a population of *S. robustus* or a related species is found in the Luangwa River in Zambia (Stauffer et al. 2021). The species is common in Lake Malawi / Shire River and their catchments, and it quite rare in the Middle Shire and an occasional vagrant in the Lower Shire (Tweddle & Willoughby 1979). It is sometimes quite common in rivers and smaller lakes, and maintains breeding populations in Lake Chilingali and other small lakes near Nkhotakota, as well as Crater Lake Kingiri in Tanzania. In Lake Malawi, it tends to stick to shallow weedy river mouths and bays and never seems to come up in trawl catches, even in very shallow waters. It seems to be a piscivore.

Fig. 877.1: Holotype of *Serranochromis robustus* at the London Natural History Museum [GFT]

Fig. 877.2: *Serranochromis robustus,* immature male, Manda Port, Tanzania, 6th Jan 2003 [Josh Hellon/GFTlab]

Fig. 877.3: *Serranochromis robustus,* juvenile. Lake Tabitabi, near Nkhotakota, Malawi, 8th Sept 2024 [GFT]

Fig. 877.4: *Serranochromis robustus,* male. Lake Chilingali, Malawi, June 2009 [GFT]

Fig. 877.5: *Serranochromis robustus,* male. Lake Kingiri, Tanzania, 15th July 2011 [GFT/MJG lab]

Coptodon Gervais 1853. MC878-879.

Family: Cichlidae; **Subfamily:** Pseudocrenilabrinae; **Tribe:** Coptodonini; **Subtribe:** none allocated.

Type species: *Acerina zillii* Gervais 1848.

Contained valid species within the Lake Malawi catchment: *C. rendalli, C. zillii.*

Proposed undescribed taxa in the catchment: none.

Taxa considered invalid (relating to taxa in the catchment): There are several invalid taxa associated with the genus, but none of these were described from the Malawi catchment.

Taxa of uncertain status: None.

Generic reviews & diagnoses: Dunz & Schliewen (2013). *Coptodon* had previously been regarded as a subgenus of *Tilapia*.

Generic diagnosis: Dunz & Schliewen (2013) provided a lengthy description of some traits of members of the genus under the caption of a diagnosis, but did not directly compare the traits to those of other taxa. Essentially every 'diagnostic' feature given overlaps with the supposedly diagnostic features of other genera/tribes of taxa formerly included in *Tilapia*. It appears that the genus (and tribe) is actually defined on the basis of forming a clade on a molecular phylogenetic tree. Taxa that were not sequenced have been included in *Coptodon* based on general similarity. In East Africa, *Coptodon* species are characterized by their deep, laterally compressed bodies, generally convex head profiles, tendency to retain the dorsal fin 'tilapia-spot' even at large sizes and tendency to develop bright red areas on the underside of the head and chest.

Field Diagnosis (Malawi catchment): Deep-bodied fish with a prominent tilapia spot.

Phylogenetic comments: Molecular analysis places the *Coptodon* clade as sister group to other West Africa substrate spawning 'tilapias' and not closely related to any other East African species.

Ecomorphological notes: East African species are large herbivorous substrate-spawners: males and females form long-term pair bonds to care for offspring and have similar colours. They are found mainly in shallow swampy areas.

Discussion: Dunz & Schliewen (2013) proposed that the genus (the only one in its tribe) contained 33 species, of which 30 were described. The centre of diversity is West Africa, where a number of lacustrine endemics are known, including adaptive radiations in Lakes Bermin and Ejagham. By contrast, in East Africa diversity is low with only a single species in most locations: *C. zillii* in the north (Nile system etc.) and *C. rendalli* in central Africa, including Lakes Malawi and Tanganyika. However, both species have been dispersed through aquaculture and attempts to enhance capture fisheries.

MC878. *Coptodon rendalli* (Boulenger 1897)

The species has a huge geographic range and many junior synonyms, but luckily for students of Lake Malawi cichlids, *Chromis rendalli* was originally described from three specimens collected in the Upper Shire River (fig. 878.1). This means that any future splitting up of the species would inevitably lead to the Lake Malawi species retaining its current specific name. In the original description, it is stated that the specimens were in bad condition. The head profile and wide tooth bands seem characteristic. The species is (i) the only cichlid fish native to both Lake Malawi and Lake Tanganyika; (ii) the only pair-bonding substrate-spawning cichlid recorded in Lake Malawi. *Coptodon rendalli* can be recognised by its laterally compressed body, characteristic head profile, dark tilapia spot in the soft dorsal fin – even when large, and it sometimes has a very distinct red underside. In contrast to *C. zillii* (which is not yet known to be established in the catchment), it has generally weaker flank barring, a more convex head profile and colour contrast in the caudal fin, with the lower half often reddish or orange.

The species inhabits shallow weedy habitats and is common throughout the rivers and smaller lakes in the Lake Malawi catchment as well as the middle and lower Shire Rivers and their catchments (Tweddle et al. 1979; Tweddle & Willoughby 1979). The species has also been recorded from Lake Chilingali, and the Tanzanian crater Lakes Kingiri, Masoko and Kyungululu. It is also found in Lake Chilwa and the Ruvuma River. The species is widely farmed and stocked in Tanzania, where fish farmers are often provided with ‘Nile Tilapia’ reared from fry collected from Lake Victoria which turn out to be a mix of *C. rendalli, O. leucostictus* and *O. niloticus*, sometimes with hybrids with whatever native species was in the area around the hatchery. These mixes are also often used to ‘re-stock’ natural water bodies where native species have been overfished. Water bodies where *C. rendalli* has been stocked include, or may include, Lake Victoria, Lake Rukwa, Lake Chala, the Ruvuma and Pangani river systems, and Crater Lakes Masoko and Kyungululu. It is thus possible that Lake Malawi may contain non-native strains of this species which presumably would interbreed with the native ones. Skelton (2024) gives a maximum size of 40cm TL and 2kg, but they are usually much smaller than that. They are said to feed mainly on macrophytes, but are opportunistic and will consume detritus, invertebrates and small fish (Skelton 2024). In Lake Malawi, they breed in shallow waters, laying their eggs on hard mud or sand, sometimes on rock, but if possible, where they can also excavate pits in which the fry develop. In Lake Malawi, they have been reported to dig extensive tunnels, and to guard the young up to as large as 40mm long. On one occasion, a cloud of fry was seen being guarded by four adults (Ribbink et al. 1981).

The species is genetically very distinct from other species in the Lake Malawi catchment. It is thought that its closest relative is *Coptodon zillii* (Dunz & Schliewen 2013).

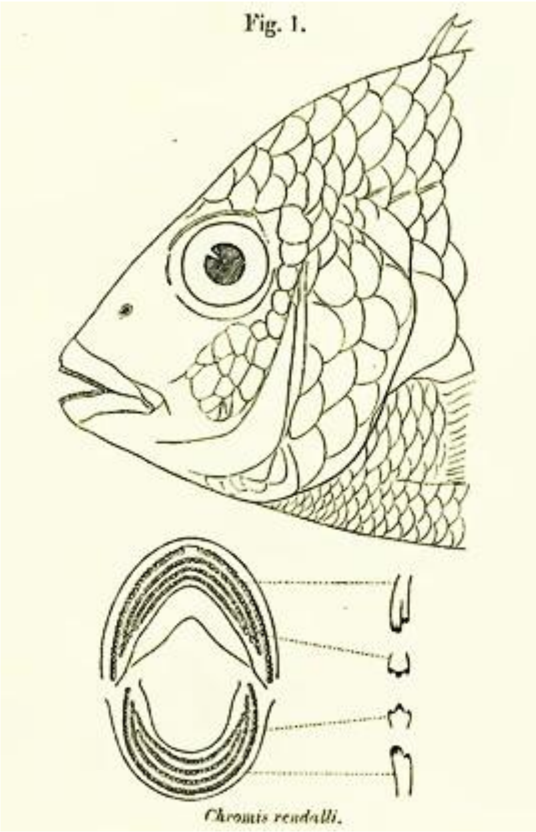


Fig. 878.1: *Coptodon rendalli*, (left) drawing of type material from original description and (below) photograph of lectotype by Seegers (1996).

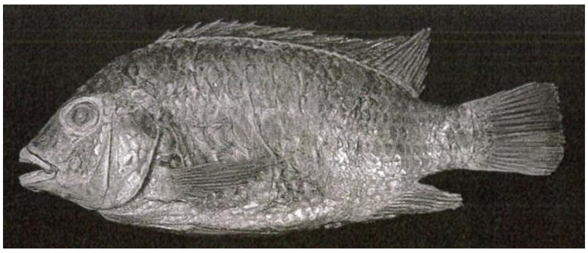


Fig. 878.2: *Coptodon rendalli,* collected from Lake Chilingali 22nd June 2006 [GFT]

Fig. 878.3: *Coptodon rendalli,* collected from Lake Kyungululu 22nd June 2011 [GFT]

Fig. 878.3: *Coptodon rendalli,* collected from Lake Kamphambe 5th Sept 2024 [GFT]

Fig. 878.4: *Coptodon rendalli,* juvenile, collected from the Ruvuma River 16th August 2013 [MJG]

MC879. *Coptodon zillii* (Gervaise 1848)

The species was first described as *Acerina zillii* from Tuggurth in Algeria, which is possibly the modern-day town of Touggourt. The species is still reported from a number of sites across north Africa, and its range extends from Morocco eastwards to Egypt and across the middle east to Israel, Jordan and Syria, as well as south to Nigeria and the Central African Republic. The range of this species extends throughout much of the Nile system, including Lake Albert in Uganda, from where it was probably introduced to Lake Victoria. The species is salt-tolerant and has been found in saline habitats in north Africa, and even photographed in the Mediterranean Sea in full seawater conditions!

The species is closely related to *C. rendalli* and they lived in different places until people introduced both of them into Lake Victoria. They might be hybridizing there, but there doesn't seem to be any real evidence for this yet. In Tanzania, government fish farms have often bred 'Nile Tilapia' for stocking in farms and for 'restocking' natural water bodies. This has been done by collecting 'Tilapia' fry from Lake Victoria where the major fishery is for Nile Tilapia. Unfortunately, in the shallow bays where it is easy to seine juvenile tilapia, there are also lots of *Coptodon* and *Oreochromis leucostictus*, and these tend to be mixed up and bred together in ponds. Most of the farms in the Lake Nyasa/Malawi catchment seem to stock *C. rendalli*, but *C. zillii* has been detected in one of them.

It is not easy to distinguish from *C. rendalli*, but it generally has a less steep head profile, stronger barring and a uniformly coloured, spotted tailfin. Of course, if the two hybridize in Lake Victoria or in fish farms, identification might get more problematic. The types of *C. zillii* are believed to be lost, but types of *Haligenes tristrami* (a junior synonym, fig. 879.1) were collected from the same location, and representative specimens from the Nile have been studied (fig. 879.2). Studies also included specimens from Lake Albert (fig. 879.3-4), the most likely source of the Lake Victoria populations now distributed around Tanzania. The specimens in the Lake Malawi catchment were stocked along with *C. rendalli*, so hybridization seems possible (fig. 879.5).

Fig.879.1: *Coptodon zillii:* type of *Haligenes tristrami* Günther 1860 from Tuggurt, Algeria BMNH 1859.11.30.6-7 [GFT].

Fig.879.2: *Coptodon zillii* from the Nile, near Sammanud, Egypt, BMNH 1907.12.2.3186-3200 [GFT].

Fig.879.3: *Coptodon zillii,* adult in breeding colours, from Lake Albert, Uganda, 4 April 2017 [Kasozi Nasser].

Fig.879.4: *Coptodon zillii,* non-breeding adult, showing uniformly spotted caudal fin, from Lake Albert, Uganda, 4 April 2017 [Kasozi Nasser].

Fig. 879.5: Probable *Coptodon zillii* (above) and *C. rendalli* (below) in a fish farm at Kiwira, Tanzania, in the Lake Nyasa catchment, 29 June 2017 [GFT].

Oreochromis Günther 1889. MC880-885.

Family: Cichlidae; **Subfamily:** Pseudocrenilabrinae; **Tribe:** Oreochromini; **Subtribe:** none allocated.

Type species: *Oreochromis hunteri* Günther 1889

Subgenera in the Malawi catchment: *Oreochromis (Nyasalapia); Oreochromis (Oreochromis).*

Contained valid species within the Lake Malawi catchment: *O. (N.) chungruruensis* (endemic)*, O. (N.) karongae* (endemic)*, O. (N.) lidole* (endemic, extinct), *O. (N.) squaminpinnis* (endemic), *O. (O.) leucostictus* (non-native, introduced), *O. (O.) niloticus* (non-native, farmed), *O. (O.) shiranus* (native).

Proposed undescribed taxa in the catchment: none.

Taxa considered invalid (relating to taxa in the catchment): *O. saka* (junior synonym of *O. karongae*).

Taxa of uncertain status: None, although geographic variation within Lake Malawi and among the crater lakes is understudied.

Generic reviews & diagnoses: Trewavas (1983). *Oreochromis* had previously been regarded as a subgenus of *Tilapia* or briefly *Sarotherodon*.

Generic diagnosis: Trewavas (1983) considers a number of morphological characters, but fundamentally, the main difference between *Oreochromis* and *Sarotherodon* is that *Oreochromis* are maternal mouthbrooders, in which males aggregate in arenas or leks and show conspicuous courtship colour and behaviour, while *Sarotherodon* are generally sexually monomorphic or nearly so, and show a variety of breeding strategies. *Sarotherodon* species are not known from the Lake Malawi catchment.

Subgeneric traits: *Oreochromis (Nyasalapia)* contains species with prominent genital tassels and complex spawning bowers with a raised central platform. This group includes the Lake Malawi ‘chambo’ species and appears to be monophyletic. The subgenus *Oreochromis* contains species with no tassels and simple crater bowers. Trewavas (1983) also recognised additional subgenera (*Alcolapia, Neotilapia, Vallicola*), but none of these are known from the Malawi catchment.

Field Diagnosis (Malawi catchment): Deep-bodied fish with a prominent tilapia spot.

Phylogenetic comments: Molecular analysis indicates that *Oreochromis* is monophyletic and derived from a group of mouthbrooding taxa including *Sarotherodon, Danakilia, Iranocichla, Tristramella* and the endemic genera of Lake Barombi Mbo (Klett & Meyer 2002; Dunz & Schliewen 2013, Ford et al. 2019, Ciezarek et al. 2024). They are not closely related to any other species found in the Lake Malawi catchment. The subgenus *Nyasalapia* also appears to be monophyletic, but *Oreochromis* (*Oreochromis*) is paraphyletic (Ciezarek et al. 2024). Lake Malawi contains two independent lineages of *Oreochromis*: the non-endemic *O. (Oreochromis) shiranus* and a small radiation of endemic ‘chambo’, *O. (Nyasalapia)* sp. comprised of *O. karongae*, *O. lidole* and *O. squamipinnis*. There are members of both lineages in the Tanzanian crater lakes, including *O. chungruruensis* which was placed in *Nyasalapia* by Trewavas (1983), but actually appears to have originated as a hybrid between the *Nyasalapia* and *O. shiranus* lineages (Ciezarek et al. 2024).

Ecomorphological notes: *Oreochromis* are largely microphagous, feeding on algae, detritus and plankton (including zooplankton). They tend to live in shoals. They are seasonal breeders with adult males aggregating on breeding areas or leks, defending a territory where they construct a spawning bowers. Females visit to mate but collect the eggs in their mouths and leave. They release their young to feed, typically in shallow vegetated areas. Small juveniles tend to live in shoals in shallow water and move deeper as they grow.

MC880. *Oreochromis* (*Nyasalapia*) *chungruruensis* (Ahl 1924)

Tilapia chungruruensis was described by Ahl in 1924, based on specimens in Berlin collected in Lake Tschungruru (modern Lake Kyungululu) in 1899 (fig. 880.1). Their identity was rather confused in later studies by Trewavas (1983), who classed some of the specimens as *Oreochromis lidole*, and also confused specimens collected from different craters lakes, such as Masoko and Kingiri. With subsequent surveys from 2011 onwards, it has become clear that *O. chungruruensis* is endemic to Lake Kyungululu (Turner et al. 2019). This tiny crater lake is only about 430m wide and is very deep (~45m), with steep sides and a small catchment, making it rather unproductive. The lake is at a very high altitude (457m above Lake Malawi) and quite isolated. The population of the species is probably very small and adults mature at a small size and seem to lose condition during the breeding season, with emaciated dying fish found drifting in the lake (Turner et al. 2019). It seems that these emaciated fish with relatively large heads may also have resorbed some of the skeletal material of their oral and pharyngeal jaws, resulting in a phenotype reminiscent of *O. lidole* (fig. 880.2, 880.6). The status of this highly marginal population is probably not helped by the presence of two additional species not found in the Berlin collection, *Coptodon rendalli* and *Tilapia sparrmanii*, which were probably stocked by Tanzanian authorities.

Molecular studies indicate that *O. chungruruensis* contains genetic material from ancestors related to *Oreochromis shiranus* and to species in the *Oreochromis (Nyasalapia)* group (Ciezarak et al. 2024). It seems likely that both lineages entered the lake and have interbred, to produce a unique species of hybrid origin. The species shows features of both ancestors and some unique traits: territorial males are black (fig. 880.3) with a small lobed genital papilla rather than the simple tube of *O. shiranus* or the long tassel of *O. (Nyasalapia)*. Adult males have enlarged jaws and can acquire a concave head profile, similar to *O. shiranus*. They sometimes show a red dorsal fin margin (like *O. shiranus*) and never a white dorsal or caudal margin (like *O. karongae*). They excavate simple craters, and do not construct a central platform of fine sand in the manner of *O. (Nyasalapia)* species. However, examination of 22 type specimens and 7 specimens collected from 2011-2013, showed that all had three anal spines, characteristic of Lake Malawi *O. (Nyasalapia)* species, while Lake Malawi populations of *O. shiranus* almost always have four. Adults in the lake did not exceed 138mm SL, and in aquaria, have grown to around 17cm SL, much smaller than either *O. shiranus* or Malawi catchment *O. karongae* or *O. squamipinnis*, suggesting a genetic basis to their small size. Juveniles and females are silvery grey with irregular vertical bars or dark blotches, sometimes turning an overall dark grey colour (fig. 880.5). Trewavas (1983) considered the species to belong to *Nyasalapia* and to be a member of the ‘chambo’ group, but given its hybrid origins, this is not straightforward. The short but lobed genital tassel is intermediate between *Oreochromis* (*Nyasalapia*) and *O. shiranus,* but the simple bower shape is more characteristic of *O. shiranus.*

Fig. 880.1: *Oreochromis chungruruensis*, type in the Natural History Museum at Berlin [GFT]

Fig. 880.2: *Oreochromis chungruruensis*, emaciated paratype in the Natural History Museum at Berlin [GFT]

Fig. 880.3: *Oreochromis chungruruensis*, territorial adult male showing signs of loss of body condition, collected in Lake Kyungululu, 2011 [GFT/MJG lab]

Fig. 880.4: *Oreochromis chungruruensis* (3D10, 127mm SL), non-territorial adult male showing good body condition, collected in Lake Kyungululu, 2011 [GFT/MJG lab]

Fig. 880.5: *Oreochromis chungruruensis*, juvenile, in Bangor University aquarium [GFT lab]

Fig. 880.6: *Oreochromis chungruruensis*, emaciated adult (2011.238a, 104mm SL), collected alive July 2011 [GFT/MJG lab]

Fig. 880.7: *Oreochromis chungruruensis*, short, lobed genital tassel of male aquarium specimen, viewed from side (left) and underneath (right) [GFT]

MC881. *Oreochromis* (*Nyasalapia*) *karongae* (Trewavas 1941)

The species was described by Trewavas (1941) as *Tilapia karongae* based on specimens collected from Karonga in the far north of Lake Malawi (fig. 881.1). These were distinguished from southern populations (*T. squamipinnis, T. lidole*) mainly by their broader, heart-shaped pharyngeal bones (fig. 881.8A). Later Lowe (1953) separated *T. saka* (fig. 881.2) and *T. squamipinnis* based mainly on male breeding dress (all-black for *T. saka* v pale blue- or white-headed *T. squamipinnnis*) and seasonality, focussing on specimens from the south of the lake and differentiating *T. karongae* on the basis of pharyngeal dentition (fig. 881.8B). Confusingly, the original type series of *Chromis squamipinnis* Günther 1864 includes specimens that clearly show black male breeding dress (fig. 881.3). Moreover, the lectotype selected by Trewavas (1941) is an apparent female with strong vertical barring, which could represent either species (fig. 886.1). Subsequently, heavy pharyngeal dentition was also found among black male specimens in various localities around the lake (fig. 881.8C), particularly in the vicinity of rocky habitats, such as Cape Maclear and Makanjila (fig. 881.6) and *O. saka* was considered a junior synonym of a single variable species, *O. karongae* (Turner & Robinson 1991, Turner 1996, Snoeks & Hanssens 2004). Specimens from rocky areas also tended to have larger numbers of oral jaw teeth, scattered in an array on fleshy gums rather than in discrete rows (fig. 881.9). Both the heart-shaped lower pharyngeal bones and the arrangement of oral teeth in the jaws were found to persist for at least 25 years in a laboratory strain derived from specimens collected at Mbamba Bay (fig. 881.7-9), suggesting a largely genetic basis to the trait.

The species can be very difficult to distinguish from *O. squamipinnis* except from male breeding dress: in southern parts of the lake, *O. karongae* females and juveniles are often a little more slender than those of *O. squamipinnis*, can be more brownish with yellow dorsal fin lappets (fig. 881.5), generally have wider pharyngeal bones with a larger toothed area and can have a greater number of oral tooth rows, generally without a clear gap between the first row and the inner rows. It is not clear if these differences hold throughout the range of the species: northern populations of *O. squamipinnis* seem to have heavier pharyngeal dentition (Turner & Robinson 1991). *Oreochromis lidole,* which also had black breeding males, was distinguished by its large jaws, thin band of oral teeth, slender pharyngeal bone and large square operculum. However, *O. lidole* (MC883) has not been reported from the lake since 2004 and is probably extinct, at least in the southern half of the lake. The three species are closely related and have apparently diversified within the lake catchment. They are generally recognised as 'chambo' within Malawi. Chambo can be distinguished from other *Oreochromis* species in the lake by their generally wide, rounded heads, tendency to strong irregular, tapering vertical barring (as opposed to horizontal elements often more strongly expressed in *O. shiranus*) and possession of three anal fin spines (versus four in *O. shiranus* in most water bodies). Like other *Oreochromis*, chambo females mouthbrood the young and males aggregate on leks. Like other *Oreochromis (Nyasalapia)* species, males develop long, branched, lobed genital tassels (fig. 881.5) and produce complex spawning bowers, consisting of an outer crater, with an inner raised platform of fine sand/mud. Lowe (1953) reported that *O. karongae* (as *Tilapia saka*) prefers to breed in shallow water in sheltered weedy areas, but Turner et al. (1991) found it breeding in exposed areas around Cape Maclear, at depths of as much as 28m. Lowe recorded a short breeding season of around September to November, but Turner (1996) reported that breeding extending to March in some areas, although the season was shorter in Lake Malombe. The species is also found in Tanzanian crater lakes Ikapu, Ilamba and Itamba. It is possibly also in Lake Itende, where males in breeding colour have not yet been observed (Turner et al. 2019; figs. 881.11-15). A synonymisation of *O. saka* with *O. karongae* is supported by an analysis of geographic variation in morphology, based on a large sample of specimens including the types. A brief abstract of the work was published in a conference proceedings by Turner & Robinson (1991: fig. 881.10). Specimens are available for further study.

Fig. 881.1: *Oreochromis karongae*, male, type specimen from Karonga (north end of lake), London Natural History Museum [GFT].

Fig. 881.2: *Oreochromis karongae*, male, type of *Tilapia saka* Lowe 1953, from south of lake, London Natural History Museum [GFT].

Fig. 881.3: *Oreochromis karongae,* male in breeding dress, from the original type series of *Chromis squamipinnis* Günther at the London Natural History Museum [GFT]

Fig. 881.4: *Oreochromis* sp., possibly *O. karongae*, ~10cm SL juvenile from Manda, Tanzania, 31 May 2003 [J.Hellon/GFTlab]

Fig. 881.5: *Oreochromis karongae*, ~15cm SL juvenile from SE Arm, 1990, showing slender body shape and brownish colour shown by some individuals of this species [GFT].

Fig. 881.6: *Oreochromis karongae*, adult male, Cape Maclear, 1st Sept 2006 [GFT]

Fig. 881.7: *Oreochromis karongae*, adult male, showing prominent genital tassel, aquarium, University of Hull, UK [GFT]

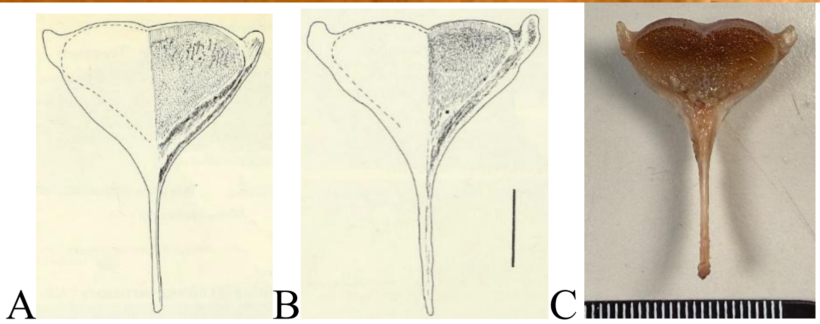


Fig. 881.8: Lower pharyngeal bones of *Oreochromis karongae:* (A) 29cm TL, northern (Karonga) population; (B) 30cm TL, southern population (*O. saka*), from Trewavas (1983), (C) 23cm SL aquarium specimen derived from Mbamba Bay [GFT].

Fig. 881.9: *Oreochromis karongae* ‘rock morph’ individuals, illustrating wide bands of up to 15 rows of oral teeth: **Left:** wild-caught at Cape Maclear (1987-92), **right:** laboratory specimen derived from individuals collected from Mbamba Bay in 1999, photographed in 2025 [GFT].

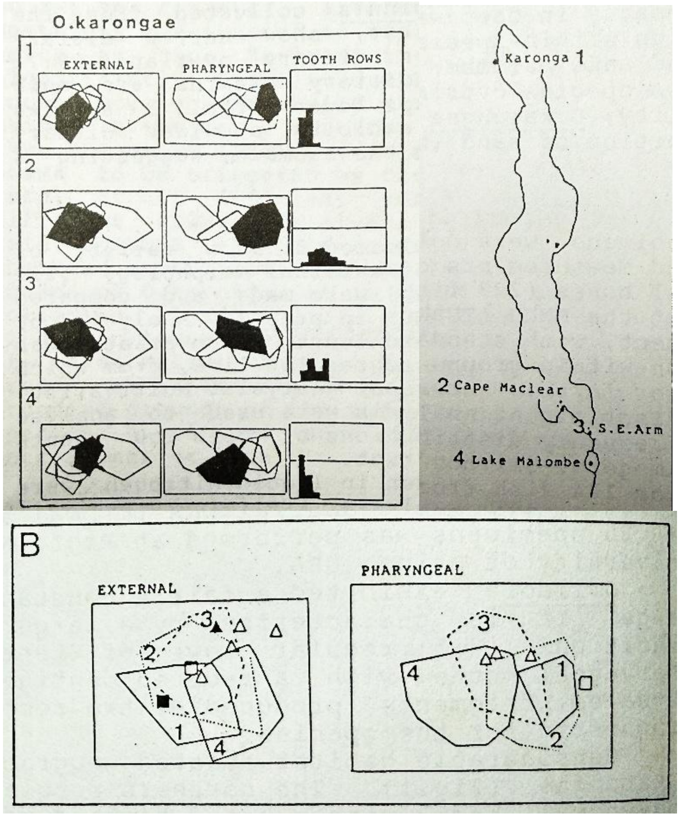


Fig. 881.10: Geographic variation in *Oreochromis karongae* from collections at four sites, using Principal Components (multivariate) Analysis of size-adjusted residuals of logged external and pharyngeal bone measurements. A sample of *O. lidole* is included for comparison in the upper left figure (the large white polygon on the right in external measurements and to the left in pharyngeal measurements). The tooth rows at Cape Maclear extend to (a low frequency) of 14, with the minimum value at 3. The lower figure (B) includes the types of *O. karongae* (□) and *O. saka* (Δ), holo-/lectotypes are filled symbols [from Turner & Robinson 1991].

Fig. 881.11: Male *Oreochromis karongae* from Tanzanian crater Lake Ikapu, March 2015 [GFT lab].

Fig. 881.12: Female *Oreochromis karongae* from Tanzanian crater Lake Ikapu, July 2011, showing golden colour [GFT lab].

Fig. 881.13: Male *Oreochromis karongae* (2011.274; 177mm SL) from Tanzanian crater Lake Itamba, 19 July 2011: large specimen showing poor body condition [GFT lab].

Fig. 881.14: Male *Oreochromis karongae* (1I1, 130mm SL) from Tanzanian crater Lake Itamba, 22 Nov. 2011, small specimen showing unusual white vertical barring [GFT].

Fig. 881.15: Female/ immature *Oreochromis cf. karongae* from Tanzanian crater Lake Itamba, 19 July 2011, showing large head, poor body condition and silver-grey background colour [GFT].

MC882. *Oreochromis leucostict*us (Trewavas 1933)

The species was described by Trewavas (1933) from specimens collected from Lakes George and Edward and the adjoining Kazinga Channel. It is also found in Lake Albert, along with catchment water bodies in the area. Specimens from Lake Albert were stocked into Lake Victoria, possibly accidentally as part of a deliberate introduction of *Coptodon zillii* made to establish a species that would exploit macrophytes (Fryer & Iles 1972). The species is generally small 32cm TL being the maximum recorded across a range of locations, with most breeding adults much smaller (Trewavas 1983). It tends to breed in very shallow muddy lagoons and bays and appears to be tolerant of low oxygen and high temperatures. It has largely replaced *O. variabilis* in this habitat in Lake Victoria, and it has been stocked widely within Tanzania apparently via hatcheries where 'Nile Tilapia' fingerlings have been cultured using mixed broodstocks reared from fry obtained from Lake Victoria. The species is known to hybridize with species of the *O. mossambicus* complex, including *O. urolepis, O. shiranus* and *O. placidus ruvumae* (Ciezarek et al. 2024). It has not been found to cross directly with *O. niloticus*, with which it naturally co-occurs, but its hybrids with other species may do so, to create 3-species hybrids (Ciezarek et al. 2024).

The species is recognised by its dark body colour with paler spotting, particularly on the soft dorsal, anal and caudal fins, but also the rear of the body. Males have vivid orange-red eyes and blue-white lower lip. Males lack a genital tassel and dig simple crater bowers. Mature males do not develop enlarged jaws as do those of the *O. mossambicus* group, such as *O. shiranus*. The caudal fin lacks the clear vertical lines seen in most populations of *O. niloticus*. The anal spine count is nearly always 3. During visits in 2012 and 2015, the species was found being cultured in the Ruhila Fish Farm, a Tanzanian Government hatchery inside the Lake Malawi/Nyasa catchment (Genner et al. 2013), that supplies aquaculture operations throughout the country. Hybrids between *O. leucostictus* and *O. shiranus* were also found in their ponds (confirmed with sequence analysis: Ciezarek et al. 2024) and juvenile *O. leucostictus* was found 'in the wild' downstream from the farm in 2015. However, it is unclear whether there is an established breeding population of this species in the wild in the Malawi catchment or if the free-ranging juveniles were escapes from the farm ponds. No sign of the species was found at the mouth of the Ruhuhu when sampled in 2015.

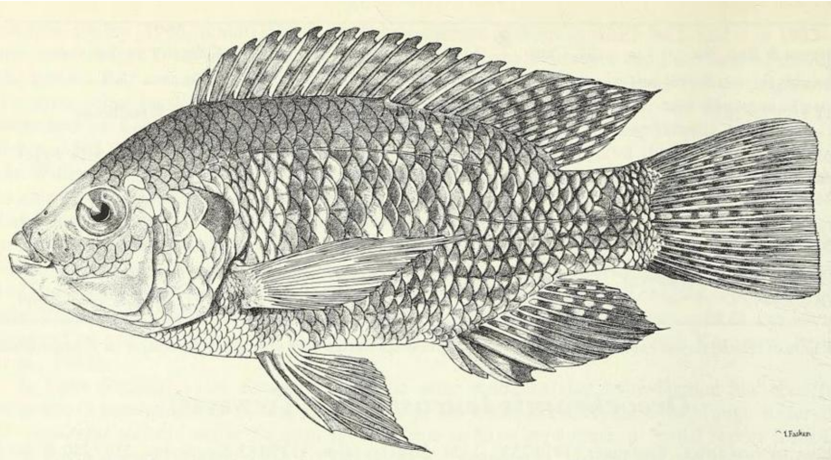


Fig. 882.1: Syntype of *Oreochromis leucostictus,* 216mm SL female, from Trewavas (1983).

Fig. 882.2: *Oreochromis leucostictus,* collected from Lake Albert [Nasser Kasozi].

Fig. 882.3: *Oreochromis leucostictus,* young male, collected from a farm pond at Ruhila Aquaculture Centre on a tributary of the Ruhuhu River, Lake Malawi catchment, Tanzania, 2012 [GFT].

Fig. 882.4:*Oreochromis leucostictus,* juveniles, collected from the Ruhila stream, downstream from the Ruhila Aquaculture Centre on a tributary of the Ruhuhu River, Lake Malawi catchment, Tanzania, 28 July 2015 [GFT].

Fig. 882.5: *Oreochromis leucostictus x shiranus* hybrid, young male, collected from a farm pond at Ruhila Aquaculture Centre on a tributary of the Ruhuhu River, Lake Malawi catchment, Tanzania, 28th July 2015 [GFT].

MC883. *Oreochromis lidole* (Trewavas 1941)

Tilapia lidole was described by Trewavas in 1941. The distinguishing characteristics include the slender lower pharyngeal bone, the large mouth with few widely separated rows of teeth (usually 3-4, occasionally 5) and the black male breeding dress. The operculum generally looks larger with a straighter, more vertical posterior margin. Females and juveniles are generally a darker grey dorsally than the other chambo species, and can be distinguished at sizes of around 15cm SL or larger. The breeding season in the south of the lake runs from September to February, but is strongly concentrated in October to November. Turner et al. (1991) found that in the Cape Maclear area, males constructed huge bowers with particularly wide central platforms at depths of 17m or deeper. Trewavas (1983) reports young being brooded up to 58mm SL. Trewavas (1983) erroneously attributed specimens collected in Lake Kyungululu and Kingiri to *O. lidole*: these are now known to be respectively *O. chungruruensis* (emaciated specimens) and *O. squamipinnis* respectively (Turner et al. 2019). *Oreochromis lidole* dominated the commercial trawl and ringnet catches in the productive southern arms of the lake up until the 1990s (Turner 1996), but apart from a single specimen collected in 2007, it has not been positively observed since and it is generally considered to have become extinct, perhaps due to overfishing. It might be worth sampling areas around Karonga and Nkhotakota during the breeding season, in case relict populations persist. The species is primarily a plankton-feeder.

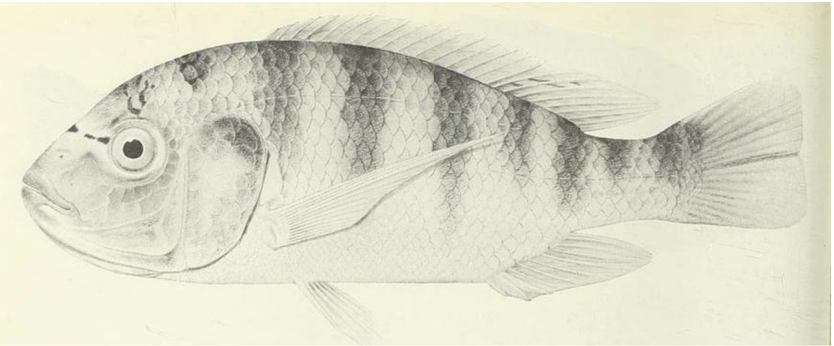


Fig**. 883.1:** Paratype of *Oreochromis lidole*, from Trewavas (1983).

Fig. 883.2: Type specimens of *O. lidole* at the London Natural History Museum, the lower one appearing to be a mature male in breeding dress [GFT].

Fig. 883.3: *O. lidole* on the deck of a commercial trawler in southern Lake Malawi, in 1987, showing characteristic dark grey colour [GFT lab].

Fig. 883.4: Adult male *O. lidole* in breeding dress, collected from bowers at Cape Maclear, 1989 [GFT].

Fig. 883.5: Adult male *O. lidole* in partially developed breeding dress, Cape Maclear, 1989 [GFT].

Fig. 883.6: Juvenile *O. lidole*, SE Arm, Lake Malawi, 1990 [GFT].

Fig. 883.7: Spent female *O. lidole*, purchased from fish trade, SW Arm at Malembo, 2nd Feb 2007. This is the last known specimen of the species [GFT].

Fig. 883.8: Adult female *O. lidole* (preserved), 278mm SL, from commercial fishery in SE Arm, between 1987-1992 [GFT].

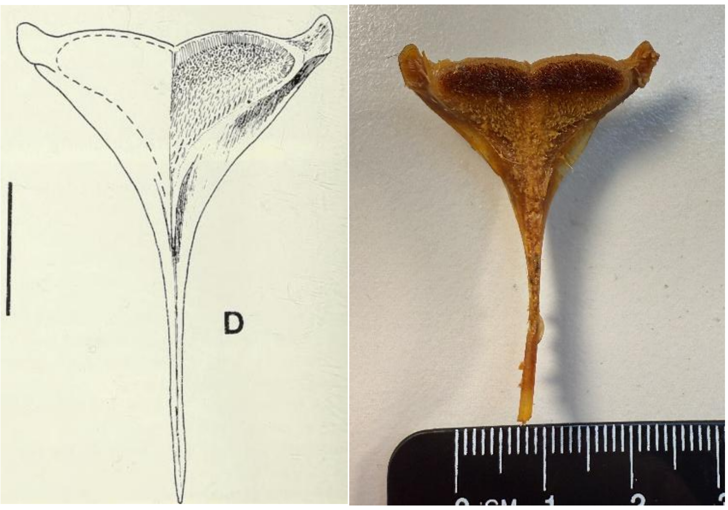


Fig. 883.8: The lower pharyngeal bone of *O. lidole* is relatively narrow with a small toothed area and long blade, in comparison to those of other chambo species, drawing from Trewavas 1983 (left) and photo of 278mm SL female collected from Maldeco Fisheries trawl catch in SE Arm between 1987-1992 [GFT]

Fig. 883.9: The oral dentition of *O. lidole* is characterised by relatively narrow bands of short erect teeth usually in 3 regular, well-separated rows (sometimes with a few extra teeth between the rows near the symphysis), set on bony gums, photo of lower jaw of 267mm SL male collected from Maldeco Fisheries trawl catch in SE Arm some time between 1987 and 1992 [GFT].

MC884. *Oreochromis niloticus* (Linnaeus 1758)

The Nile tilapia was originally described by Linnaeus in 1758, making it probably the first cichlid to be described. Confusingly, it was described as *Perca nilotica* – which means the Nile Perch, but that is something completely different (*Lates niloticus*) which was originally described also by Linnaeus as *Labrus nilotica* (Trewavas 1983 mistakenly assigned this as the original name of the Nile Tilapia). The type material is known but does not appear to have been illustrated. It was collected from the Nile near Cairo, which does not completely rule out *O. aureus*, which has been confused with this species in the past. However, it is now conventional to recognise *O. niloticus* in this locality at least on the basis of its clear, regular caudal fin striping (fig. 884.1). The species is prized among aquaculturalists because of its rapid growth, particularly 'improved' farm strains which may not be 100% pure *O. niloticus*, but certainly present a similar phenotype. Consequently, the species is essentially becoming globally distributed in freshwaters warm enough for it to survive. It appears to be competitively superior to many congeneric species, particular in lake habitats. It is also prone to hybridize with many species, forming fertile hybrids. It was introduced into Lake Victoria probably from Lake Albert as a contaminant of the deliberate introduction of *Coptodon zillii* to feed on macrophytes. Initially, it did not seem to establish, but populations appeared to build up in synchrony with those of the introduced Nile Perch, perhaps because these species were co-adapted, while the native *O. esculentus* was naïve to the predator. Nile Tilapia is extensively cultured in Tanzania and often stocked into dams and natural water bodies in response to complaints of overfishing of native tilapias. The species has been recorded in farms on the Ruhuhu and Kiwira rivers in the Lake Malawi/Nyasa catchment in Tanzania (figs. 884.2-4), and it was being cultivated in the lake in cages in 2016. There are also unconfirmed reports that it is being cultivated in Mozambique. It is not clear whether any of these activities have led to the species establishing self-sustaining populations in the catchment. The species has proved to be invasive and competitively superior to native species in Lake Victoria, Lake Kyoga, Lake Jipe on the Pangani, the Kidatu Reservoir on the Great Ruaha, Lake Nala on the Wami and the Mindu Reservoir on the (southern) Ruvu River. It has also been shown to hybridize with *O. shiranus* in ponds. However, it is native to the Lake Tanganyika catchment (having apparently naturally invaded from Lake Kivu during the formation of the Ruzizi River) and seems unable to get very well established in the main Lake Tanganyika, perhaps because of competition with the endemic lacustrine specialist *Oreochromis tanganicae*.

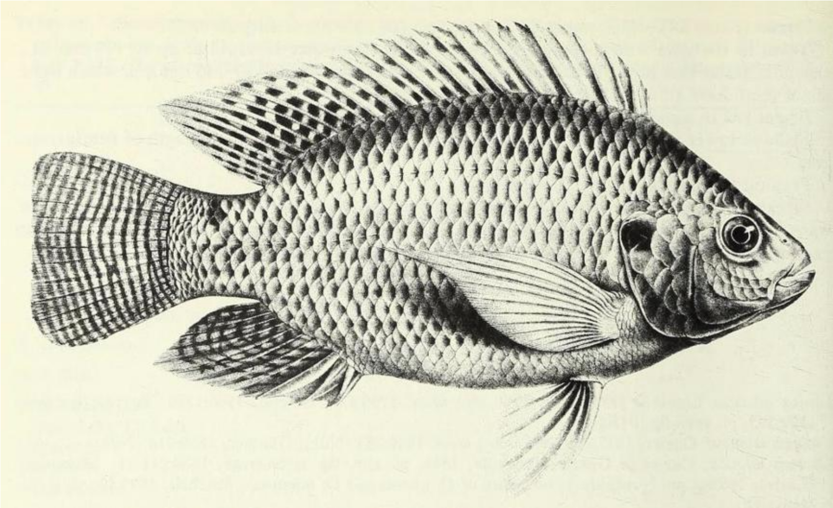


Fig. 884.1: *Oreochromis niloticus* from Trewavas 1983, originally from Boulenger 1907.

Fig. 884.2: *Oreochromis niloticus* male, with partly developed breeding dress, from Ruhila Fish Farm on the Ruhuhu, 28th July 2015 [GFT].

Fig. 884.3: *Oreochromis niloticus* apparent female, from Ruhila Fish Farm on the Ruhuhu, 28th July 2015 [GFT].

Fig. 884.4: *Oreochromis niloticus* apparent male, from Riverside Fish Farm on the Kiwira River, Lake Nyasa catchment, 29th June 2017 [GFT].

MC885. *Oreochromis shiranus* Boulenger 1897

Oreochromis shiranus was described by Boulenger in 1897 (according to Fricke et al, although the issue is dated as 1896) from 5 specimens of 92-225mm SL from a collection of specimens from the Upper Shire River by Dr Percy Rendall, said to be in 'very bad condition'. Illustrations were given only of the heads and jaws, and it was noted that nothing could be said of their colour because of their condition. However, the specimens appear to be straightforward to identify, as they are clearly an *Oreochromis* with a strongly concave head upper head profile (associated with enlarged jaws on the apparently adult male: fig. 885.1), numerous small bicuspid/tricuspid teeth in 5-6 rows, 15-18 short lower gillrakers, a deep caudal peduncle and very unusually among Malawi cichlids, 4 anal fin spines (Boulenger 1897). Trewavas (1983) considers there to be a second species, *O. shiranus chilwae* from Lakes Chilwa and Chiuta and gives a more extensive description of the Lake Malawi subspecies (*O. shiranus shiranus*) based on 30 specimens overall, noting that anal spine count is occasionally 3 or 5, but is generally 4. She gives maximum size of 37cm TL. She also notes that the live fish are generally a dark olive green with a bright yellow or white ventral surface, brownish horizontal bands may be shown, and males are generally dark green to black with orange margins to the dorsal and caudal fins. However, smaller juveniles often show faint, thin vertical bars (rather than the bold, broad tapering bars of *O. (Nyasalapia)* species) instead of horizontal elements, generally on a metallic golden background, although they may be silvery at the smaller sizes.

Trewavas (1983) reports that the species mainly feeds by scraping biofilm from reeds and other emergent macrophytes, but that it may also switch to plankton feeding during blooms. Breeding occurs from September to March or April, constructing simple basin-shaped nests in shallow water. It is an abundant species in shallow vegetated areas in Lake Malawi, the Upper and middle Shire and Lake Malombe as well many catchment rivers, streams and smaller lakes, including many of the lakes in the vicinity of Nkhotakota, including Lake Chilingali, and also several of the Tanzanian crater lakes, notably Lakes Kingiri, Ilamba, Ikapu and Itamba (Turner et al. 2019). Anal fin spine counts are variable within the crater lake populations, with 3 being more commonly found, possibly reflecting hybridization with co-occurring *O. (Nyasalapia)* populations (Turner et al. 2019). More convincingly, *O. chungruruensis* from Lake Kyungululu is revealed by genomic analysis (Ciezarek et al. 2024) to have evolved from a hybrid population with relationships to both *O. shiranus* and *O. (Nyasalapia)*: neither pure form co-exists in the current lake.

Phylogenetically, *O. shiranus* is a member of the *O. mossambicus* group, along with *O. urolepis* and *O. korogwe* (Ciezarek et al. 2024). Its relationship with *O. placidus* is complex: Trewavas (1983) split *O. shiranus* into two subspecies, one in Lakes Chilwa and Chiuta and the other in the Lake Malawi catchment. Likewise, *O. placidus* was split into *O. placidus placidus* from the Lower Shire/Zambezi southwards and *O. placidus ruvumae* in the Ruvuma system and further north. However, Lakes Chilwa and Chiuta do not really have much to do with Lake Malawi, but were strongly associated with tributaries of the Ruvuma system, and molecular analysis indicates that the sister taxon to *O. shiranus shiranus* is *O. placidus placidus*, while *O. shiranus chilwae* is more closely related to *O. placidus ruvumae* (Ciezarek et al. 2024). Trewavas (1983) didn't really provide much justification for her classification, rather focussing on distinguishing among the subspecies of *O. shiranus* and *O. placidus* or differentiating the latter from the co-occurring *O. mossambicus*. Males from Lakes Chilwa and the Ruvuma are generally rather slender, black with white scales on their flanks, particularly the upper half of the body and with bright red dorsal and caudal fin margins (figs. 885.9-10). Females are also more silvery and less yellowish in both Chilwa (Trewavas 1983) and the Ruvuma (fig. 885.11). Oddly Trewavas (1983), quoting D. Tweddle, states that Lake Chiuta specimens look more like Lake Malawi *O. shiranus shiranus,* but no recent images are available. Assuming there really are significant differences between *O. shiranus shiranus* and *O. placidus placidus*, it might make more sense to consider raising *O. ruvumae* back to a full species, and to regard the Chilwa/Chiuta populations as conspecific, perhaps as a subspecies (*O. ruvumae chilwae*), if indeed any trenchant differences can be found among them.

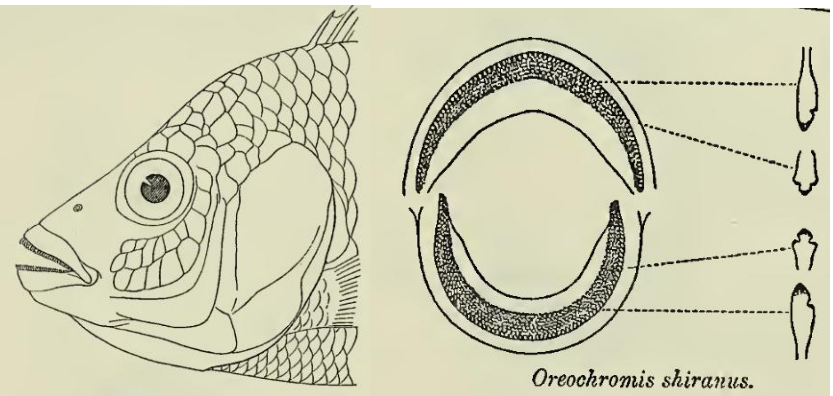


Fig. 885.1: *Oreochromis shiranus*: line drawings of head and jaws from original description by Boulenger 1897.

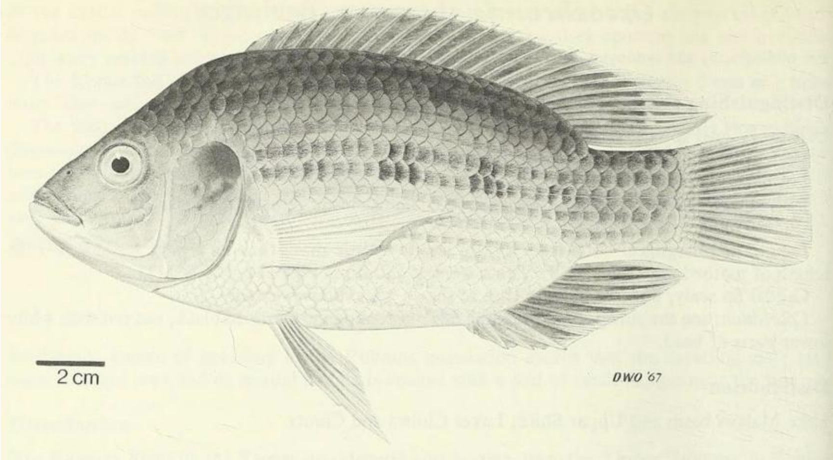


Fig. 885.2: *Oreochromis shiranus shiranus,* female from Liwonde on the Upper Shire River, from Trewavas 1983.

Fig. 885.3: *Oreochromis shiranus shiranus,* Lake Chilingali, Nkhotakota district, 2009 [GFT].

Fig. 885.4: *Oreochromis shiranus shiranus,* Manda, Lake Malawi, Tanzania, 6th Jan 2003 [GFT lab].

Fig. 885.5: *Oreochromis shiranus shiranus,* juvenile, Sept 2024, Lake Nadzenje, Nkhotakota district, Malawi, Tanzania, 6th Jan 2003 [GFT lab].

Fig. 885.6: *Oreochromis shiranus shiranus,* female, 21 July 2011, Lake Kingiri, Tanzania [GFT lab].

Fig. 885.7: *Oreochromis shiranus shiranus,* male, showing dark breeding dress and orange dorsal margin, 3 July 2018, Lake Ilamba, Tanzania [GFT].

Fig. 885.8: *Oreochromis shiranus shiranus,* male, showing dark breeding dress, enlarged jaws and red dorsal margin, 22 Nov. 2011, Lake Itamba, Tanzania [GFT].

Fig. 885.9: *Oreochromis shiranus chilwae,* adult male, showing dark breeding dress, white flank spotting, concave upper head profile, enlarged jaws and red dorsal margin, Bangor University aquarium strain [GFT].

Fig. 885.10: *Oreochromis placidus ruvumae,* adult male, showing dark breeding dress, white flank spotting, partly overlain with dark vertical barring and red dorsal margin, Lake Chidya, Ruvuma catchment, Tanzania, 17 Aug 2013 [MJG lab].

Fig. 885.11: *Oreochromis placidus ruvumae,* female, showing generally silvery-brown colour, lack of horizontal elements and slender body shape, Namiungu River, Tunduru, Ruvuma catchment, Tanzania, 16 Aug 2013 [MJG lab].

MC886. *Oreochromis squamipinnis* (Günther 1864)

The species was described as *Chromis squamipinnis* by Günther in 1864, based on a series of dried skins. Having examined them, it is clear that none of them can be unambiguously assigned to *O. squamipinnis*, and at least 3 of them seem to be male *O. karongae* in breeding dress (fig. 881.3), so really a neotype should be designated. Eschmeyer's catalogue indicates 12 syntypes, but a lectotype was designated by Trewavas (1941: fig. 886.1). Unfortunately, it does not show male breeding dress, and thus could easily be a female or immature specimen of what we now recognise as *O. karongae*. Lowe (1953) designated two specimens that were collected subsequently as 'hypotypes' to try to fix the identity of the species, but this term is not regulated by the ICZN code and thus does not appear to be taxonomically valid. It may be that the male specimen indicated by Lowe could be designated as a neotype, but this would require a petition to the ICZN Commission to set aside the existing lectotype as unidentifiable.

As presently recognised, *O. squamipinnis* can be distinguished from other Lake Malawi chambo species by its male breeding dress, which in full development is black with a paler head, generally blue, but sometimes white or green (fig. 886.2-4). There is considerable geographic variation in oral and pharyngeal dentition, body shape and male breeding dress, with specimens from sheltered muddy areas generally being deeper-bodied, with lighter dentition and having a generally paler breeding male, generally with white heads and backs (fig. 886.3). Fish from the north of the lake are generally more slender with heavier pharyngeal dentition and males have dark bodies and pale blue heads (fig. 886.2). At some locations, white-headed and blue-headed males are found together, occasionally with the odd green-headed male, as at Lake Chiwondo near Karonga (fig. 886.4). It is still unclear how much this represents phenotypic plasticity and how much is due to genetic differentiation among populations, perhaps even cryptic speciation. A laboratory strain at Bangor University, derived from a single male from Lake Masoko and a single female from Lake Kingiri has consistently shown dark males with blue heads, as has been observed in both water bodies (fig. 886.5). Lowe (1953) reported the species as preferring to breed in deeper water than *O. karongae* (=*Tilapia saka*), at depths of around 16m, off more exposed shores. However, the species breeds in Lake Malombe, which is nowhere deeper than 5m, and has been observed by snorkelling in Monkey Bay. It also breeds in shallow water in Lake Masoko (Turner et al. 2019). It was not reported to breed in the Cape Maclear area by Turner et al. (1991). Lowe (1953) reported that breeding is primarily in the rainy season (December to February).

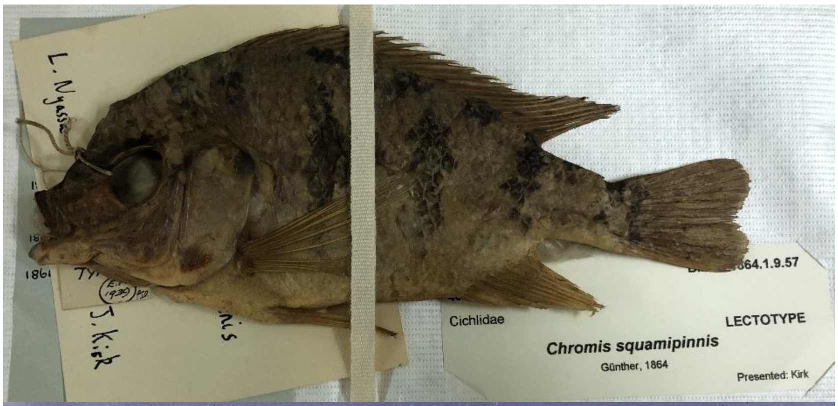


Fig. 886.1: Lectotype of *Oreochromis squamipinnnis*, at the London Natural History Museum in 2025. This specimen does not show male breeding dress and could as well be O. karongae. Three specimens in the type series clearly showed black male breeding dress [GFT]

Fig. 886.2: *Oreochromis squamipinnnis*, male, collected from Karonga, illustrating dark breeding dress and genital tassel [D. Tweddle]

Fig. 886.3: *Oreochromis squamipinnnis*, male, collected from Lake Malombe, 3rd Feb 2007, illustrating pale breeding dress and genital tassel [GFT]

Fig. 886.4: *Oreochromis squamipinnnis*, breeding pair in aquarium derived from crater lake populations (Masoko x Kingiri), showing female with male's genital tassel in her mouth [GFT]

Fig. 886.5: Male *Oreochromis squamipinnnis*, collected from Lake Chiwondo near Karonga in 1989, showing variation in male breeding dress [GFT]

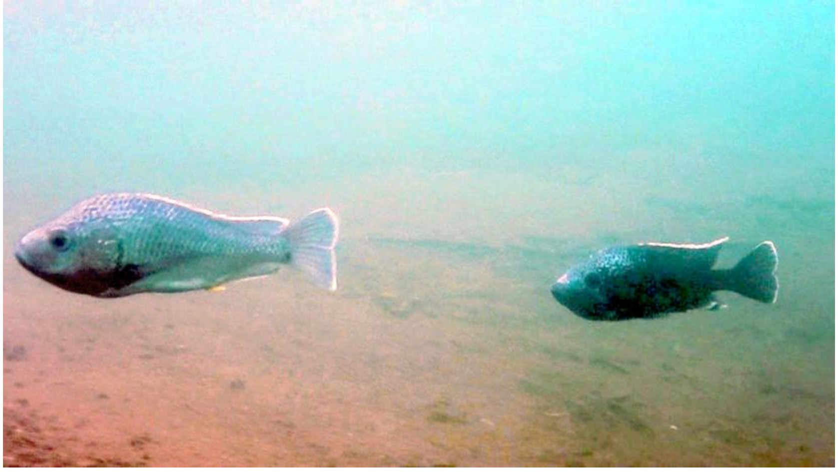


Fig. 886.6: Territorial male *Oreochromis squamipinnnis*, photographed underwater in Lake Masoko. In this lake, males show the dark body and blue head typical of northern populations of *O. squamipinnis*. They also have a generally slender morphology with large heads reminiscent of *O. lidole* [GFT]

Fig. 886.7: *Oreochromis squamipinnnis* bower at ~2m depth in Lake Masoko. [GFT]

Fig. 886.8: Territorial male *O. squamipinnis* from Lake Masoko in aquarium at Bangor university, showing bower construction leading to a central platform of fine sand (falls through the operculum while the fish 'winnows' the material picked up in its mouth), with coarser material piled up in outer ring (spat out of the mouth) [GFT].

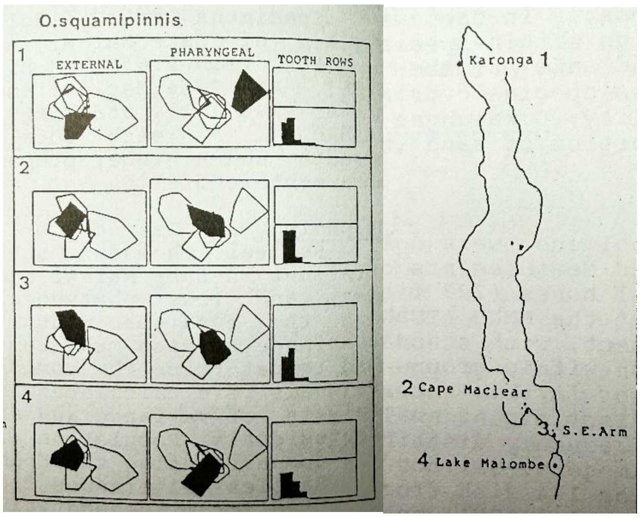


Fig. 886.9: Geographic variation in *Oreochromis squamipinnis* from collections at 4 sites, using Principal Components (multivariate) Analysis of size-adjusted residuals of logged external and pharyngeal bone measurements. A sample of *O. lidole* is included for comparison in the upper left figure (the large white polygon on the right in external measurements and to the left in pharyngeal measurements). The tooth rows counts are less variable than in *O. karongae*, but there is similar substantial pharyngeal bone variation, with the Karonga population an outlier [from Turner & Robinson 1991].

MC887. *Tilapia sparrmanii* Smith 1840

The type specimens were collected from tributaries north of the Orange River, in Namaqualand, which straddles Namibia and South Africa, and described by Smith in 1840. It is the type species of the genus *Tilapia*, which is now much reduced to contain only 4 species (the others are *Tilapia baloni, T. guinasana, T. ruweti*, with a further 3 in the limbo state of quotation marks). This follows the separation of the mouthbrooders into *Oreochromis* and *Sarotherodon* (summarised by Trewavas 1983) and the later splitting of the substrate spawning 'tilapias' based on mitochondrial DNA clades by Dunz & Schliewen (2013). The original illustration in Smith's description (fig. 887.1) looks rather slender with long fins and a rather anteriorly placed dorsal fin spot, but aspects of the markings are appropriate, and it seems to be the only fish of this general appearance in this location, so the ID is not really in doubt. A more realistic representation of the type appeared in Boulenger's (1915) Catalogue of the Freshwater Fishes of Africa (Fig. 887.2).

The species as currently recognised has a wide distribution in southern Africa (including southern Congo tributaries and the Zambezi) and it extends to the Lake Malawi catchment, where it has a distribution that largely matches that of *Pseudocrenilabrus philander* (MC876), apparently being absent from the main lake, but abundant in the catchment from the lakes and inflowing rivers of Nkhotakota area up to the northern Tanzanian shore around Kyela to Matema. Its occurrence elsewhere in the Tanzanian-sector of the catchment is reported (B.P. Ngatunga pers. comm.) but unconfirmed by collections or images, apart from presumed stocked populations in ponds or reservoirs near Njombe (fig. 887.7). In the Nkhotakota area, it was known from Lake Chilingali prior to the 2012 dam collapse, but has not been seen there since, although it was found in the outflowing Kaombe River in 2024. It has also been recorded in Lake Tabitabi on the Kayanjamwano River, and Kamphambe and Nadzenje on the Kang'ona River (Turner et al. 2025). In the north, it has been recorded from the Mbaka river, as well as Lakes Ikapu and Kyungululu (introduced in the latter and possibly in both: Turner et al. 2019).

Beyond the Malawi/Nyasa catchment, it also occurs in the little Ruaha River (fig. 887.6), although it has not been reported further downstream in the Rufiji catchment. Tweddle & Willoughby (1979) were sceptical of records from Chilwa, Chiuta and the Lower Shire. The species is intensely coloured at all stages of its life history, with smaller fish being bright golden to olive-green, sometimes with dark brown bars and highlights of red and blue. Breeding adults are very dark. Skelton (2024) reports a maximum size of 230mm SL, but it is usually much smaller, and often breeds at half this size. It is generally found in shallow weedy areas. Skelton reports it to be omnivorous, taking plant and invertebrate material as well as small fish. It is a biparental substrate spawner.

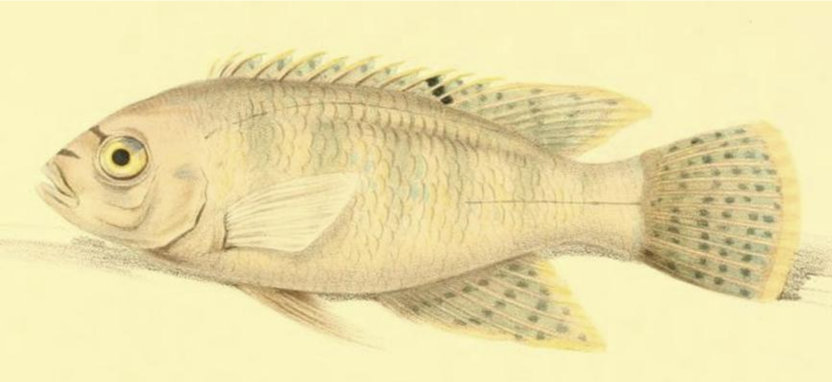


Fig. 887.1: *Tilapia sparrmanii*, type from original description.

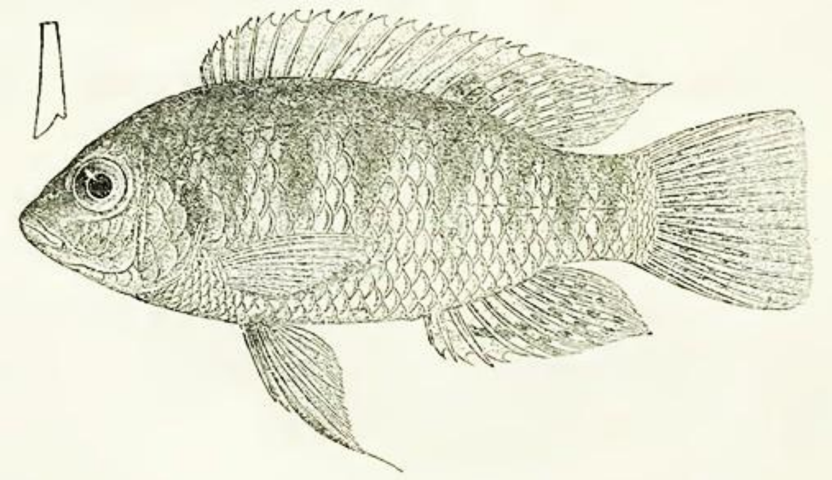


Fig. 887.2: *Tilapia sparrmanii*, type, from Boulenger 1915.


Fig. 887.3: *Tilapia sparrmanii*, young adult from Lake Chilingali 2009 [GFT lab].


Fig. 887.4: *Tilapia sparrmanii*, juvenile, Lake Nadzenje, September 2024 [GFT].

Fig. 887.5: *Tilapia sparrmanii*, young adult, Lake Kyungululu, September 2011 [GFT lab].

Fig. 887.6: *Tilapia sparrmanii*, Little Ruaha River near Mafinga, -8.4548, 35.1713, Tanzania, 1 Dec 2011 [MJG, GFT].

Fig. 887.7: *Tilapia sparrmanii*, large mature territorial adult, stocked in a reservoir at Njombe, Tanzania, 20 June 2017 [B.P. Ngatunga].

Discussion

This work is the third of three linked monographs dealing with the identification of Lake Malawi cichlid fishes, and collectively these will support ongoing and new genome sequencing programmes, alongside other research. This volume deals with the endemic pelagic cichlids, subtribe Rhamphochromina, comprised of the endemic genera *Diplotaxodon, Pallidochromis* and *Rhamphochromis*. It also covers the cichlids belonging to non-endemic genera (*Astatotilapia, Coptodon, Oreochromis, Pseudocrenilabrus, Serranochromis* and *Tilapia*), most of which inhabit shallow vegetated areas, river mouths and smaller water bodies in the catchment of Lakes Malawi and Malombe and the upper reaches of the Shire River.

Here, we have dealt with 57 taxa, of which 31 are presently regarded as valid described species, leaving 26 undescribed. Some of the described species have not yet been confidently identified in the field since their original description: for example, *D. ecclesi*, while others are still a challenge, or have only really been reliably separated from other taxa in the present work (*D. altus, D. dentatus, R. lucius*). Identification of *Diplotaxodon* has proved challenging because it is clear that there are many species with extremely similar morphologies. These often have distinctive male breeding colours which are only visible on a subset of specimens, available for collection at certain times and places. Molecular analysis has consistently shown that these do fall into genetically distinctive groups representing genetically isolated sympatric species (Genner et al. 2007a), often not even particularly closely related within the genus (Blumer et al. 2025, Camacho Garcia et al. 2025). After years of investigating many specimens, it is possible that we have not looked carefully enough, which in our defence is to some extent a reflection of the huge number of species and the relatively low survey effort. But, we think it is most likely that many of these species simply lack any morphological traits that can be used to differentiate female and juvenile individuals. Future investigations where identification to the species level is important will most likely need to focus either on adult males in breeding dress, or with individuals where molecular analysis can be used for identification (which in itself requires calibration with data from adult breeding males). There may be a few morphologically distinctive species, such as *D. greenwoodi*, but even their differentiation from *D.* sp. ‘brevimaxillaris’ is not straightforward and the possibility of cryptic species cannot be discounted.

Rhamphochromis presents its own challenges. Many species were described in the early years of the 20th Century. Descriptions were often very brief, lacked illustrations and were based on small individuals with no information on male breeding dress. In contrast to most other genera, the coverage of this genus by Eccles & Trewavas (1989) was cursory and examination of material in the London Natural History Museum indicates that much of the non-type material has been misidentified. Consequently, these old names have hung around, being frequently misused, and preventing adequate identification of field-collections. As with *Diplotaxodon*, it has become clear that calibration of species identification through examination of a large number of individuals showing male breeding dress is essential. Generally, *Rhamphochromis* show a lot of within-species variation in key traits such as gape and snout angle, and the extent of premaxillary pedicel projection. Relative trait measurements are sometimes useful, but can be misleading. For example, the angle of the head profile and projection of the premaxillary pedicel are considered to distinguish *R. woodi* and *R.* sp. 'nkhwazi', but misled previous workers into distinguish '*R. leptosoma*' specimens from *R. esox*. However, with practice, large individuals of most species can probably be distinguished, even when male breeding colours are not apparent. Smaller specimens can be very difficult to differentiate.

Most of the species of non-endemic genera are pretty unproblematic, as they have no relatives within the lake catchment. Issues arise with the *Oreochromis (Nyasalapia)* complex and *Astatotilapia calliptera*. In the case of *Oreochromis*, the juveniles of the three species are essentially indistinguishable, as are the adults of *O. squamipinnis* and *O. karongae*, apart from males in breeding dress. In addition, the issues of geographic / habitat-related variation in trophic traits within species have not been investigated genetically. It is possible that there is substantial hidden diversity in this group. In *Astatotilapia calliptera*, it may make sense to recognise as species the geographically restricted taxa that differ in male breeding dress (and other traits, as in the case of the deep-water Masoko ecotype). There is some evidence for preferences for assortative mating among these (Tyers & Turner 2013). As issue would be that this would render the widespread 'yellow' *A. calliptera* paraphyletic or ancestral, but there are good grounds for this being an acceptable situation (Turner 2024). Moreover, it will be valuable to recognise unique geographically-restricted forms as new species that are interesting biologically and vulnerable to anthropogenic threats (Turner 2024). A particularly interesting situation is in Lake Masoko, where the littoral ecotype shows little obvious phenotypic differentiation from the ancestral form in the nearby river, despite the substantial genetic and epigenetic differences between them (Vernaz et al. 2022). Meanwhile, the littoral form is currently exchanging genes with the well-differentiated benthic ecotype (Malinsky et al. 2015).

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