Identification and Biology of Diplotaxodon, Rhamphochromis and Pallidochromis

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Abstract

We present preliminary morphological and molecular taxonomic studies of the genera *Rhamphochromis, Diplotaxodon* and *Pallidochromis*, along with notes on their identification, distribution and ecology. We suggest that *Rhamphochromis* is comprised of eight to ten species: *R. longiceps, R. woodi, R. macrophthalmus, R. esox,* possibly *R. ferox* and four or five undescribed species. We suggest that *R. lucius* and *R. brevis* may be junior synonyms of *R. woodi*. We also believe that *Rhamphochromis leptosoma* and *R. melanotus* are junior synonyms of *R. esox.* We consider that the two types of *R. ferox* are not conspecific and we designate a lectotype. However, we have not yet been able to positively identify this species from recent collections. *Diplotaxodon* may contain anything from 11 to 22 or more species. Valid species of *Diplotaxodon* that we identified in the field were *D. aeneus, D. apogon, D. argenteus, D. greenwoodi, D. limnothrissa* and *D. macrops*. We were not able to positively identify *D. ecclesi*, apart from the holotype. In addition, we characterise a further 5 undescribed species, while as many as 10 further species may remain to be characterised adequately. *Pallidochromis tokolosh* remains a monotypic genus, but from mitochondrial DNA sequence data, it appears to be derived from *Diplotaxodon*, which would thus be rendered paraphyletic. A mitochondrial phylogeny suggests that *Rhamphochromis* is monophyletic, with a clade comprised of *Diplotaxodon* and *Pallidochromis* as its sister group. Within *Rhamphochromis*, *R. esox* appears to occupy a basal position, although not all species were included in the analysis. Little else could be resolved within the *Rhamphochromis* and *Diplotaxodon/Pallidochromis* clades. Incomplete lineage sorting of mitochondrial sequences proved to be as much of a problem as with other Malawian endemic haplochromine groups, such as the mbuna.

Introduction

The genera *Rhamphochromis* Regan, 1922 and *Diplotaxodon* Trewavas, 1935 include the most pelagic of Lake Malawi's cichlids (Turner, 1996). *Pallidochromis* Turner, 1994, a more benthic form, is also considered in this chapter, as it appears morphologically intermediate between *Diplotaxodon* and *Rhamphochromis* (Turner 1994a). *Rhamphochromis* species are streamlined elongated predators of fish and zooplankton. They usually have large teeth and jaws. *Diplotaxodon* comprises a heterogeneous mix of small-toothed silvery species with upwardly-angled jaws. The genus includes zooplanktivores and predators of small pelagic fish.

The genus *Rhamphochromis* was described by Regan (1922), who took the type species as *Rhamphochromis longiceps* (Günther, 1864). At the time of description, other species included were *R. esox*, (Boulenger, 1908) and the new species *R. macrophthalmus*, *R. ferox*, *R. leptosoma* and *R. woodi*. The original diagnosis was really a long description, but the genus was keyed out on the basis of the anterior beak-like expansion of the premaxillae. Subsequently, the following species were described: *R. lucius* Ahl, 1927, *R. melanotus* Ahl, 1927 and *R. brevis* Trewavas, 1935. In Trewavas' (1935) key, it was noticed that the monotypic genus *Hemitilapia* Boulenger, 1902 also exhibited beaklike premaxillae, but had very different teeth and fewer vertebrae. Since then, no new species have been described, and there has been little further work at the species- or genus-level, although Stiassny (1981) presented a detailed comparative anatomical study of *Rhamphochromis* and the Tanganyikan ecomorphological equivalent *Bathybates* Boulenger, 1898. Eccles and Trewavas (1989) presented a revised diagnosis, a key to the species and brief descriptions. Their generic diagnosis was also a detailed description, but the key to the genera contradicts the diagnosis in that *Rhamphochromis* can be keyed out from either option of dichotomy 5, where a distinction is made on the basis that the anterior teeth of the inner row are enlarged or not. More recent studies by Allison *et al.* (1995a) and Turner (1996) made some progress in identification of newly collected material, but were hampered by the small number of specimens examined and limited study of type material.

The genus *Diplotaxodon* was described by Trewavas (1935) based on the single species *D. argenteus* Trewavas, 1935. Subsequently, Fryer & Iles (1972) noted that the genus was represented by a large number of species, but more detailed information was not presented. Species descriptions that followed were those of *D. ecclesi* Burgess & Axelrod, 1973 and *D. greenwoodi* Stauffer & McKaye, 1986. In 1989, Eccles & Trewavas estimated that a further seven or more species remained to be described. Since then, four more species have been described: *D. limnothrissa* Turner, 1994, *D. apogon* Turner & Stauffer, 1998, *D. macrops* Turner & Stauffer, 1998 and *D. aeneus* Turner & Stauffer, 1998. The original generic diagnosis (Trewavas 1935) was based on an osteological character: the inferior vertebral apophyses for the retractor muscles of the pharyngeal jaws were short and did not meet below the aorta. At this time, the genus was considered monotypic. Eccles & Trewavas (1989) did not examine this character in the species described since 1935, and gave their diagnosis in terms of external appearance: lack of distinct dark bars or stripes, mouth oblique, lower jaw projecting and moderately strong, teeth simple in 2 - 4 rows. Turner (1994b) examined the vertebral apophyses of a number of species. The apophyses of *D. greenwoodi* did meet below the aorta, while those of *Copadichromis virginalis* (Iles, 1960) and a specimen of *Rhamphochromis* did not. The continued use of Eccles & Trewavas's diagnosis was recommended.

Turner (1994a) erected the monotypic genus *Pallidochromis* to contain the single species *P. tokolosh*. The genus was diagnosed as lacking distinct spots or stripes, lacking the enlarged anterior inner row teeth or high vertebral count of *Rhamphochromis* and in having a shallower gape inclination and more widely-spaced teeth than *Diplotaxodon* and *Copadichromis* (Eccles & Trewavas, 1989). Thus, like many other Malawian haplochromine genera, *Pallidochromis* lacked any defining apomorphies.

Here, we present the results of further collections, examination of new material and type specimens, and molecular studies of mitochondrial DNA sequences to clarify the status of the species and their interrelationships with other Malawian haplochromine cichlids. This work is still very preliminary, as many of the specimens we have collected have been tentatively allocated to particular species without being fully examined or measured.

Material and methods

Specimens were collected from artisanal fishery catches from all major regions of the Malawian shore, namely Karonga, Nkhata Bay, Nkhotakota, Salima, the South East (SE) and South West (SW) Arms and the associated water bodies Lake Malombe, the Shire River, Chia River and Chia Lagoon. Samples were also obtained from the Malawian islands of Likoma and Chisumulu, which lie in the east of the lake, very close to the Mozambique shore. More than 4,500 individually-labelled specimens were collected from more than 18 weeks of fieldwork. Samples were also obtained from artisanal fisheries from around the entire Tanzanian coast of the lake, including Kyela Market, Itungi Port, Matema, Lupingu, Liuli and Mbamba Bay. This work was carried out by Dr. B.P. Ngatunga, J. Mwambungu, J. Kihedu and their colleagues. Collections were also made from the trawl fishery at Maldeco in the SE Arm, and from experimental trawls of the research vessels Ethelwynn Trewavas (SE and SW Arms up to Kambiri point, 1996), Ndunduma (autumn 1998) and Usipa (March 1999). In 1998, between January 18th to January 27th, one of us (RLR) participated in an 11-day pelagic trawl survey on the RV Usipa, obtaining a total of 1,044 kg of fish from which more than 3,300 tissue samples were collected for DNA analysis, in addition to many hundreds of whole specimens. A total of 1,355 specimens collected by the SADC/GEF project from 1996 - 1999 were examined by GFT in March 1999. The GEF project undertook demersal trawl surveys at a number of stations throughout the lake, supplemented by experimental gillnetting, particularly over rocky areas unsuitable for trawling, and a small number of ad hoc purchases from artisanal fishers. Critically, the GEF project was also able to sample deep shelf areas throughout the lake, including the Mozambican sector. Further samples were obtained (by GFT) from the Mozambican sector during a demersal trawl cruise (1999) chartered by the EU Demersal Ecology Project. In addition, we re-examined 525 specimens, including type material, previously collected by GFT during the FAO Chambo Fisheries Research Project and by the ODA-funded UK/SADC Pelagic Fish Resources Project, completed in 1995, plus a further 15 type specimens and 10 non-type specimens from the

Natural History Museum London and 2 types and 4 non-type specimens from Zoologisch Museum, Humboldt Universität, Berlin. Measurements of the type of *D. ecclesi* were made by Prof. J.R. Stauffer (Penn State University, USA).

Measurements and counts followed the methods of Turner (1994b), which were based largely on those of Barel *et al.* (1977). We carried out Principal Components Analysis or Discriminant Function Analysis based on residuals from common within-groups regressions of individual logged measurements against log SL.

Despite extensive investigation, we did not find multivariate analysis to be of great benefit. In general, we found that these methods did not enable us to see discontinuities or density foci, which might indicate whether a sample of unknown specimens consists of one or more than one morphological species. Instead, they merely provided us with a graphical and numerical confirmation of morphological differences already determined by eye, univariate or bivariate comparisons. Consequently, we have not presented many results of multivariate studies here, and in fact, largely discontinued such investigations at an early stage in the project.

Furthermore, due to the immense number of specimens available, we did not carry out full sets of measurements on the majority of specimens. In most comparisons, it became apparent after study of a few individuals, which measurements were of no use for distinguishing species, and so we discontinued such measurements to concentrate on those potentially providing useful information. Thus, we focus below on informative characters rather than presenting extensive tables of counts and morphometric ratios.

Several of the photographs presented here have been edited electronically with the aim of presenting a useful impression of the overall body proportions and shape for use in identification. They should not necessarily be taken as accurate representations of features such as scales and fin rays, where such features are visible.

Results

Rhamphochromis Regan, 1922

Type species: *Hemichromis longiceps* (Günther, 1864).

Diagnosis: Cichlid fishes endemic to Lake Malawi, Lake Malombe, the Shire River and associated water bodies. Teeth simple, erect or recurved at tips. Premaxillae beaked. Melanin pattern usually absent, apart from countershading. Sometimes one or two horizontal stripes or occasionally faint, thin vertical bars. Individuals with large widely-spaced teeth have one to three enlarged anterior teeth in the inner series.

Discussion: Trewavas's (1935) key to the genera of Lake Malawi cichlids lists three genera, apart from *Rhamphochromis*, as being characterised by their beaked premaxillae: *Hemitilapia* Boulenger, 1902, *Aristochromis* Trewavas, 1935 and *Lichnochromis* Trewavas, 1935. We have not critically re-examined material from the latter three genera, but all seem readily distinguished from *Rhamphochromis*. All three genera are monotypic. *Aristochromis christyi* Trewavas, 1935 and *Lichnochromis acuticeps* Trewavas, 1935 are a very laterally compressed species with prominent oblique dark stripes. *Hemitilapia oxyrhynchus* Boulenger, 1902 (Maréchal's, 1991a, amendment to *H. oxyrhyncha* does not seem to have been subsequently employed) is a deep-bodied laterally compressed species with several dark flank blotches and rather specialised spatulate teeth with obliquely-truncate crowns (Eccles & Trewavas 1989). Snoeks (pers. comm.) does not consider *Hemitilapia* to have strongly beaked premaxillae. *Pallidochromis tokolosh* which was described subsequent to Trewavas's key, also has strongly beaked premaxillae. It has widely-spaced teeth, but does not have enlarged anterior teeth in the inner tooth rows. Among *Rhamphochromis* species, *R. longiceps*, *R.* sp. 'grey' and *R.* sp. 'slender' have relatively small, closely-packed teeth and sometimes appear to lack enlarged anterior inner row teeth. However, it is unclear whether this is simply due to loss of these teeth, perhaps during preservation and handling of specimens. Molecular data (see below) place *Pallidochromis* within the *Diplotaxodon* clade and not among the *Rhamphochromis*. This has influenced our decision to frame the diagnosis of *Rhamphochromis* to exclude *P. tokolosh*.

Rhamphochromis longiceps (Günther, 1864) (fig. 1)

Rhamphochromis longiceps was the first haplochromine cichlid from Lake Malawi to be described, as *Hemichromis longiceps*. The lectotype (fig. 2) is a dried half skin (left side), BMNH 1863.12.21:5.

Distinguishing features: Compared to other members of the genus, *R. longiceps* has smaller, more closely-packed teeth. It attains a relatively small maximum size. These traits are shared with *R.* sp. 'slender', and the two species are difficult to tell apart, if indeed they are distinct species. Larger individuals of *R. longiceps* tend to have longer and deeper heads, a larger opercular area, and a larger eye than similar-sized *R.* sp. 'slender'. The snout tends to be less acutely pointed. The back sometimes seems more arched, and the body wider and deeper than in *R.* sp. 'slender'. The dorsal fin base is generally also relatively longer. The easiest way to distinguish the two species is from live colour (R.L. Robinson, pers. obs.). When freshly caught, many larger specimens of *R. longiceps* have a bright greenish metallic iridescence on the upper surface of the body. Mature males can be more bluish-grey. Unfortunately, some specimens seem to lack the iridescence entirely.

Description: A small, streamlined fish with a smaller mouth and teeth than most other *Rhamphochromis*. The operculum has a relatively large surface area, and a 'squarish' appearance. The cheek is relatively deep and the eye large. The teeth are very small and closely-packed. The gillrakers are usually long, unbranched and closely packed. The body is countershaded, dark grey dorsally, sometimes with a green metallic iridescence on the dorsal surface. Immature fish and mature individuals of both sexes may have grey-white or orange-yellow ventral fins. There can be 3 - 6 yellow or pinkish egg spots on the anal fin. Aquarium-kept speci-

Fig. 1. *Rhamphochromis longiceps* freshly seined from Lake Malombe, uncatalogued.

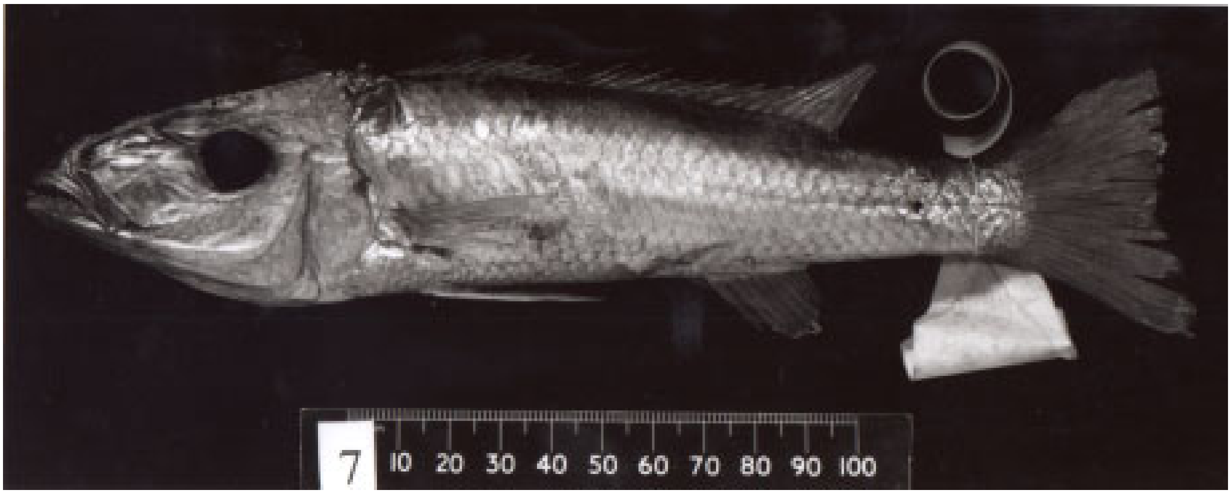

Fig. 2. *Rhamphochromis longiceps*: lectotype of *Hemichromis longiceps* (BMNH 1863.12.21:5).

mens sometimes show faint thin vertical bars. The maximum length recorded was 197 mm SL.

Ecology and Distribution: Getting accurate ecological information was complicated by our difficulty in distinguishing this species from *R.* sp. 'slender'. In this light, the following information should be treated with caution. The species is abundant and widely distributed, from the extreme shallows to depths of 148 m (fig. 3). It is found in reedy bays and lagoons, open sandy beaches, throughout the shelf and reef zones and in the open water right out in the middle of the lake. This species seems to be the most abundant *Rhamphochromis* in sheltered muddy areas, such as Lake Malombe and the Chia Lagoon. As far as we are aware, there has been no investigation of the diet of smaller, small-toothed *Rhamphochromis* where this species has been accurately distinguished from *R.* sp. 'slender'. Small fish of the *R. longiceps*/sp. 'slender' morphotype eat mostly crustacean zooplankton, whereas adults eat predominantly larvae and juveniles of the small shoaling zooplanktivorous cyprinid *Engraulicypris sardella* (Günther, 1868), locally known as Usipa (Allison *et al.*1995b). The smallest sexually mature male recorded was 109 mm SL, and the smallest female 130 mm SL. Ovaries of ripe females contained 52 - 76 eggs, of diameters up to 4 mm (rarely 5 mm). Ripe fish were collected in the months of February, March, July, August, September and October, indicating that reproduction is probably nonseasonal. Ripe fish have been reported from the SE Arm, Salima, Nkhotakota, Nkhata Bay, Chisumulu and Karonga. The species probably breeds throughout the lake. Mouthbrooding females and juveniles are commonly found inshore, generally in surface water in the shelf and littoral zones, often in reedy bays and lagoons. The species has been seen in the catches of midwater, pair and bottom trawls, handline fishermen, chirimilas, beach seines and occasionally in gillnet catches. It can sometimes be a significant component of the catch.

Discussion: Maréchal (1991b) lists the type material as syntypes: "BMNH 1863.12.21:5 and one skin". Our investigations indicated that this accession number refers to a jar containing two half-skins. One specimen of 192 mm SL is labelled as collected by Kirk from Songwe in 1861 and as the type of *Hemichromis longiceps*. In his description of *R. ferox*, Regan (1922) states that "Günther's second type-specimen of *H. longiceps* probably belongs to this species" (i.e. *ferox*). However, he does not seem to have been sufficiently confident in his identification to designate this specimen as one of the types of *R. ferox*. This specimen (172 mm SL, labelled as collected by Livingstone, presented by Russell)

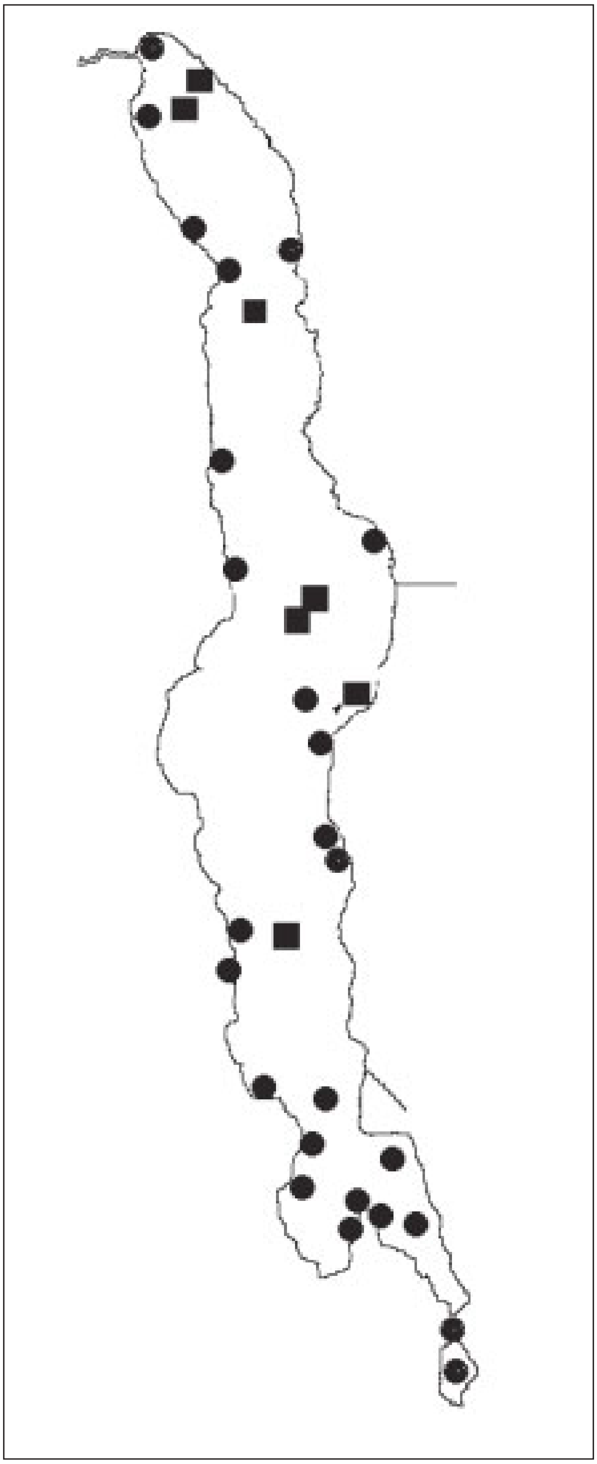

Fig. 3. Distribution records for *Rhamphochromis longiceps*. Square symbols indicate catches from over the anoxic bottom, round symbols over oxygenated bottom.

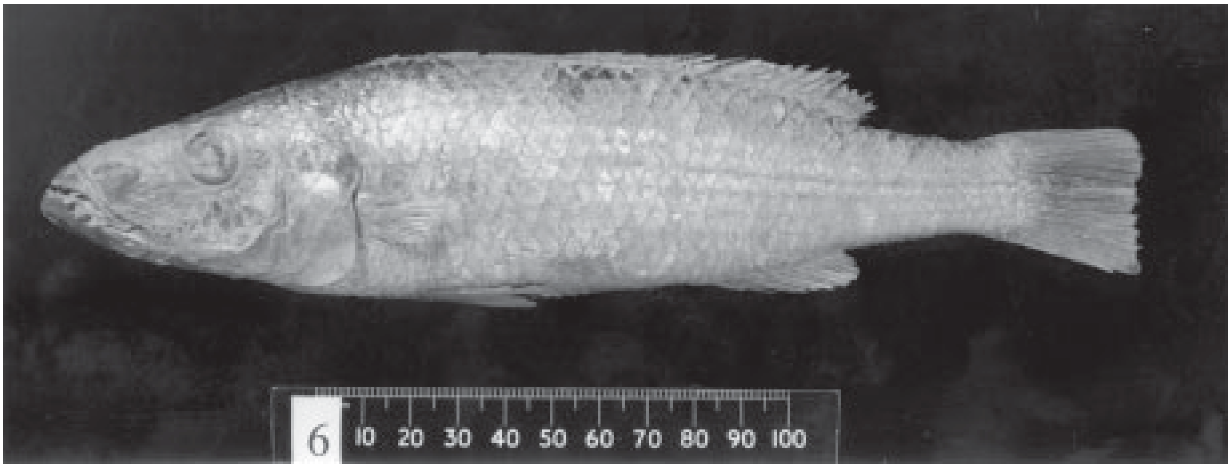

Fig. 4. *Rhamphochromis longiceps*?: syntype of *Champsochromis ferox* (BMNH 1896.10.25.28).

seems to have a more slender snout and more widely-spaced teeth than is typical for *R. longiceps*, and we agree that it seems to be conspecific with one of the syntypes of *R. ferox* (BMNH 1906.9.7:22, 179 mm SL). Thus, we consider that the Kirk specimen was effectively designated by Regan as the lectotype of *H. longiceps*. To our knowledge, no illustration of the type has previously been published. Eccles & Trewavas (1989) show a drawing of the non-type BMNH 1935.6.14.2177, and a photograph of the same specimen appears in Turner (1996). We are satisfied that this individual is conspecific with the type.

We believe that one of the syntypes of *R. ferox* (fig. 4: BMNH 1896.10. 25.28, 203.5 mm SL, collected from the Shire River) is possibly *R. longiceps*. Turner (1996) considered that this form might represent an undescribed species, nicknamed *Rhamphochromis* 'shire ferox'. The freshly caught specimen illustrated under this name by Turner (1996: p.51), we now consider is certainly *R. longiceps*.

Rhamphochromis esox (Boulenger, 1908) (fig. 5)

Described as *Paratilapia esox* by Boulenger in 1908 from three specimens. BMNH 1908.10.27.63, 331 mm SL, was taken by Regan (1922) as the type of *R. leptosoma*, but we consider this to be a junior synonym of *R. esox*. Thus, we designate BMNH 1908. 10.27.62 (319 mm SL) as the lectotype of *Paratilapia esox*. This is probably the specimen illustrated by Boulenger (1915). The third specimen mentioned in the original description may be the skeleton also mentioned by Boulenger (1915). We have not examined this specimen. Maréchal (1991b) lists other synonyms, including *Rhamphochromis melanotus* Ahl, 1927.

Distinguishing features: *Rhamphochromis esox* has an elongated and very streamlined shape. The body is rather more rounded in cross-section than other species of the genus. Apart from *R.* sp. 'deep stripe', this species appears to be the only *Rhamphochromis* to frequently exhibit a horizontal stripe in nature.

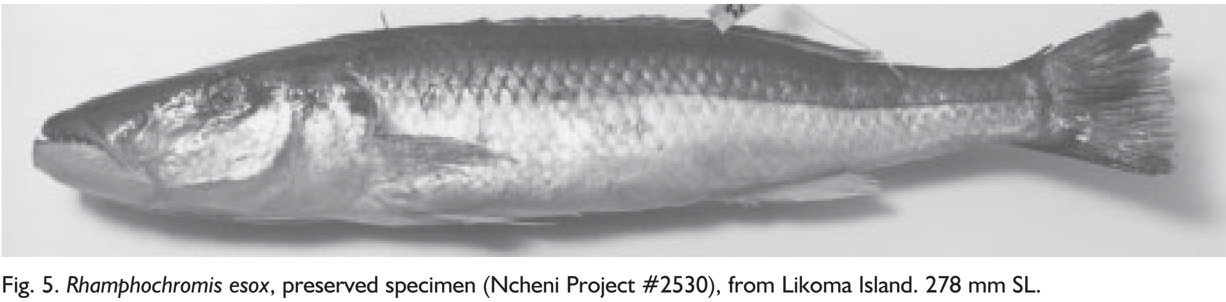

Fig. 5. *Rhamphochromis esox*, preserved specimen (Ncheni Project #2530), from Likoma Island. 278 mm SL.

Description: A large, elongate, and rather cylindrical species with a very slender body. The lower jaw is very deep, and has a smooth surface, a trait shared with *R.* sp. 'maldeco'. The teeth are short, straight and widely spaced. They are generally not visible with the mouth closed. Individuals are countershaded, dark grey dorsally usually with a blue metallic iridescence in life. There is usually an indistinct dark horizontal stripe on the flanks. The pelvic and anal fins may be either grey-white or orange. There are sometimes 2 - 9 orange-yellow egg-spots on the anal fin. The maximum length recorded is 42 cm SL.

Ecology and Distribution: We have never found this species in large numbers at any site, but it is very widely distributed (fig. 6) in shelf and rocky reef zones, usually in areas where the bottom is fairly shallow. We have collected samples from above bottom depths of 2 - 65 m. Although the streamlined morphology of this species made us predict that it would be found in surface waters right out over the anoxic zone, it was rarely found offshore. The smallest mature males that we collected were 204 mm SL, and the smallest females 187 mm SL. The ovaries of ripe females contained 117 to 680 eggs, of a diameter up to 5 mm. Ripe females were caught in June, but as few were collected, the breeding season may be longer. Ripe fish were only recorded from Nkhata Bay, but it is probable that it breeds elsewhere: certainly small juveniles were widely distributed in the littoral zone in swampy, sandy and rocky habitats. The species is mostly caught by hand lines, gillnets, and sometimes in chirimila nets. It is often caught by demersal and midwater trawls, but has not been seen to comprise a significant component of the catch. Juveniles are caught in beach seines.

Discussion: Maréchal (1991b) lists the type material as 'syntypes BMNH not registered (skin)'. This appears to be erroneous, as the types we examined were whole specimens. We consider that both *R. leptosoma* and *R. melanotus* are probably junior synonyms of *R. esox*. If this is accepted, *R. esox* can be considered the most distinctive and most readily identified species of the genus.

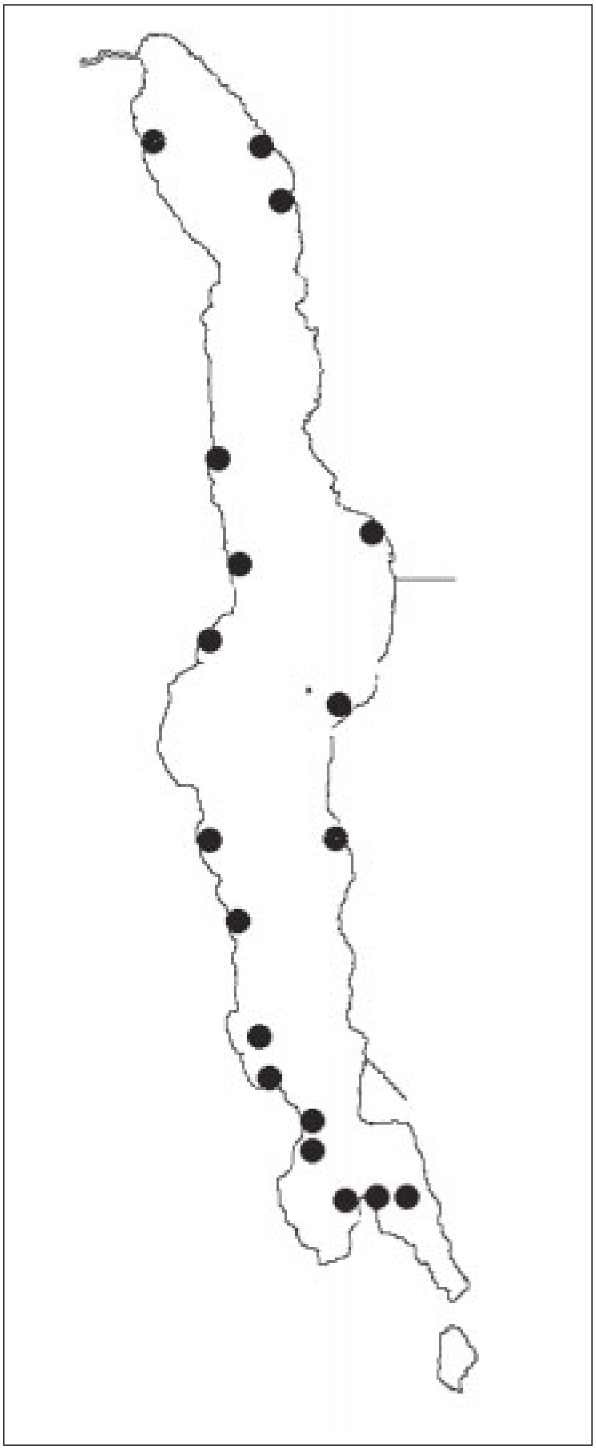

Fig. 6. Distribution records for *Rhamphochromis esox*.

Rhamphochromis ferox Regan, 1922
(fig. 7)

Rhamphochromis ferox was described from two syntypes, which we do not consider conspecific. One specimen (BMNH 1896.10.25.28, 203.5 mm SL, collected from the Shire River) is possibly *R. longiceps*. Neither Eccles & Trewavas (1989) nor Maréchal (1991b) list a lectotype. Thus, we designate the lectotype of *R. ferox* as BMNH 1906.9.7:22. This is a small slender fish (179 mm SL) with delicate jaws. We have not yet positively identified this species from recent collections.

Distinguishing features: The teeth are longer and more widely spaced than those of *R. longiceps* or *R.* sp. 'slender'. The premaxillary pedicel and jaws are shorter than those of similar-sized *R. woodi*. The eye is smaller and the cheek depth greater than most similarly-sized *R. macrophthalmus*.

Description: A small, slender, streamlined fish with an acutely pointed snout and small mouth. The teeth are slender and curved and relatively widely-spaced.

Ecology and Distribution: As this species has not been identified in recent collections, nothing is known of its ecology and distribution. The lectotype shows little gonadal development and may be an immature male.

Discussion: This is a real problem species. Because of the order in which Regan (1922) presented the species descriptions, *R. ferox* has to be considered the third *Rhamphochromis* species to be described, after *R. longiceps* and *R. esox*. The lectotype seems clearly distinct from both of these species, and so the name is most likely taxonomically valid. Unfortunately, this specimen is a small and rather undistinguished-looking and badly bent out of shape. Trewavas (1935) decided that the types of *R. ferox* were conspecific with several much larger specimens, and based her entry in the key to the species on 14 specimens, ranging from 190 to 430 mm TL. We have not examined all of these, and indeed it is not clear which specimens these were, as accession numbers are not listed in the 1935 paper. However, several of the larger specimens in the British Natural History Museum (BMNH) collection on which Trewavas worked, which are labelled as *R. ferox* and date from prior to 1935, seem to us to be very different from the lectotype of this nominal species. Other workers have followed Trewavas' definition (e.g. Eccles & Trewavas 1989; Allison *et al.* 1995a; Konings, 2001) and assigned many large specimens to *R. ferox*. We have assigned most similar individuals to *R. woodi* or *R. macrophthalmus*. However, should it be found that the lectotype of *R. ferox* is indeed a juvenile of one of the larger forms, it is possible that *R. woodi* or *R. macrophthalmus* may be junior synonyms of *R. ferox*.

The specimen BMNH 1896.10.25.28 (fig. 4) was included in Regan's description of *R. ferox*. We do not think that this is conspecific with the other type. It has a deep head and rather short straight teeth. It may be *R. longiceps*. However, the specimen is in poor condition. It is soft with many scales missing and the ends of most of the fins are broken off. The body surface is covered with a cloudy brownish substance, perhaps the remains of fungal growths or decayed skin and mucus. Thus, it is not easy to get a good impression of the body shape, but the deep cheek and squarish operculum seem more

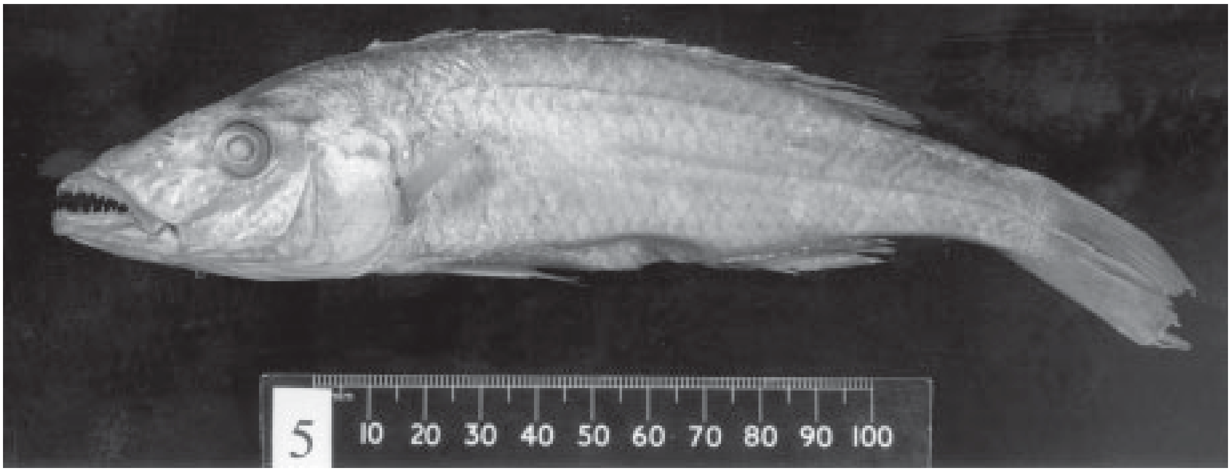

Fig. 7. *Rhamphochromis ferox.* Lectotype BMNH 1906.9.7.22.

similar to *R. longiceps* or *R.* sp. 'maldeco' than to the lectotype of *R. ferox*. The upper jaw seems rather heavy in comparison to a typical *R. longiceps*, particularly at the rostral end. In this respect, the specimen is more similar to *R.* sp. 'maldeco'. However, the body shape is atypical for that species, being rather shallow in the mid-body region. We have generally identified with confidence only fairly large specimens of *R.* sp. 'maldeco', so perhaps the discrepancy would not be apparent if we compared this specimen with smaller *R.* sp. 'maldeco'. This *R. ferox* type was collected from the Shire River. We have generally found *R.* sp. 'maldeco' in deeper water, and we have never recorded it from an inshore habitat such as the Shire River.

Rhamphochromis macrophthalmus Regan, 1922 (fig. 8)

The species was described from 3 syntypes (BMNH 1921.9.6:217-219), collected by Wood. These are smallish individuals of 167 - 197 mm SL, and we consider them to be probably conspecific. Neither Eccles & Trewavas (1989) nor Maréchal (1991b) list a lectotype, although Turner (1996) showed a photograph of the smallest specimen as lectotype [this is probably an unpublished designation from the BMNH catalogue]. This small specimen has a slightly less arched back and a rather straighter snout than the other two, and least resembles the easily diagnosable larger specimens we have collected of this species. The three syntypes are presently placed in the same jar without individually assigned catalogue numbers. We have assembled a series of individuals showing continuous variation in body proportions in relation to overall length ranging from the size of the types to that of the larger specimens readily assigned to one of our 'field species', nicknamed *R.* sp. 'longsnout'. In this, we follow Eccles & Trewavas (1989) and Allison *et al.* (1995a) in referring *R. macrophthalmus* to the large brownish species common in demersal trawl catches in the southern arms and not to the smaller slender species normally referred to in aquarist literature.

Distinguishing features: This is a large, big-toothed brownish species usually found in trawl catches in the shelf areas. Specimens usually have proportionally larger eyes and shorter premaxillary pedicels than those of *R. woodi*.

Description: A large fish often with a decurved snout and a fairly large mouth and eyes. The lower jaw is moderately to strongly protruding. Larger specimens in particular tend to have a relatively arched back and a flabby, rather rounded lower profile. The premaxillary pedicel bone is variable in length, but usually shorter than that of similarly-sized *R. woodi*. The teeth are fairly long and slender, but variable. Some individuals have extremely long teeth, e.g. those collected from Young's Bay in the north of Malawi and Chilola Bay in Mozambique. In other specimens, the teeth are shorter and few are visible when the mouth is closed. Females and non-breeding males are countershaded, dark grey-brown dorsally. The overall brownish cast is especially marked in juveniles. The caudal fin is dark grey. The pelvic fins are long in some individuals. In a collection of sexually mature and largely ripe fish made at Metangula, Mozambique, all males had orange and all females had white ventral fins. The throat may be flushed with orange, or

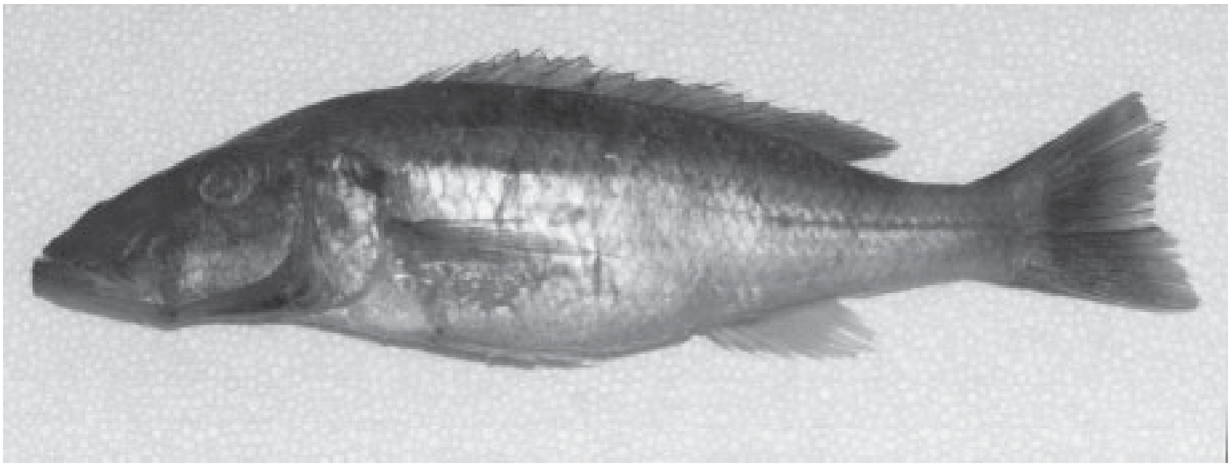

Fig. 8. *Rhamphochromis macrophthalmus*. Preserved specimen (Chambo Project #24.1) from SE Arm Lake Malawi, 229 mm SL.

may be white. No egg-spots were present on the anal fin of the specimens we examined. The largest known specimen is 298 mm SL.

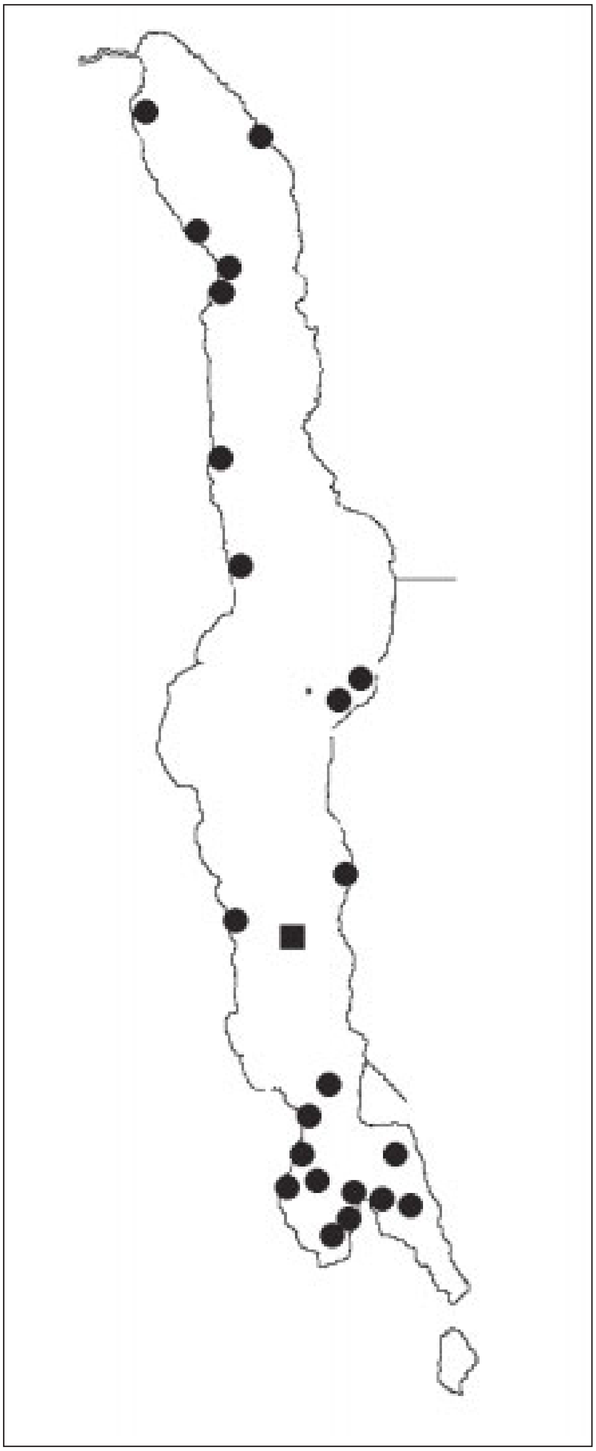

Fig. 9. Distribution records for *Rhamphochromis macrophthalmus*. Square symbols indicate catches from over the anoxic bottom, round symbols over oxygenated bottom.

Ecology and Distribution: This species is common on the shelf zone at 50 - 100 m, but the known depth range is 30 - 109 m. It was also occasionally found off reefs and has been reported from 35 m depth in the water column over the anoxic zone, although it was not commonly recorded from the middle of the lake (fig. 9). Little remains of the gonads of the types, although the 184 mm specimen appears to be sexually immature. In our collections, we found males to be sexually mature at around 199 mm SL and females at 186 mm SL. The ripe females examined contained 154 - 202 eggs, of a diameter up to almost 5 mm. Ripe fish were collected on a breeding ground at around 100m depth off Metangula in March 1999, indicating that the species probably forms breeding leks on or near the bottom. Juveniles are common in the adult habitat. The species was common in bottom and semi-pelagic trawl catches in the south of the lake, and has also been recorded from hand-line and gillnet catches in the north.

Discussion: The form commonly referred to as *R. macrophthalmus* in the aquarium literature we refer to *R.* sp. 'slender'. The species we have now assigned to *R. macrophthalmus* is what Turner (1996, photo: p.50) referred to as *R.* 'longsnout'. We have several reasons for our decision. Like the types of *R. macrophthalmus*, both *R.* sp. 'longsnout' and *R.* sp. 'slender' have relatively large eyes. All of the types of *R. macrophthalmus* range from 200 - 230 mm TL, or 167 - 197 mm SL. This is around the maximum size of the species we have assigned to *R.* sp. 'slender', yet none of the types show any indications of gonadal development, suggesting they are immature specimens of a species with a larger size at maturity. The snouts of the types of *R. macrophthalmus* are rather decurved, and their backs somewhat arched. This is typical of *R.* sp. 'longsnout', but not of *R.* sp. 'slender'. The drawing accompanying the original description (Regan, 1922), and also presented in Eccles & Trewavas's (1989) monograph, is rather misleading in this regard. The back appears less arched, and the snout less decurved than in the types. Furthermore, both upper and lower lateral lines appear to be marked with a conspicuous dark horizontal stripe, which was not in evidence when we examined the type material. We think this is possibly the result of shrinkage of the specimens causing concavities, and thus shadow at the lateral lines, although it is possible that the stripes were visible when the original drawing was made and they have since faded. Regan, in his original description, noted that the pelvic and anal fins of the specimens were orange. As the orange colour fades much more rapdily in alcohol than dark markings, Regan must have made colour notes on relatively fresh material. Regan (1922) does not mention dark horizontal stripes in *R. macrophthalmus*, although he notes their presence on *R. woodi* and *R. leptosoma*. This is significant, as *R.* sp. 'slender' sometimes shows such stripes (at least in aquaria), but we have never seen horizontal stripes in *R.* sp. 'longsnout' specimens. Lastly, both the types of *R. macrophthalmus* and our collections of *R.* sp. 'longsnout' have large, widely-spaced teeth, while *R.* sp. 'slender' typically has smaller more closely-packed teeth. Although this indicates that *R.* sp. 'slender' is not *R. macrophthalmus*, it is not much help with the identification of specimens in aquarist literature, where the teeth are not easily seen on photographs.

Rhamphochromis woodi Regan, 1922
(fig. 10)

The specimen of 184 mm SL, BMNH 1921.9.6.214, was designated as the lectotype by Eccles & Trewavas (1989). Two further specimens, BMNH 1921.9.6.215-216; 152 and 173 mm SL were recorded as paralectotypes. *Rhamphochromis brevis* Trewavas, 1935 is almost certainly a junior synonym, and *Rhamphochromis lucius* Ahl, 1927 may be also.

Distinguishing features: This is the really big nasty-looking species that is almost always called *R. ferox* in other accounts. This species has a very large mouth and big stout teeth. Individuals usually have less ventrally angled snouts, and relatively longer premaxillary pedicels than those of *R. macrophthalmus* (fig. 11). They also usually have relatively smaller eyes, and in particular, the eye seems very small compared to the scaled area of the cheek beneath. When viewed in profile, the upper surface of the tip of the premaxilla often extends almost horizontally for a considerable distance.

Description: A large species, with a very large head and mouth. The lower jaw is moderately to strongly protruding, with a prominent mental process. It has small eyes and deep cheeks. The teeth are large, thick, fairly straight and widely-spaced. In many individuals, only the tips of those near the front of the jaw are visible when the mouth is closed. The body is generally counter-shaded. The belly, chin and gular region may be silver-grey, white or yellow. Adults of both sexes may have white, grey or orange/yellow ventral fins, sometimes with black trailing edge. No egg-spots are present on the anal fins of the fish we have examined. The caudal fin is dark grey to black, sometimes with white spots in membrane. Some individuals have white spots on the membranes of the soft dorsal fin. The maximum length recorded is 402 mm SL.

Ecology and Distribution: Specimens have been found all over the lake, including the reef and shelf zone of inshore areas and also offshore in the true pelagic zone, at depths of 8 to 121 m (fig. 12). This is probably an extremely abundant species. The large '*Rhamphochromis ferox*' of Allison *et al.* (1995a) are almost certainly this species. These authors report that the largest individuals of over 40 cm TL

Fig. 10. *Rhamphochromis woodi*. BMNH 1935.6.14.2193. Approximately 32 cm SL.

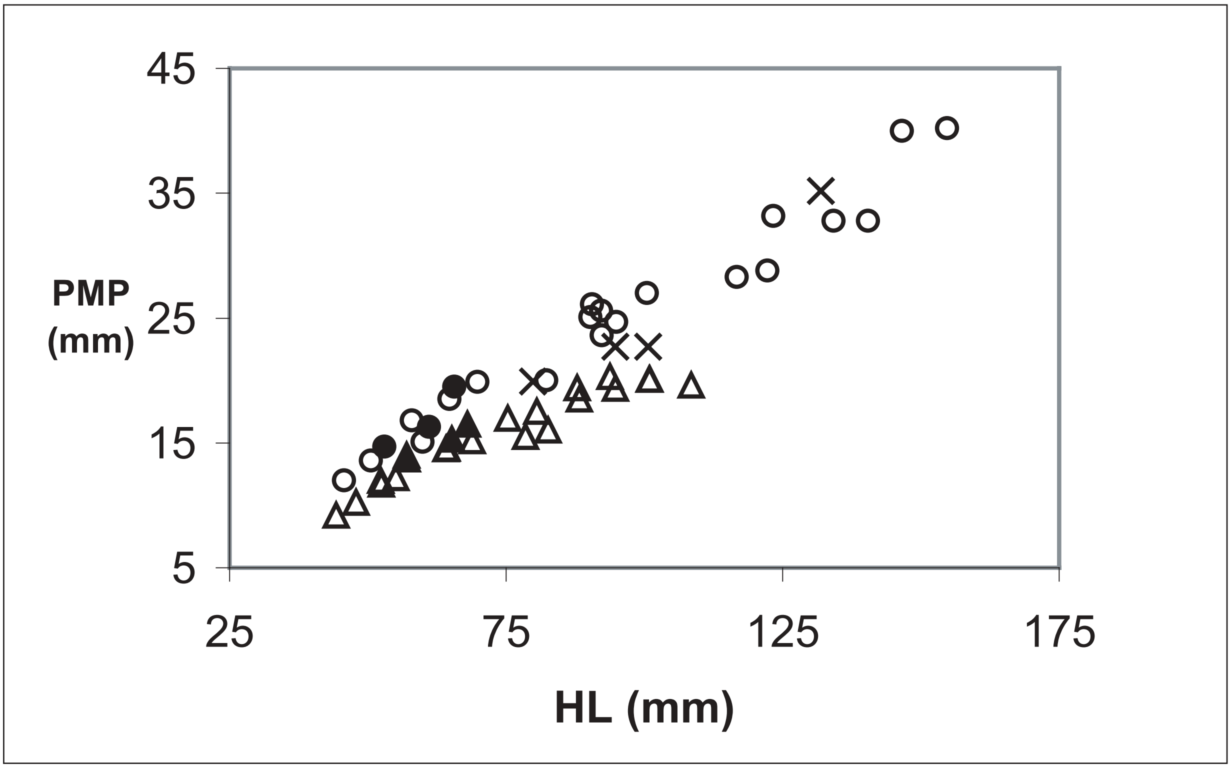

Fig. 11. The premaxillary pedicel (PMP) of *Rhamphochromis woodi* (○; types:●) is relatively longer than that of *Rhamphochromis macrophthalmus* (▲; types: △), but this difference is not so clear at the small sizes of the types. The types of *Rhamphochromis brevis* (×) are generally more similar in PMP length to *R. woodi*, although the relationship is really only clear-cut for the largest specimen.

fed mainly on *Diplotaxodon* sp. 'big-eye' (= mainly *D.* sp. 'offshore') and *D. limnothrissa*, but also took *Rhamphochromis* and the cyprinid *Engraulicypris*. Individuals of 30 - 40 cm TL ate mostly *Engraulicypris*, but about half of the diet was *D. limnothrissa* and *D.* sp. 'offshore'. The smallest size class of 20 - 30 cm TL overwhelmingly fed on *Engraulicypris* (about 70 %), with lesser amounts of *Diplotaxodon*. The largest individuals are the top predators in the pelagic zone of Lake Malawi. The smallest ripe fish known are a male of 164 mm SL and a female of 198 mm SL. Ripe females were recorded with up to 546 eggs, of up to almost 5 mm in diameter. Breeding grounds are not well documented: two mouthbrooding females (both longer than 40 cm TL) with fry were found in midwater at 30 - 50 m depth in the water column over a bottom depth of 138 m near Karonga. Mouthbrooding females and ripe males have also been found at Nkhata Bay, Ruarwe and in the SE Arm. Juveniles have been found in the inshore shelf regions, including the benthic zone of SE Arm, some in the main trawling areas. Many juveniles were taken by midwater and bottom trawls in the south, along with a few adults. We observed that adults were also caught by hand lines and gillnets, predominantly in the north.

Discussion: Regan's (1922) original description mentions four specimens, 'the one figured by Boulenger, 330 mm long (Rhoades) and three of 160 to 215 mm (Wood)'. He also mentions a skeleton. Boulenger's (1915) figure was captioned as "*Champsochromis longiceps*". However, Eccles & Trewavas (1989) and Maréchal (1991b) list only the three smaller specimens as types (BMNH 1921. 9.6.214-216). The whereabouts of the Boulenger specimen and skeleton are unknown. We have not been able to find any characteristics to differentiate distinct species among the really large big-mouthed *Rhamphochromis*, and so we have tentatively considered them all as belonging to *R. woodi*. Within the range of material we have examined, we have found apparently continuous variation in the length of the premaxillary pedicel and in the snout angle. Some of the very large specimens show a strongly decurved snout and less prominent premaxillary

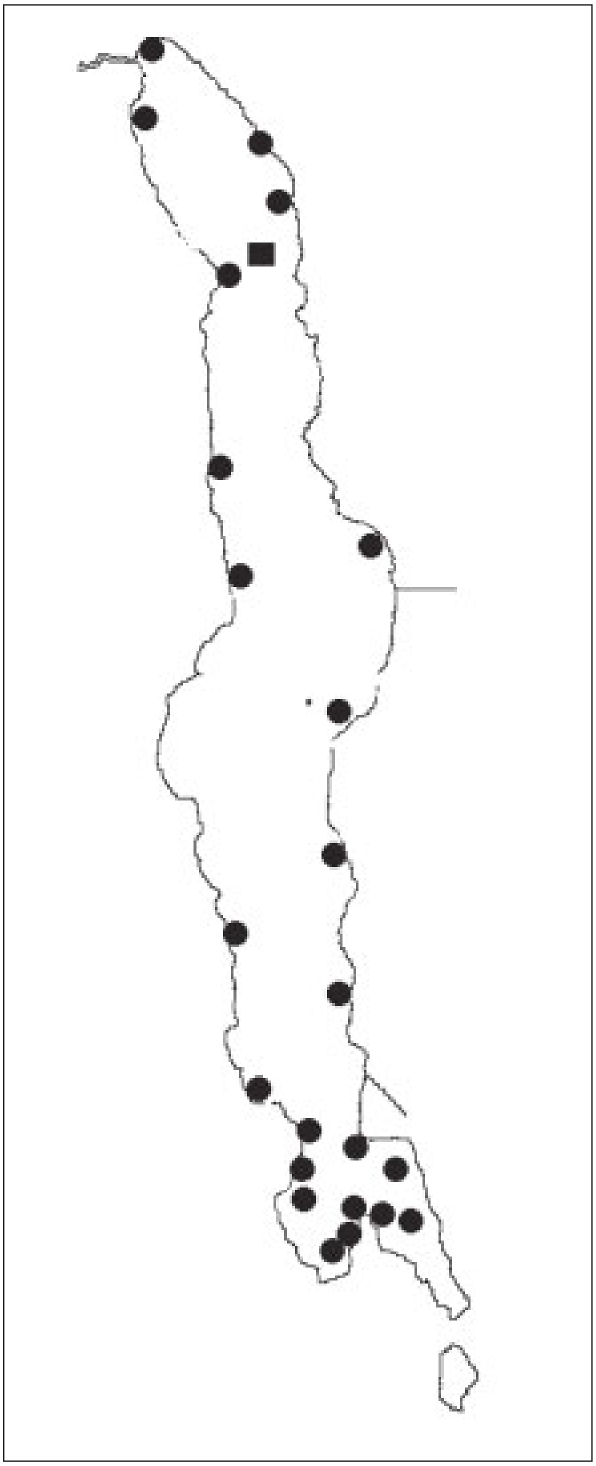

Fig. 12. Distribution records for *Rhamphochromis woodi*. Square symbols indicate catches from over the anoxic bottom, round symbols over oxygenated bottom.

pedicels (fig. 13). At first we thought that these specimens might be very large individuals of *R. macrophthalmus*. However, we did not find any intermediate-sized individuals, and the large specimens were often found in locations, such as Nkhata Bay, where more clear-cut *R. macrophthalmus* were rare. A similar situation was found with *R. esox*, where some of the larger individuals showed the *R. leptosoma* morphotype with decurved snouts and less prominent premaxillary pedicels. We have tentatively concluded that these represent old individuals with a hump-backed morphology, as is commonly found in many fish species. In any case, there seems to be some variation in these traits even in smaller individuals. For example, the types of *R. brevis* are very similar to *R. woodi*, but have a slightly deeper body and more decurved snout, while the larger type of *R. lucius* has a more streamlined form with a less decurved snout than the types of *R. woodi*. We were unable to find any demarcation between these forms. Among the smaller individuals in our collection, many show the clear *R. woodi* morphology, with small eyes, deep cheeks and long prominent premaxillary pedicels. Others, such as the individual illustrated by Turner (1996) as *R.* 'kolowilo' show a less distinctive morphology. We have tentatively regarded these as conspecific, but we cannot yet rule out the possibility that they represent an additional species that simply lacks any distinctive traits that we have noticed. Given our doubts over the identification in life of *R. lucius*, *R. brevis* and *R. ferox*, the taxonomic status of these forms cannot be regarded as definitively resolved. Contrary to Eccles & Trewavas (1989), we do not consider the presence of whitish spots in the caudal and soft dorsal fins to be diagnostic of the species, as very similar specimens from the same location were collected with or without such spots.

Fig. 13. *Rhamphochromis woodi*. 'Hump-backed' specimen, 368 mm SL, Ncheni Project #4250, caught in open water pelagic trawl haul PT 18 (S13° 53.05', E034° 44.15' - S13° 55.55', E034° 48.38') at 20 - 50 m water depth over approximately 100 m bottom.

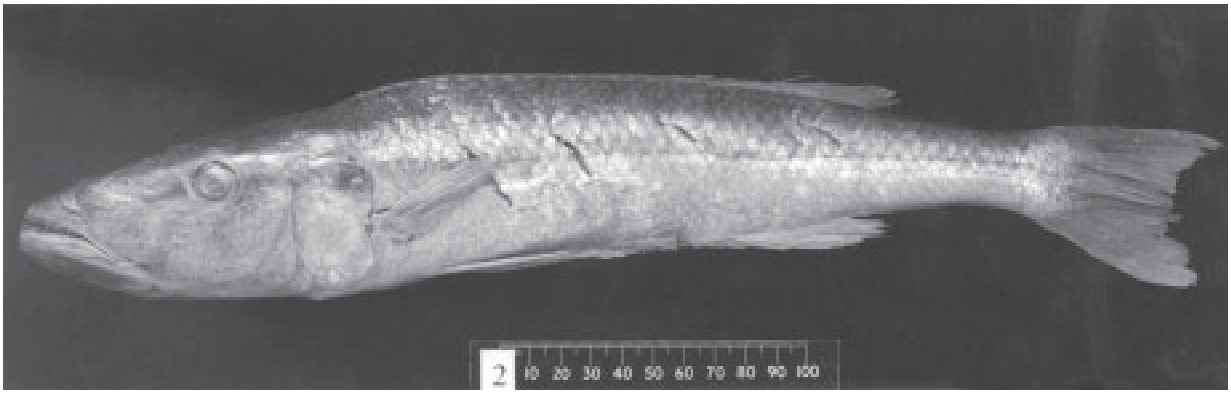

Fig. 14. *Rhamphochromis esox.* BMNH 1908.10.27:63. 331 mm SL. Syntype of *Paratilapia esox*, later taken as holotype of *Rhamphochromis leptosoma*.

Rhamphochromis leptosoma Regan, 1922
(fig. 14)

One of the types (BMNH 1908.10.27.63) of *Paratilapia esox* was taken by Regan (1922) as the type of *R. leptosoma*. We consider that *R. leptosoma* should be considered as a junior synonym of *R. esox*. The type of *R. esox* has a more prominent premaxillary pedicel, while the type of *R. leptosoma* has a more downward-angled snout. With a larger number of specimens to examine, we could not find a clear dichotomy between these two sets of character states. Also, we found similar variation in many other *Rhamphochromis* specimens that, like *R. esox* and *R. leptosoma*, did not seem to differ in any other traits. Furthermore, it seems that within *Rhamphochromis* a more prominent premaxillary pedicel is often associated with a more horizontal snout angle. We consider it likely that the two character states are the result of a single developmental change and thus should not be considered independent. Thus, there is no evidence of linkage disequilibrium between a pair of traits likely to result from non-interbreeding, and so we consider the two forms to be almost certainly conspecific.

Rhamphochromis lucius Ahl, 1927 (fig. 15)

We examined the two syntypes, ZMB 226 and ZMB 303, 169 and 307 mm SL. Contrary to the statement of Maréchal (1991b), they are not lost. The larger specimen is catalogued as the lectotype, although we are not aware that this designation has previously been published. This specimen (illustrated by Turner, 1996, p. 43) appears to us to be a large, rather slender specimen of *R. woodi*. It has small eyes, deep cheeks and long jaws. Thus, we think that *R. lucius* may be a junior synonym of *R. woodi*. However, the specimen has short premaxillary pedicels and the upper surface of the tip of premaxilla makes a fairly smooth continuation of the head profile. So, if it is *R. woodi*, it is not a nice distinctive one, and some doubts must remain. If the specimen had a clearly marked horizontal stripe and a jutting premaxillary pedicel, it could be *R.* sp. 'stripe'. We did not consider a jutting premaxillary pedicel a sufficiently invariant trait to justify the distinction of *R. esox* and *R. leptosoma*. The stripe may have faded on the specimen, or it may be that it is only sometimes expressed according to mood or background. The paralectotype (photograph in Turner, 1996, p. 43, as *R.* 'short tooth brown') is probably not conspecific and is discussed briefly below, under 'other material'.

Rhamphochromis melanotus Ahl, 1927

Trewavas (1935) considered that one of the types of *R. melanotus* was almost certainly *R. leptosoma,* while the other was probably *R. esox*. In the light of our views on the synonymy of *R. leptosoma with R. esox,* we did not consider it necessary to examine the types of *R. melanotus* to conclude that it too is a junior synonym of *R. esox*.

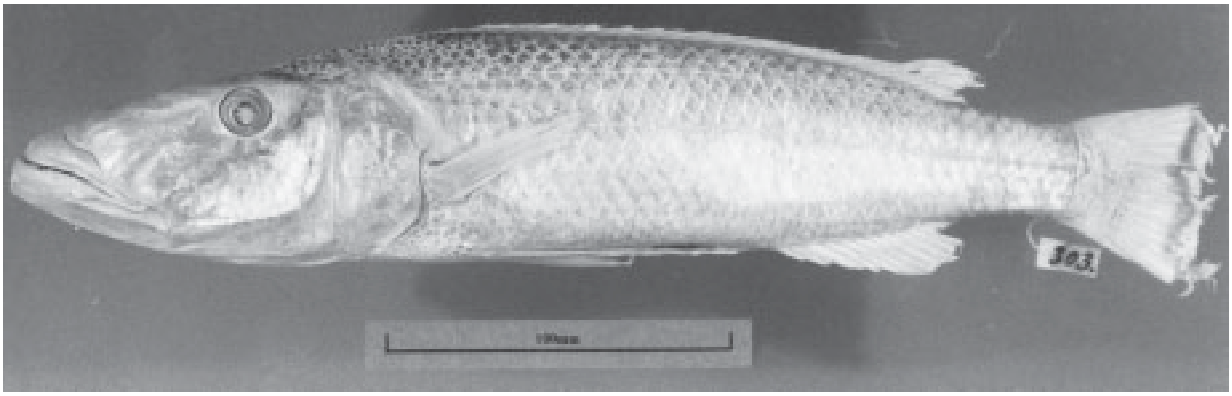

Fig. 15. *Rhamphochromis woodi*? Lectotype of *Rhamphochromis lucius*. ZMB 303. 307 mmSL, collected from Langenburg, Tanzania.

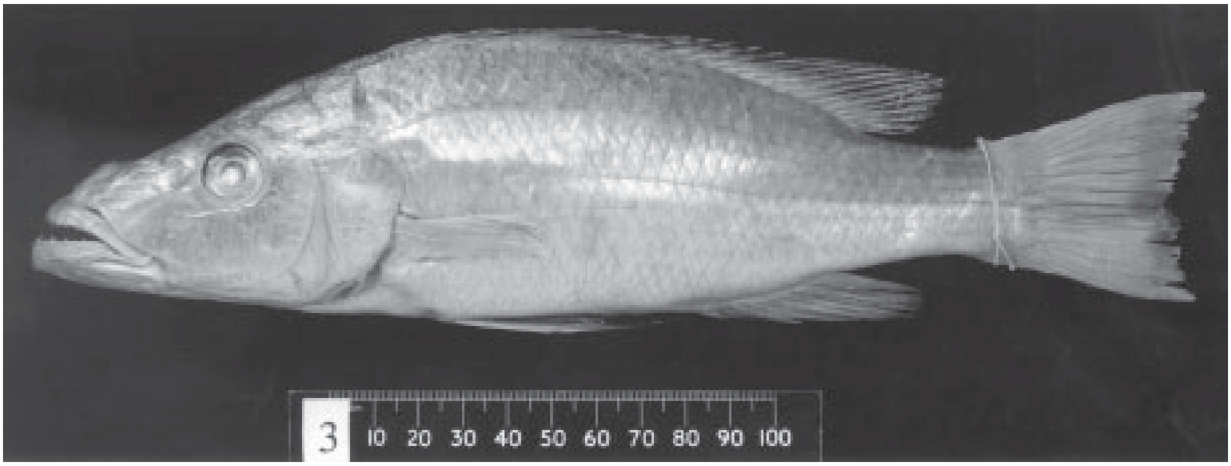

Fig. 16. *Rhamphochromis woodi*? Lectotype of *Rhamphochromis brevis*. BMNH 1935.6.14.2182. 218 mm SL.

Rhamphochromis brevis Trewavas, 1935 (fig. 16)

We examined four types of *R. brevis* (BMNH 1935.6.14:2182-2183), which measure 218-308 mm SL. Trewavas' (1935) original description lists five types (255 to 400 mm in total length). Maréchal (1991b) also lists five types under a shared range of accession numbers (BMNH 1935.56.14:2182-2183). The whereabouts of the fifth specimen is not known. We are reasonably confident that the largest remaining specimen is a rather deep-bodied *R. woodi*. It certainly has the long premaxillary pedicel, small eye and deep cheek of that species. Eccles & Trewavas (1989) designated the smallest specimen (BMNH 1935.56.14:2182) as the lectotype. This has a rather larger eye and shorter premaxillary pedicel than the largest specimen. We cannot completely exclude the possibility that this, and the two smaller paralectotypes are deep-bodied specimens of *R. macrophthalmus*, but plots of premaxillary pedicel against head length are more indicative of *R. woodi*. We conclude that *R. brevis* is almost certainly a junior synonym of *R. woodi*.

Rhamphochromis sp. 'slender' (fig. 17)

Rhamphochromis sp. 'slender' is readily confused with *R. longiceps*, from which it is only tentatively regarded as distinct. This species was illustrated by Turner (1996: p.50) as *R. cf. longiceps* and by Turner *et al.* (2001, 2002) as *R. cf. ferox*. Although this form resembles both of these nominal species, we now consider it rather confusing terminology, and have thus adopted the present designation. To further confuse the issue, this species is known in many aquarist accounts as *R. macrophthalmus*.

Distinguishing features: Like *R. longiceps*, with which it is readily confused, *R.* sp. 'slender' is a small species with a small mouth, slender jaws and small closely-packed teeth. The teeth are more widely spaced. For other differences between these species, refer to the section on *R. longiceps*.

Description: A small, slender, streamlined fish with an acutely pointed snout and small mouth. The teeth are small, slender and closely-packed. The body is countershaded, dark grey dorsally, sometimes with a bluish metallic sheen on the dorsal surface, and pinkish or purple tinges on the snout. The maximum recorded length is 209 mm SL. We have made several attempts to develop a diagnosis of this species using morphometrics and meristics. These have unsuccessful so far because we do not have a clear reference sample of specimens that can be unambiguously assigned to this species as opposed to *R. longiceps*.

Ecology and Distribution: This form is very abundant, and widely distributed throughout the lake (fig. 18), but less inclined to frequent swampy areas than *R. longiceps*. It is common in all other habitats, from inshore reef, shelf and littoral zones to offshore pelagic. It seems to be more frequent than *R. longiceps* in areas where the bottom depth exceeds 50 m. It has been caught at 20 - 90 m depth over the anoxic zone, but its depth range is probably wider, and almost certainly includes surface waters. As far as we are aware, there has been no investigation of the diet of smaller, small-toothed *Rhamphochromis* where this species has been accurately distinguished from *R. longiceps*. The smallest mature males recorded were 138 mm SL and females 143 cm SL. The ovaries of ripe females contained 27 - 68 eggs, of diameters up to 4 mm (rarely 5 mm). Ripe individuals have been collected in January, February, March, July, September and October. Reproduction is probably all year round.

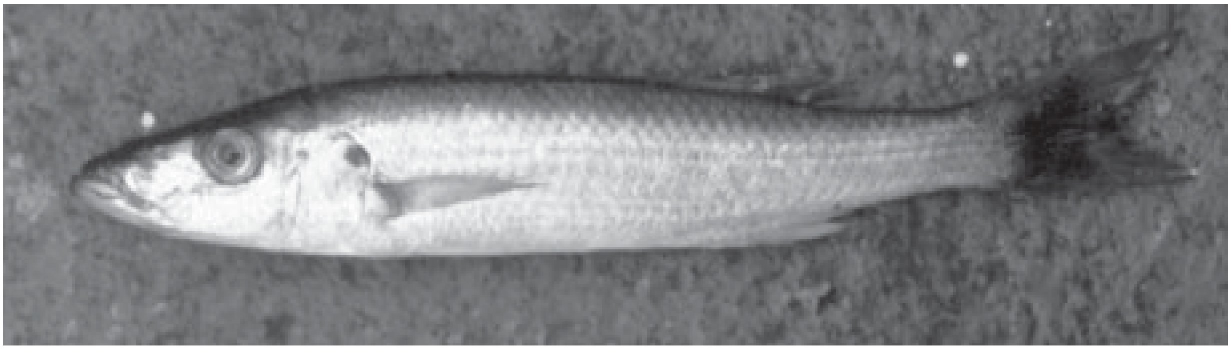

Fig. 17. *Rhamphochromis* sp. 'slender'. Uncatalogued specimen, freshly trawled from SE Arm Lake Malawi.

Carr's (1996) account of keeping and breeding *R. macrophthalmus* probably refers to this species. Breeding was said to be easily achieved in captivity, the fish being rather unaggressive for Malawi cichlids. Breeding took place when the fish attained a total length of 5-inches SL (ca 125 mm). The male had bright yellow pelvic and anal fins, even at a size of 2.5 inches (63 mm SL), while the female's fins were colourless. Spawning was observed to take place near the water surface, with the eggs released singly and retrieved by the female before they touched the substrate. The female was reported as mouthing at the male's vent, and not (as is usual in haplochromines) at the anal fin. Nine days after spawning, 30 yolk-sac fry of 7 - 8 mm total length were released as a result of the stress of catching the brooding female. Our data indicate that breeding grounds include the SE & SW Arms, Salima, Nkhotakota, Nkhata Bay, Ruarwe, Chisumulu and Karonga. Juveniles were usually found inshore and near the surface, in the shelf and littoral zones. This form was caught in large numbers by all trawl fisheries, by beach seines and chirimila nets, and sometimes in gillnets and by angling.

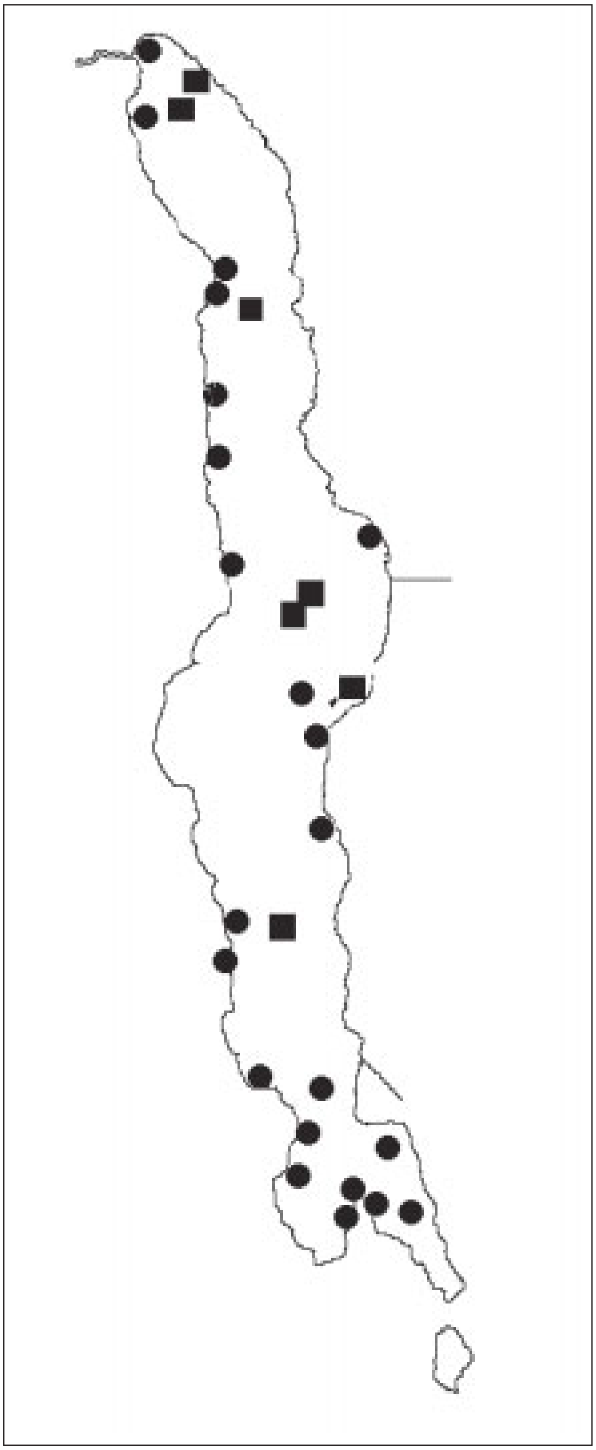

Fig. 18. Distribution records for *Rhamphochromis* sp. 'slender'. Square symbols indicate catches from over the anoxic bottom, round symbols over oxygenated bottom.

Discussion: In many previous publications, mainly from the aquarist literature, this form has been identified as *R. macrophthalmus*. We are inclined to agree with Allison *et al.* (1995a) that *R. macrophthalmus* is actually a large brownish benthic species.

Rhamphochromis sp. 'stripe' (fig. 19)

Distinguishing features: The prominent midlateral black stripe distinguishes this species from adults of all other *Rhamphochromis*, except the much more slender *R. esox*. Morphologically, the species most closely resembles *R. woodi*. Both species have small eyes, large mouths, deep cheeks and large stout teeth. *Rhamphochromis woodi* generally has a more upwardly-angled gape and a longer premaxillary pedicel. When viewed in profile, the anterior upper edge of the tip of the premaxilla does not project so far forwards as in *R. woodi*, and generally curves smoothly downwards following line of the head profile.

Description: A large fish, with a small eye and dark horizontal stripe. The body is less laterally compressed than that of many other *Rhamphochromis*. Specimens we examined had short and prominent premaxillary pedicels and terminal mouths. The teeth were large and widely spaced.

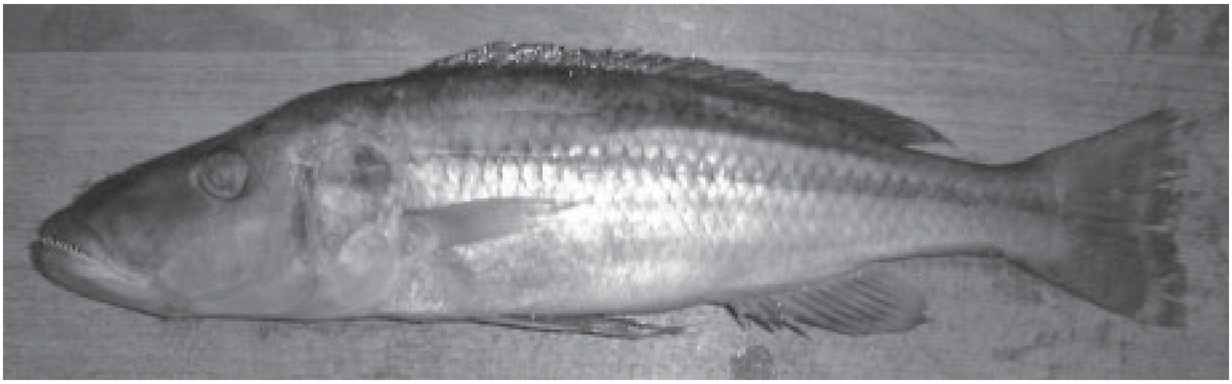

Fig. 19. *Rhamphochromis* sp. 'stripe'. Preserved specimen, collected from off Likoma Island. Ncheni Project # 2445. 322 mm SL.

The body was countershaded, dark grey dorsally with silver flanks and a white belly. Some aquarium-held specimens have shown faint vertical barring and a second dark stripe midway between the lateral stripe and the dorsal fin. The snout, and the dorsal, caudal and anal fins were dark grey. The pelvic fins were dark grey, sometimes suffused with yellow. There were 7 - 12 elongated yellow egg dummies at the edge of the anal fin, on a translucent membrane. The proximal part of anal fin was often dark grey. The maximum recorded length was 322 mm SL.

Ecology and Distribution: This species has been collected from the northern part of the Malawian coast and in Tanzania and Mozambique, as far south as Metangula (fig. 20). It is probably found on all rocky shores, and there are possible records from Cape Maclear in the south. We did not collect many specimens, but this may due to the nature of the habitat. The depth of sampling is known for only two of the individuals we have examined, which were caught between 29 - 32 m. However, small specimens almost certainly of this species are frequently seen by Scuba divers on rocky shores, sometimes in much shallower water. Individuals seem to stay close to the bottom, often in a head-up orientation. They tend to be restless, moving around rapidly, aiming rapid strikes at benthic as well as midwater fishes. Small specimens are occasionally exported for the ornamental fish trade, and adapt well to the aquarium. They can be acclimatized to feed on flake and pellet food, as well as frozen fish and shellfish. In aquaria, we have found them to be extremely aggressive to other *Rhamphochromis*, and they will try to eat any fish that might fit inside their mouths. The large 'canine' teeth at the front of the jaws can quickly cause a lot of damage to smaller fish, as can the rasping action of the pharyngeal jaws. However, they can be maintained without difficulty with other large fishes. It is not yet known if they can be bred in captivity. They are caught by hand-line fisheries around Likoma Island and off Metangula, and probably elsewhere too.

Discussion: This form is similar to *R. woodi* in its large maximum size, big mouth, long widely-spaced teeth, small eye and deep cheek. We distinguish them on the basis of two apparently unlinked traits: the head profile (shorter, more prominent premaxillary pedicel and less horizontal upper profile of tip of premaxilla) and the presence of marked horizontal stripes. As we have already pointed out in discussion of *R. woodi* and *R. esox*, the premaxillary pedicel prominence is often variable in *Rhamphochromis*. Also, species that rarely if ever exhibit horizontal stripes may do so under certain circumstances, such as confinement in aquaria. However, there is a third trait distinguishing these forms, namely the preference of *R.* sp. 'stripe' for rocky shores.

One specimen (BMNH 1986.2.5:52-53) in the Natural History Museum, London, labelled as *R. ferox* (not type material), may be this species. As we have said above, it is possible that *R.* sp. 'stripe' may be *R. lucius*.

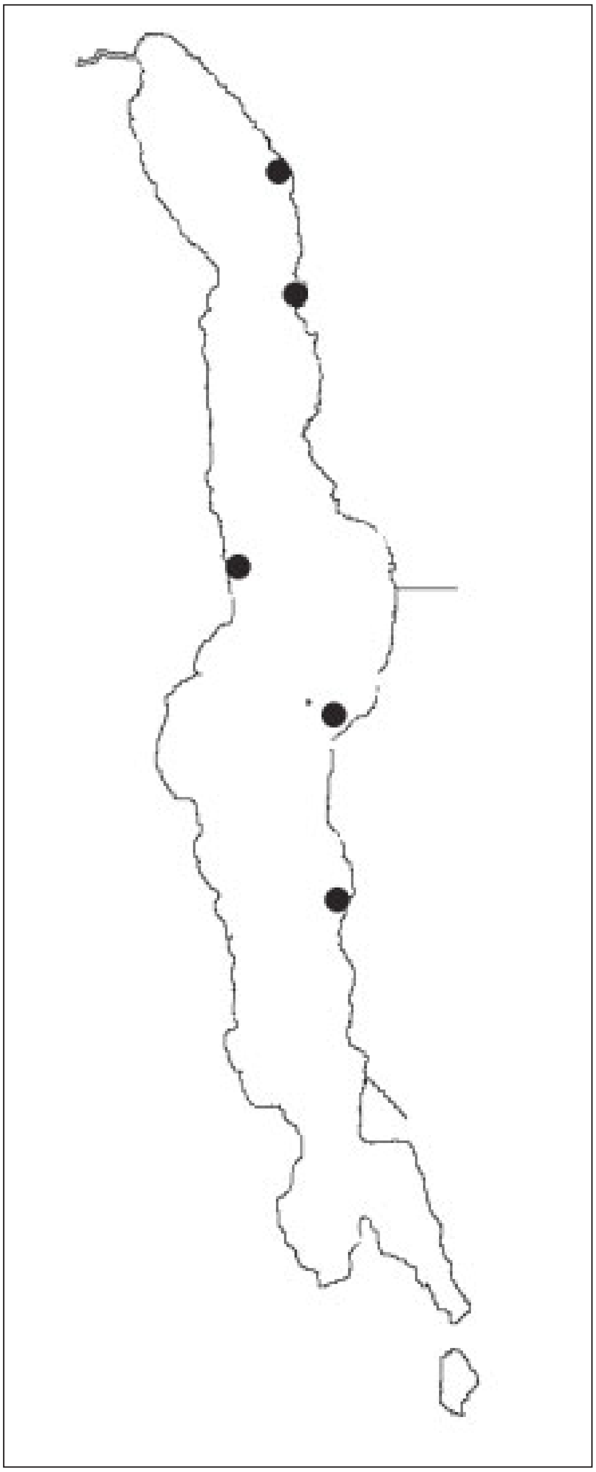

Fig. 20. Distribution records for *Rhamphochromis* sp. 'stripe'.

Rhamphochromis sp. 'grey'
(fig. 21)

Distinguishing features: Their long, laterally compressed snout, small eyes and mouths, along with their dark colour make the adults easily identified. The small closely-packed teeth are otherwise only known from *R. longiceps* and *R.* sp. 'slender' which have much smaller maximum sizes, and lack the long laterally compressed snout of *R.* sp. 'grey'. Immatures have not yet been identified and may have been confused with *R.* sp. 'slender' and *R. longiceps*.

Description: These are fairly large, sleek fish with smallish, pointed heads and small mouths. The snout is long and strongly laterally compressed. The caudal peduncle is narrow, but the body is deep in the middle. Unlike other larger *Rhamphochromis*, the teeth are very small and closely-packed. All individuals examined alive were dark grey on the flanks and dorsal surface. In many individuals, the lower body surface and throat were also dark grey, sometimes with a yellow-orange cast. Individuals of both sexes may have white, grey-black or orange anal and pelvic fins. This is apparently not related to the state of gonadal maturity. The dorsal fins of all specimens were predominantly dark grey but may be suffused with an orange cast. The maximum recorded length was 347 mm SL.

Ecology and Distribution: This species was commonly found around the Nkhata Bay region, where artisanal fishermen reported catching it from very deep rocky reefs (fig. 22). In experimental surveys, it was taken by pelagic trawls at 35 m depth over the anoxic bottom near Lupingu (Tanzania) and Chilumba. One smallish individual from Lukoma Bay, Tanzania, (48 - 60 m depth) was tentatively assigned to this species. A photo, apparently of this species, in Konings (1995, p. 340; 2001, p. 341) is labelled as 'Pallidochromis chicken' — local fishermen apparently call this species 'chicken'. It was caught by angling near Makanjila, just north of the SE Arm. Minimum size for mature males was recorded as 232 mm SL, and 218 mm for females. Ripe females contained 94 - 195 ovarian eggs, of diameter up to 5 mm. Exploitation was mainly by hand lines and gillnets in Nkhata Bay, and probably elsewhere.

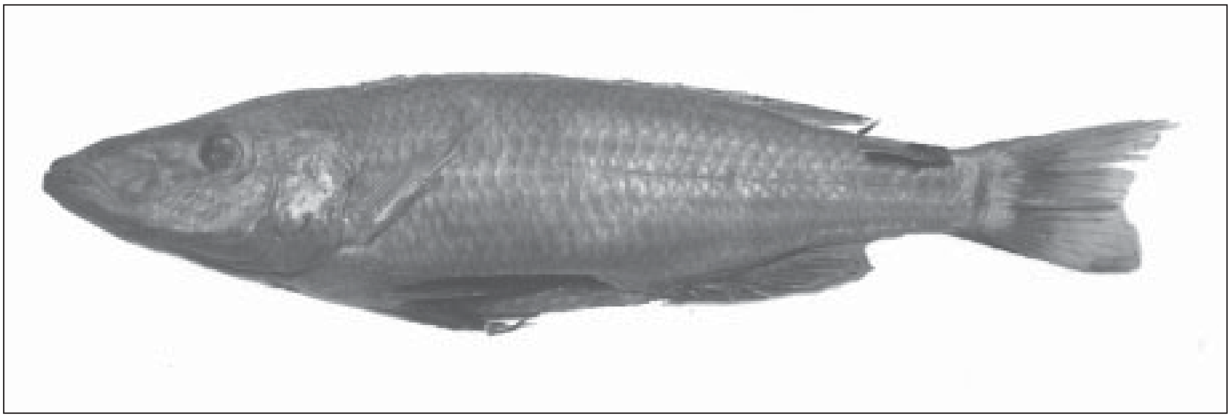

Fig. 21. *Rhamphochromis* sp. 'grey'. Preserved specimen from Nkhata Bay, Lake Malawi. Ncheni Project #437, 253 mm SL.

Discussion: We are confident that this is an undescribed species. It was first mentioned by Allison *et al.* (1995a), as a large dark grey form similar to *R. longiceps*. We examined some of their voucher specimens. Turner (1996) discussed these under *R. ferox*, but without strongly suggesting that this was the true identity of this form.

Rhamphochromis sp. 'maldeco'
(fig. 23)

Distinguishing features: The shape is smooth and streamlined like *R. esox*, but much deeper-bodied. We have never seen a trace of a horizontal stripe. The cheek depth is greater than *R.* sp. 'grey', and individuals have smaller mouths than those of *R. woodi* and *R. macrophthalmus*, wider interorbital distances than *R. macrophthalmus*, and longer pelvic fins than *R. esox*.

Description: A plump-looking fish with a streamlined head. The teeth are hardly visible when the mouth is closed. The lower jaw is deep and smooth. The anterior profile of the fish is smoother than most *Rhamphochromis*. This is a reflection of several features. The premaxillary pedicel is not prominent, indeed it is scarcely detectable in profile. The lower jaw does not jut much beyond the end of the upper jaw. In profile, the upper surface of the tip of the premaxilla follows the slope of the head and premaxillary pedicel. There is little or no mental process. Countershaded grey dorsally, with paler flanks. Specimens usually, if not always, have an overall yellowish sheen and brownish snout. The dorsal fin and tail are grey, usually suffused with

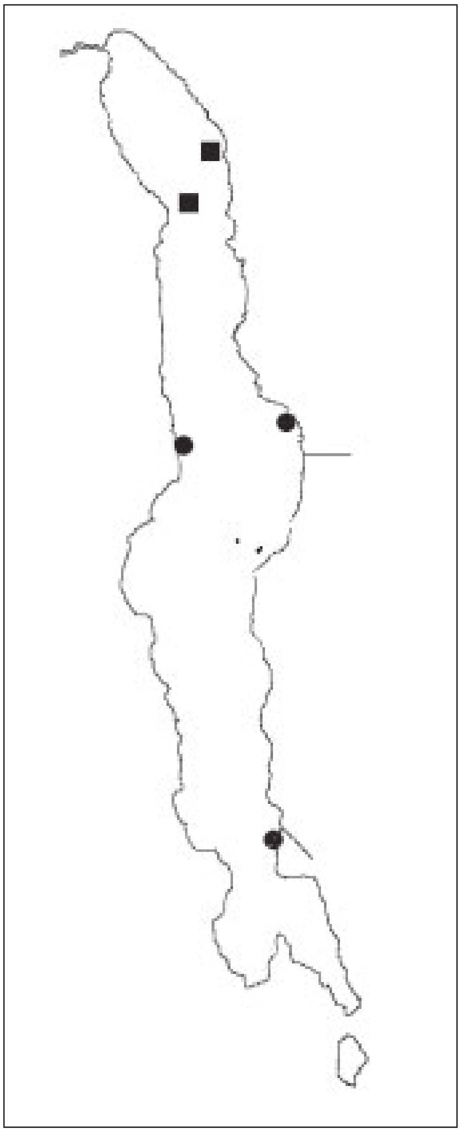

Fig. 22. Distribution records for *Rhamphochromis* sp. 'grey'. Square symbols indicate catches from over the anoxic bottom, round symbols over oxygenated bottom.

Fig. 23. *Rhamphochromis* sp. 'maldeco'. Ncheni Project # 355. Freshly trawled from SE Arm Lake Malawi, off Monkey Bay.

yellow-orange. Many larger individuals of both sexes have a bright yellow belly and orange & black ventral fins. There may be one yellow egg-spot on the anal fin. The maximum length we recorded was 312 mm SL.

Ecology and Distribution: This species is very common in the southern arms, particularly on shelf regions at 60 - 80 m depth. We also recorded it, rather tentatively, from near Nkhata Bay and Lukoma Bay, Tanzania (fig. 24). Males mature at 17 cm SL, females at about 16cm. The species comprises a small, but regular component of demersal and midwater trawl catches in the southern arms.

Discussion: We think there is little doubt that this is an undescribed species. Although it is possible that the paralectotype of *R. ferox* is conspecific with these specimens, we have proposed that this specimens is not conspecific with the lectotype of *R. ferox*. Turner (1996) mentioned some large deeper-bodied specimens that could be referable to *R.* 'kolowilo', which we have now treated as a form of *R. woodi*. We have now characterised these as *R.* sp. 'maldeco'.

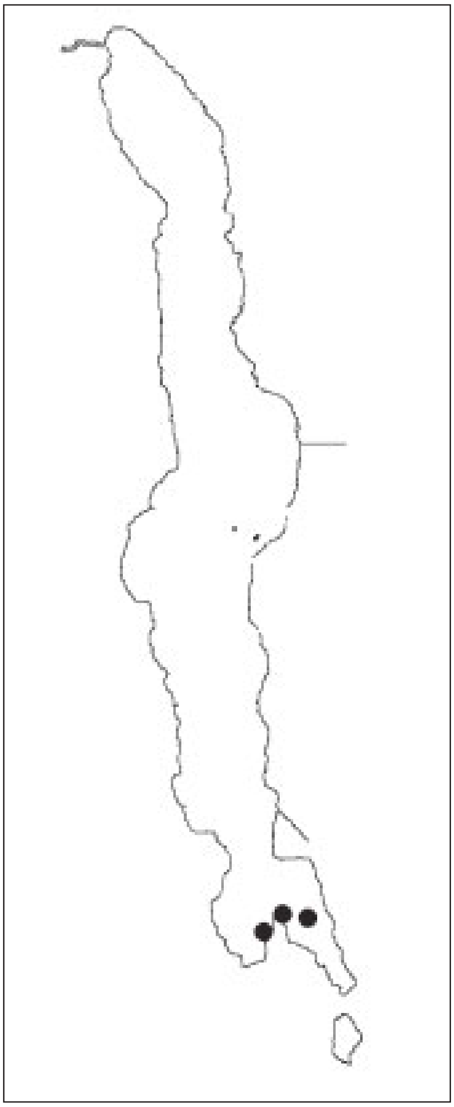

Fig. 24. Distribution records for *Rhamphochromis* sp. 'maldeco' from Ncheni Project. Additional specimens collected by SADC/GEF Project indicate a wider distribution (see text).

Fig. 25. *Rhamphochromis* sp. 'longfin'. Mature male, 184 mm SL, SE Arm, Lake Malawi, Chambo Project #6.5.

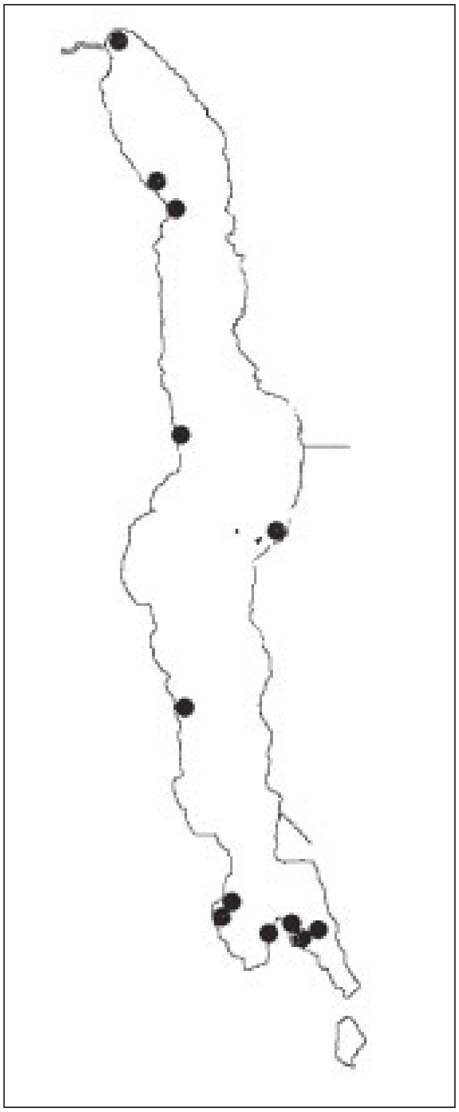

Fig. 26. Distribution records for *Rhamphochromis* sp. 'longfin'.

Rhamphochromis sp. 'longfin' (fig. 25)

Turner (1996) referred to this species as *R.* 'longfin yellow'.

Distinguishing features: This species is distinguished by its large eye, short prominent premaxillary pedicel, and long, slender teeth. Ripe males have greatly elongated pelvic fins and are bright yellow-orange. Small specimens could be confused with *R. macrophthalmus,* but the teeth are longer, the cheek deeper, the gape more upwardly-angled and the snout not so decurved as a typical individual of that species. Compared to *R. woodi*, the species matures at a much smaller size and has larger eyes and a deeper body.

Description: A small, relatively deep, short-bodied species. It has large eyes, but a deep cheek. The head is laterally compressed. The mouth is large and upwardly angled, and the premaxillary pedicel short and prominent. In profile, the anterior end of the upper surface of the tip of the premaxilla projects almost horizontally and a long distance beyond the end of the snout, as does that of *R. woodi*. The teeth are very long, prominent and widely-spaced. The lower jaw juts far beyond the upper. Females and non-breeding males are silver with a slightly brownish hue. Males in full breeding dress are spectacular, being almost entirely bright yellow, shading to orange ventrally. They may be brownish-yellow dorsally but the whole ventral surface and the ventral fins are bright orange. The pelvic fins of ripe males are extremely long, extending beyond the start of the anal fin. The maximum recorded length is 25 cm TL.

Ecology and Distribution: The species seems to be widely distributed but uncommon. It has been found in the southern arms, and off Nkhotakota, Chilumba, Chilola Bay, Wismann Bay and Chitande Island (fig. 26). It is usually found in deep water (87 - 145 m), but occasionally shallower (4 individuals from 24 - 40 m in the SE Arm, and 1 individual from 55 - 61 in Wismann Bay). A large male in breeding dress was found at 145 - 150 m at Chilola Bay, Mozambique, in April 1998. Ripe males have also been collected in deep waters in the southern arms. The smallest male with developed secondary sexual traits (orange belly, elongated pelvic fins) was 182 mm SL, almost 2 cm shorter than the smallest known apparently mature *R. macrophthalmus*.

Discussion: There can be little doubt that this is a new species. At the time of writing, Oliver (http://malawicichlids.com/mw08095.htm) illustrated this form as *R. brevis*, although making clear in the accompanying text that the identification was uncertain. Oliver's specimen was trawled on 14 August 1971 at a depth of 100 - 120 feet (30 - 37 m) at trawl station Mpemba I (between Boadzulu Island and Namiasi, in the SE Arm of Lake Malawi). This was the only individual captured on that occasion. The specimen illustrated as *R.* sp. 'big-tooth brown' by Turner (1996: p.41) may be a small specimen of this species.

Other Specimens

We are uncertain of the affinities of the specimens discussed by Turner (1996) as *R.* 'short-tooth brown', including the paralectotype of *R. lucius*. In overall body shape these smallish specimens resemble *R. longiceps*. The short, straight teeth are rather stouter and more widely-spaced than is usual for that species, however.

Diplotaxodon Trewavas, 1935

Type species: *Diplotaxodon argenteus* Trewavas, 1935.

Diagnosis: 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.

Discussion: Some *Copadichromis* species, notably those of the *C. virginalis* and *C. eucinostomus* complexes also have small teeth and lack bars, stripes or flank spots. In these species, the gape is much less upwardly angled. According to Eccles & Trewavas (1989), *C. eucinostomus* (Regan, 1922) and *C. inornatus* (Boulenger, 1908) have bicuspid or tricuspid teeth, as well as simple teeth. Iles (1960) described the teeth of *C. virginalis* and *C. mloto* (Iles, 1960) as having expanded or notched crowns, which we have not found in *Diplotaxodon*. Molecular studies (see below) suggest that *C. virginalis* and *C. cf. eucinostomus* are not members of the *Diplotaxodon* clade. Although molecular data suggest that *P. tokolosh* is a member of the *Diplotaxodon* clade, it is phenotypically very different, with a less upwardly-angled gape and larger, more widely-spaced teeth.

Diplotaxodon limnothrissa Turner 1994 (fig. 27)

Described by Turner (1994b) from 33 specimens. Holotype: BMNH 1992.3.25.1. Paratypes: BMNH 1992.3.25.2-30; PSU 255.

Distinguishing features: *Diplotaxodon limnothrissa* is a more slender, elongate fish than other members of the genus. Individuals have smaller heads, eyes and mouths than those of the other *Diplotaxodon* species, except for *D.* sp. 'holochromis'. The latter species can be distinguished by its slightly deeper body. Ripe male *D.* sp. 'holochromis' lack the yellow-white dorsal 'blaze' of *D. limnothrissa* males.

Description: *Diplotaxodon limnothrissa* is a relatively elongate cichlid with a small head and a small mouth. The eye size is variable, but the diameter is usually, but not always, less than the snout length. The overall appearance is of a more slender

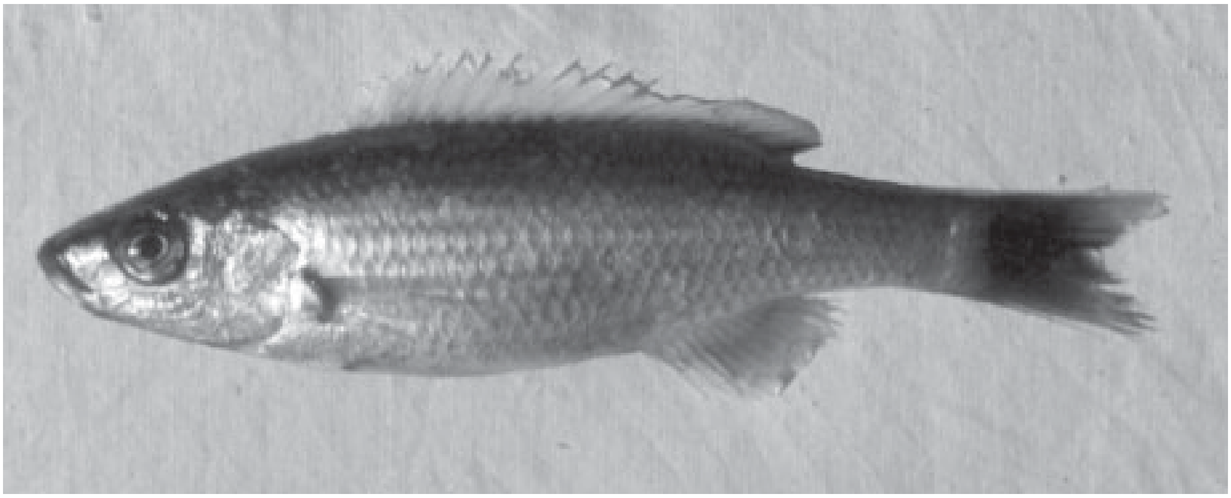

Fig. 27. *Diplotaxodon limnothrissa.* Mature male. SADC/GEF Project.

Copadichromis virginalis, and females and juveniles are superficially similar to those of the Lake Tanganyika cichlid *Benthochromis tricoti* (Poll, 1948) in general body shape. Like these species, *D. limnothrissa* has the typical appearance of a small pelagic zooplankton feeder, with a small upwardly-angled protrusible mouth, long closely-packed gillrakers and a silvery countershaded body. Live females and non-breeding males often exhibit a bright metallic purple sheen. The males in breeding dress are dark grey to black, with a bright yellow dorsal 'blaze'. In trawl catches maturing males are found which are dark grey dorsally, silver-grey on the flanks and pale ventrally. The dorsal fin is grey-white or yellow, although sometimes this colour is only present on the dorsal part of the dorsal fin, the lower part being dark grey or black. There is a dorsal 'blaze' of white or yellow, sometimes peppered with black spots, extending from the snout to the dorsal fin, and sometimes all along the upper body surface to the caudal peduncle. The caudal fin is grey, sometimes with yellowish upper and lower borders. The pelvic and anal fins can be white, grey or yellow. There are 1 - 2 large, pale yellow egg spots on the anal fin. The maximum length we recorded was 15.4 cm SL, but Duponchelle *et al.* (2000a) recorded occasional fish up to 17 cm SL, although few were over 14.5 cm. Maximum recorded live weight was around 60g, but most adults were around 30g.

Ecology and Distribution: The species is abundant throughout the lake, except in shallow areas (fig. 28). It is found inshore and offshore, on reefs and over the shelf. It is abundant over the anoxic zone, and has been recorded from depths of 20 - 220 m. It has not been collected from shallow inshore areas (< 20 m depth), and, to our knowledge, has never been observed whilst Scuba diving. Offshore, most individuals were either longer than 11 cm TL or small fry. Intermediate sized fish were abundant in the SE Arm, although they have been found elsewhere. *Diplotaxodon limnothrissa* is probably the most abundant cichlid in the lake. Menz (1995) estimated a total biomass of 87,000 t in the offshore pelagic zone. Duponchelle *et al.* (2000a) estimated that, in bottom trawls in the SW Arm in 1998 - 99, this species comprised around 4 % of the biomass at 50 m, 8 % at 75 m, 10 % at 100 m and 2 % at 125 m. We estimated average length at maturity for males at 13.5 cm TL and for females at 14.5 cm TL. Ovaries of ripe females contained an average of 15 eggs, with a maximum of 30. The maximum egg diameter was up to 5 mm. During our surveys, males in breeding dress were found throughout the year, but we did not carry out intensive year-round sampling in any single location. In the SW Arm, Duponchelle *et al.* (2000a) recorded that breeding began in March, peaked in April to June and tailed off again in August. We recorded ripe adults and mouthbrooding females at depths of 50 to 125 m. Duponchelle *et al.* (2000a) found the same range, but noted that more ripe females were found at the greatest depth, while most males in breeding dress were found at 75 - 100 m. The largest fry found in the mouths of females were around 3 cm TL, but a maximum of only 1 - 2 such large fry were found per female. Juveniles of 4 - 5 cm were found in many locations, including large numbers in the southern arms. Stomach contents analysis by Allison *et al.* (1995b) indicated that the diet was mainly

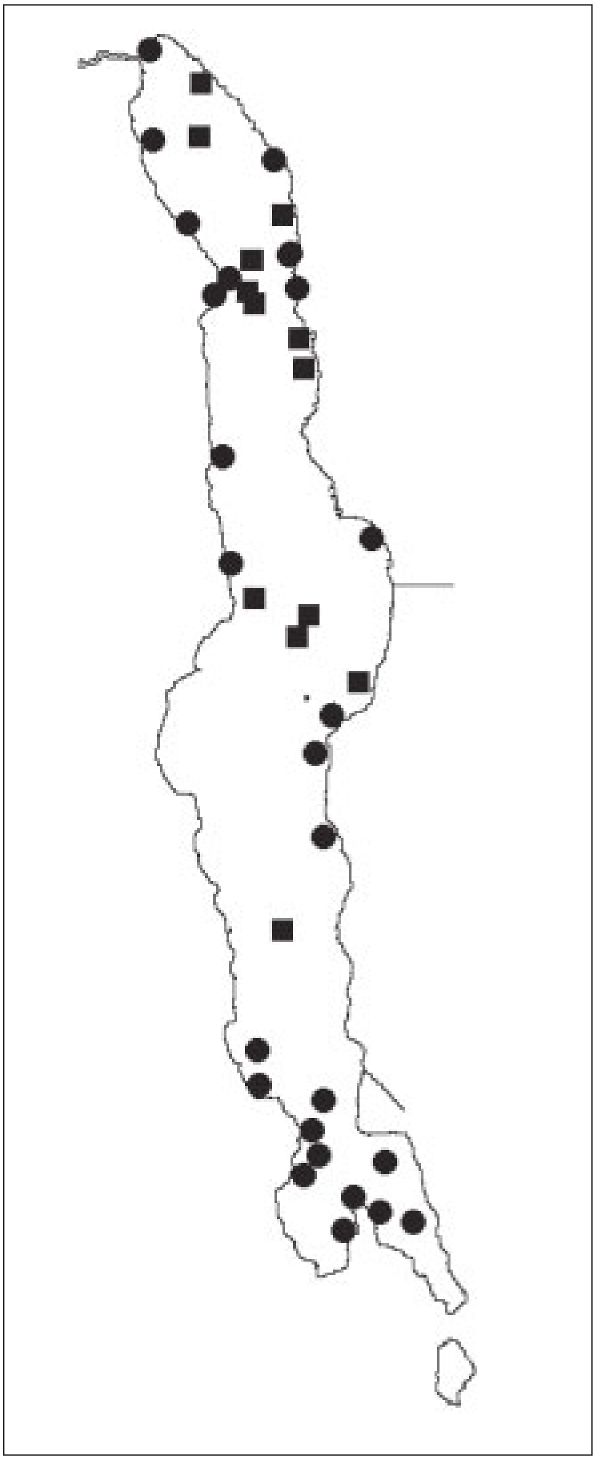

Fig. 28. Distribution records for *Diplotaxodon limnothrissa*. Square symbols indicate catches from over anoxic bottom, round symbols over oxygenated bottom.

zooplankton, particularly crustaceans such as *Tropodiaptomus*, *Mesocyclops*, and *Diaphanosoma*, but occasionally also *Chaoborus* larvae and pupae, fry of the cyprinid fish *Engraulicypris*, as well as filamentous diatoms, particularly *Aulacoseira*. These results were broadly confirmed by Duponchelle *et al.* (2000a). During the early 1990s, the species was abundant in commercial trawl catches in the southern arms, and was occasionally seen in large numbers in chirimila catches elsewhere. It was estimated to comprise over 70 % of the semi-pelagic trawl haplochromine catch in the SE Arm in the early 1990s (Turner, 1995). It has occasionally been seen in artisanal gillnet catches.

Discussion: At one stage during our project, we thought that there might be two species: one that had larger eyes, deeper bodies and longer jaws. However, these traits seemed to represent continuous variation and no diagnostic traits could be found in other aspects of morphology, in male courtship dress or in molecular genetics.

Diplotaxodon sp. 'holochromis'
(fig. 29)

It appears that this form was originally collected and named by T.D. Iles, who deposited specimens in the Malawi Fisheries Department museum in the 1950s. However, the species remains undescribed. Turner (1996) referred to smaller immature specimens from the southern arms as *D.* 'intermediate', but also discussed the Iles specimens as *D.* 'holochromis'. We are now satisfied they are the same species.

Distinguishing features: This species looks very similar to *D. limnothrissa*, but it has a deeper body (fig. 30), and a different male breeding dress, lacking entirely the dorsal blaze. In comparison to *D.* sp. 'deep', *D.* sp. 'holochromis' has a proportionally greater inter-orbital width and a less deep head. The pectoral fin is shorter, not reaching the vent and the predorsal fin distance is proportionally less. It has as a shallower head, shorter lower jaw, and narrower opercular width when compared to the *D.* sp. 'bigeye' group (*D. macrops*, *D. apogon*, *D. aeneus*, *D.* sp. 'offshore'), as well as a longer dorsal fin base and shorter distances between snout-dorsal fin and snout-pelvic fins. In comparison to the *D. argenteus* group, this species has a greater dorsal fin base length and greater inter-orbital width, but a shorter lower jaw.

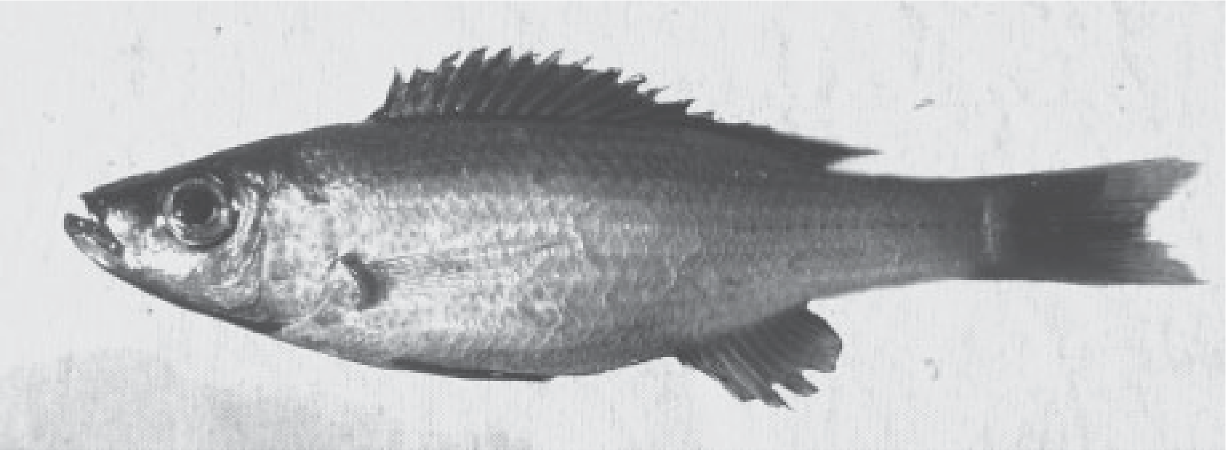

Fig. 29. *Diplotaxodon* sp. 'holochromis' mature male. SADC/GEF Project.

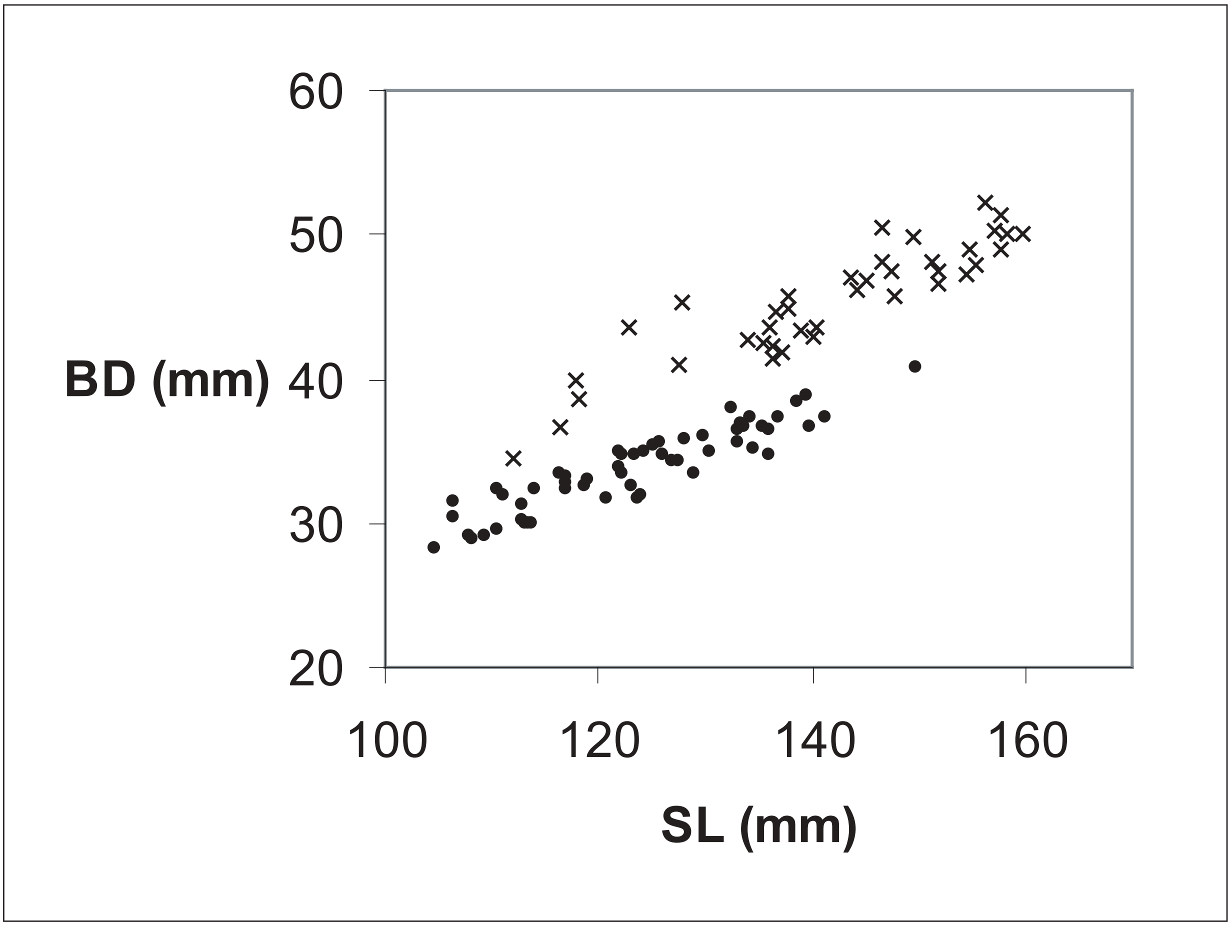

Fig. 30. *Diplotaxodon* sp. 'holochromis' (×; n=39) has a relatively deeper body (BD) than *Diplotaxodon limnothrissa* (●; n=56, including all intact types). This difference may not be apparent below 110 mm SL.

Description: Like other *Diplotaxodon* species, immature *D.* sp. 'holochromis' are pale, silvery countershaded fish. The snout, which is often dark grey, often has a purplish sheen. The dorsal fin is grey or, in ripening fish, very dark grey or black, sometimes with white lappets. Ripe males are uniformly black, except for a broad white margin to the dorsal fin and up to 3 large white egg spots on

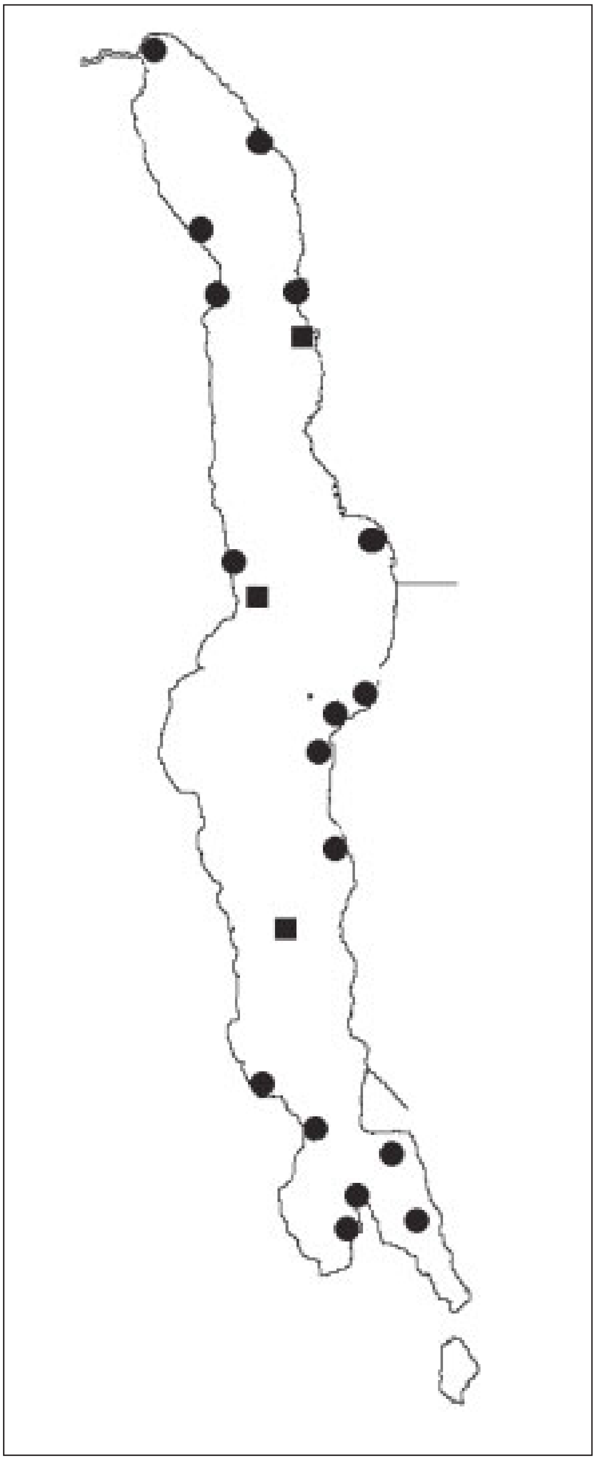

Fig. 31. Distribution records for *Diplotaxodon* sp. 'holochromis'. Square symbols indicate catches from over anoxic bottom, round symbols over oxygenated bottom.

the anal fin. The maximum recorded length is 16 cm SL.

Ecology and Distribution: The species was mostly collected from above steeply-shelving bottoms, in the vicinity of rocky coasts and reefs, but it was also sometimes found on the shelf zone (fig. 31). It was only occasionally encountered over the anoxic bottom. The depth preference was 35 - 160 m. The species was common at Nkhata Bay, occasionally found in SE Arm, but apparently uncommon elsewhere. We collected ripe specimens from April to June in the south of the lake, and in September near Chilumba, but the breeding season may be longer. Ripe fish were mostly taken from artisanal catches from deep water (69 - 122 m) near rocky reefs, at Cape Maclear, Domira Bay, Likoma Island and Chiwanga Bay. Juveniles were trawled from as shallow as 30 m in the SE Arm. Allison *et al.* (1995b) report that the species feeds on juvenile *Engraulicypris*. Occasionally caught in artisanal gears (gillnets and chirimilas). This species was sometimes encountered in small numbers in trawl catches in the south.

Diplotaxodon argenteus Trewavas, 1935
(fig. 32)

Described by Trewavas in 1935, from 3 syntypes (BMNH 1935.6.14:2281-2283) collected from the south end of the lake. *Diplotaxodon argenteus* was the only described species in the genus until the 1970s.

Distinguishing features: In comparison to *D.* sp. 'similis', *D. argenteus* has a shallower body with a flatter dorsal profile, a more upwardly-pointing mouth, a relatively wider inter-orbital distance, a large number of gillrakers, and a comparatively shorter pectoral fin. It has a relatively larger mouth and longer lower jaw than *D. limnothrissa* and *D.* sp. 'holochromis'. The dorsal fin base and inter-orbital distance are comparatively shorter than those of *D.* sp. 'holochromis'. The body is generally shallower than *D.* sp. 'deep', *D. greenwoodi* and *D.* sp. 'brevimaxillaris'.

Description: A rather 'typical' *Diplotaxodon* in appearance, moderately elongated with fairly large teeth and a predatory facies. For a *Diplotaxodon*, the eyes are not particularly large. Most specimens have a relatively large upturned mouth, with a strongly protruding lower jaw. The snout is narrow and

Fig. 32. *Diplotaxodon argenteus*. Ncheni project # 763, freshly trawled from commercial trawler in SE Arm, Lake Malawi.

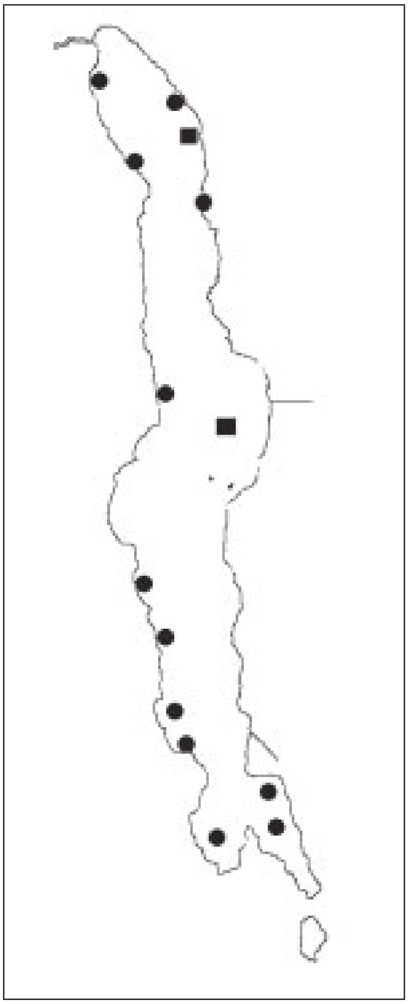

Fig. 33. Distribution records for *Diplotaxodon argenteus*. Square symbols indicate catches from over anoxic bottom, round symbols over oxygenated bottom.

fairly concave in profile, with a prominent premaxillary pedicel. The mental process is moderate to prominent. Females and non-breeding males have a silvery counter-shaded body, which is grey dorsally. The snout is dark and the body has an overall silver sheen. Fins are generally grey, though ventral fins may also be white. Males in breeding dress develop a darker head and dorsum, black eyes, snout and fins (both paired and unpaired). The anal fin is marked by 1 - 2 large yellow egg-spots. The largest specimen we recorded was 20.4 cm SL.

Ecology and Distribution: *Diplotaxodon argenteus* was common in the south, particularly on shelf zone, but was also reported near inshore reefs (fig. 33). It was collected from near the bottom, where the depth ranged from 34 - 114 m, and it was also collected from 35 m depth over the deep anoxic bottom. Duponchelle *et al.* (2000a) estimated that *D. argenteus* and *D.* sp. 'similis' (which were not distinguished; see under *D.* sp. 'similis' for further observations) comprised about 3 % of the demersal trawl fish biomass at 75 - 100 m and roughly 1.5 % at 125 m in the SW Arm from 1998 - 99. A few individuals were found at 50 m. Stomach contents of the *D. argenteus* group were reported as being mainly juvenile usipa, *Engraulicypris sardella* (Allison *et al.*, 1995b). Ripe males and brooding females were commonly found in trawl catches from depths of 40 - 70 m in the SE Arm. A male in breeding dress was collected by the SADC/GEF project from 34 - 35 m in the southern part of the SE Arm in November 1997, and another from 66 - 69 m off

Fig. 34. *Diplotaxodon* sp. 'similis'. Uncatalogued specimen freshly trawled from SE Arm, Lake Malawi.

Msaka in the SW Arm in May 1997. In the 1990s, the species was caught in fairly high numbers in midwater and bottom trawls, as well as occasionally by chirimila nets and hand lines.

Diplotaxodon sp. 'similis' (fig. 34)

An undescribed species almost certainly confused with *D. argenteus* in many previous studies.

Distinguishing features: *Diplotaxodon sp.* 'similis' belongs to a group of species generally resembling *D. argenteus* in overall appearance. The two can be readily distinguished at a glance from overall appearance, with a bit of practice. *Diplotaxodon* sp. 'similis' has a less upwardly directed gape and more prominent teeth than other members of the genus. Compared to *D. argenteus*, it generally has a more arched back, a deeper and wider body, a relatively larger eye and narrower inter-orbital, fewer gillrakers (fig. 35), comparatively longer pectoral fins and snout, and a less prominent premaxillary pedicel. *D.* sp. 'similis' has a more slender body than *D.* sp. 'deep', *D. greenwoodi* and *D.* sp. 'brevimaxillaris'. *Pallidochromis tokolosh,* which is similar in general appearance, has a less upwardly directed mouth and larger teeth.

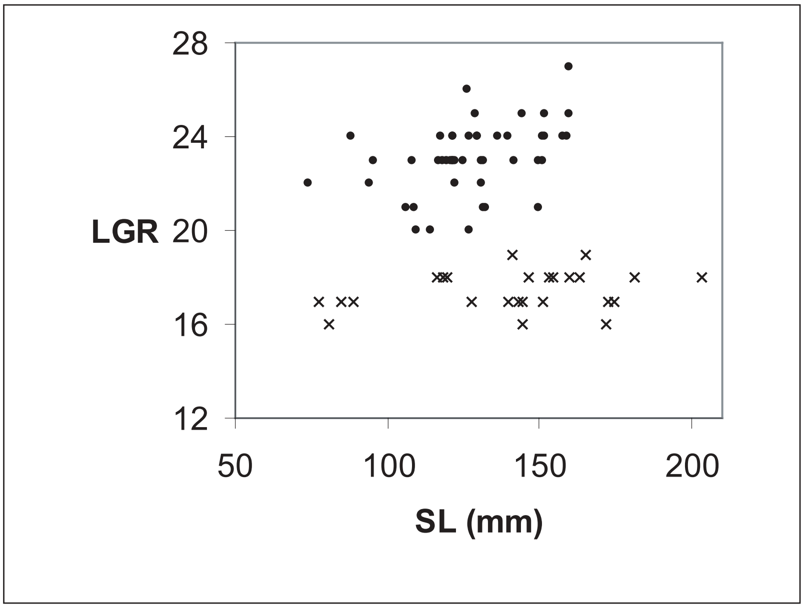

Fig. 35. *Diplotaxodon* sp. 'similis' (×; n=25) has consistently fewer ceratobranchial gillrakers (LGR) than *Diplotaxodon argenteus* (●; n=46, including all 3 types). Within *D. argenteus*, LGR is significantly positively correlated to SL (r=0.413, 46df, P<0.01), suggesting that this feature would probably not be diagnostic among smaller specimens. These taxa are also statistically significantly different in shape, as assessed from t-tests on both the second and third principal components based on 21 measurements (Student's t-test, not assuming homogeneity of variances: PC2: t=6.36, 57.3df, P<0.01; PC3: t=2.805, 55df, P<0.01).

Description: *Diplotaxodon* sp. 'similis' has a relatively large mouth and snout and a fairly large eye.

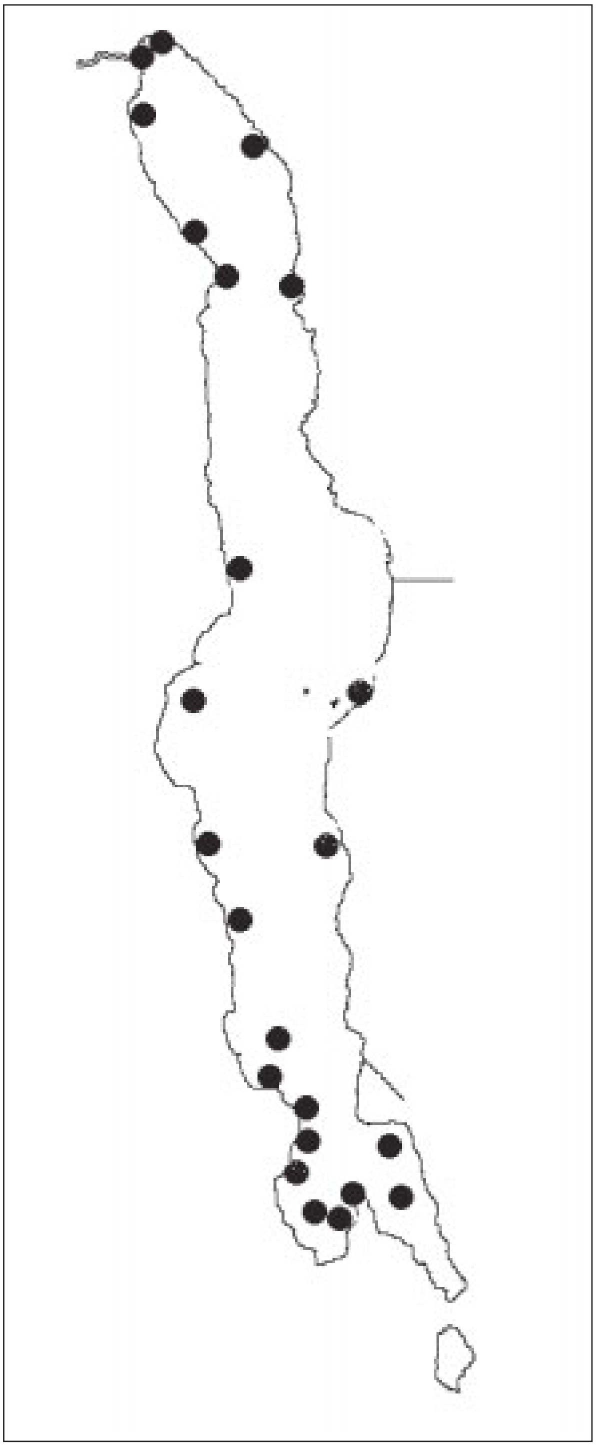

Fig. 36. Distribution records for *Diplotaxodon* sp. 'similis'.

The snout length is greater than the eye diameter. Females and non-breeding males are silver and counter-shaded. Most individuals have a yellowish-brown cast. Ripe males usually have darkened unpaired and pelvic fins, and a dark snout, nape, chin and belly. Some specimens have exaggerated countershading (dark back, pale belly), a white dorsal fin and dark pelvic fins. Perhaps these represent another species, but we were unable to find any diagnostic features. The anal fin has up to three large, pale yellow or white egg spots. The maximum length we recorded was 20.3 cm SL.

Ecology and Distribution: This species was commonly found at many sites throughout the lake, mainly in deep water, but occasionally over inshore reefs (fig. 36). No specimens have been recorded from the water column above the anoxic zone. Our records indicate a depth range of 69 - 145 m (and one individual from 30 - 45 m at Nkhotakota). Duponchelle *et al.* (2000a) estimated that *D. argenteus* and *D.* sp. 'similis' (which were not distinguished) comprised about 3 % of the demersal trawl fish biomass at 75 - 100 m and roughly 1.5 % at 125 m in the SW Arm from 1998 - 99. A few individuals were found at 50m. Stomach contents of the *D. argenteus* group were reported as being mainly juvenile usipa, *E. sardella* (Allison *et al.*, 1995b). Duponchelle *et al.* (2000a) estimated size at first maturity at an average of 140 mm SL, with a few females ripe at as little as 10 cm SL. The ovaries of ripe females contained 22 - 50 eggs, each of a mean weight of 70 mg (Duponchelle *et al.*, 2000a). Duponchelle *et al.* (2000a) recorded males in breeding dress in all months, except June (and September when no sample was taken) and ripe females in October, November and from February to May. Ripe adults have been recorded mainly from the deep waters of the shelf zone. We examined males in breeding dress collected from Domira Bay, Nkhotakota and Chilola Bay, Mozambique, at depths of 92 - 148 m (in one case 76 - 78 m in the SW Arm) in the months of January, April, June, September and October. No specific nursery areas were apparent, and juveniles less than 10 cm TL were generally distributed as the larger individuals, but were occasionally sampled depths as shallow as 53 - 61 m. The species has been observed to be exploited in small numbers in the midwater and bottom trawls in the southern part of the lake and by hand lines, chirimila seines and gillnets throughout the deepwater coastal areas around the lake.

Fig. 37. *Diplotaxodon* sp. 'deep'. Ncheni Project # 752. Freshly trawled from SE Arm, Lake Malawi.

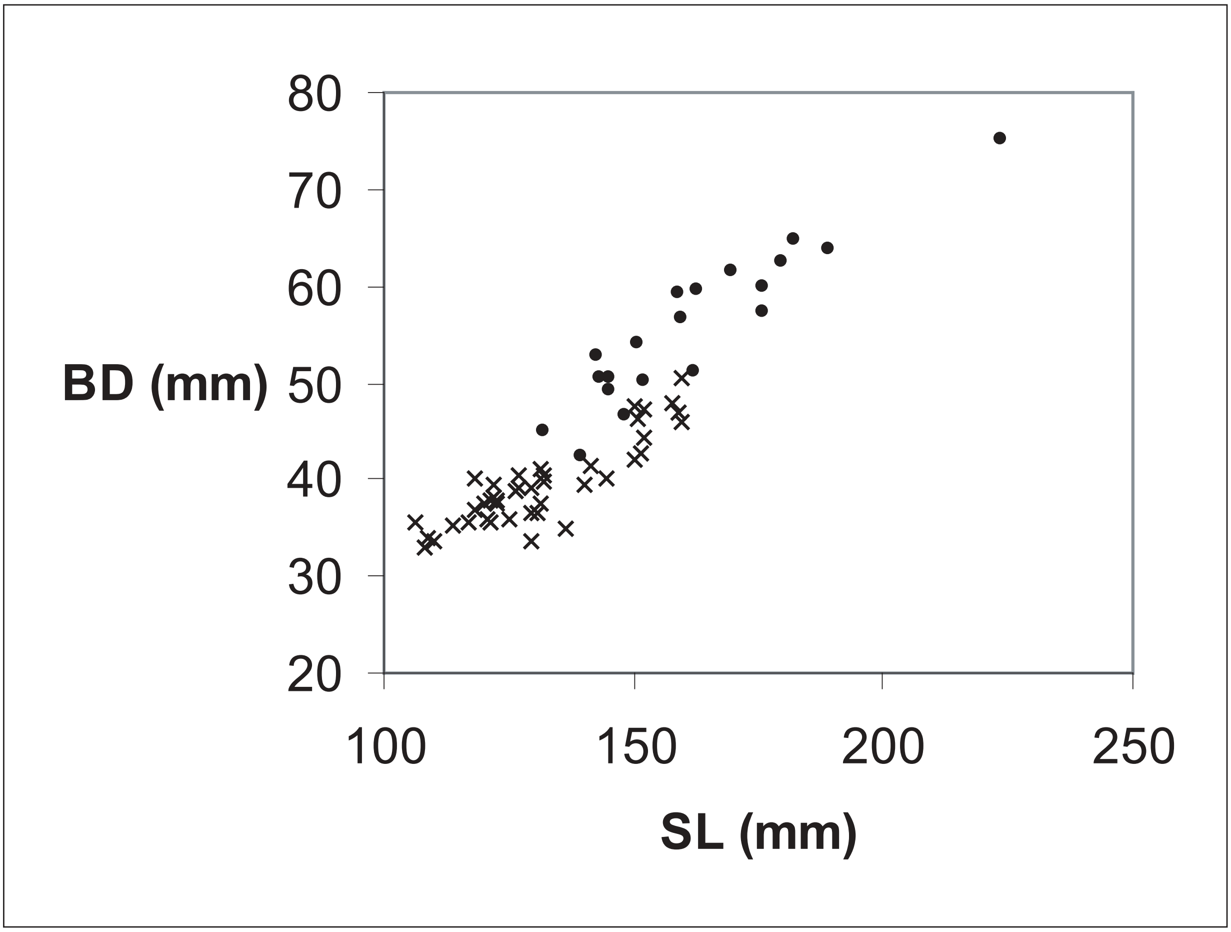

Fig. 38. *Diplotaxodon* sp. 'deep' (X; n=20) generally has a relatively deeper body (BD) than *Diplotaxodon argenteus* (●; n=46, including all 3 types).

Diplotaxodon sp. 'deep'
(fig. 37)

Another undescribed species, it was first illustrated by Turner (1996).

Distinguishing features: A fairly large, deep-bodied species which as a less steeply angled mouth than *D. greenwoodi* and *D.* sp. 'brevimaxillaris'. The ceratobranchial gillraker count (19 - 24) is usually higher than either *D.* sp. 'brevimaxillaris' (15 - 18) or *D. greenwoodi* (16 - 19). In comparison to *D.* sp. 'holochromis', *D.* sp. 'deep' has a relatively deeper head, longer pectoral fin (reaching beyond vent), narrower interorbital and larger snout to dorsal distance. It has a relatively smaller eye than *D. apogon*, *D. macrops*, *D. aeneus* and *D.* sp. 'offshore', and all of those species have a proportionally greater interorbital distance and larger opercular width. It has a relatively deeper body than *D. argenteus* (fig. 38).

Description: A fairly large, deep-bodied fish, with large eyes and a narrow interorbital distance. Females and non-breeding males are countershaded silver with a yellowish-brown hue. Male breeding colour is unknown. Maximum length recorded was 22.4 cm SL.

Ecology and Distribution: We did not collect many specimens, although it was often encountered in trawl catches in the south of the lake. We also found the species at Nkhata Bay and possibly on Tanzanian shores (fig. 39). Most specimens were collected from the shelf zone at depths of 50 - 90 m. No males in breeding dress or mouthbrooding females have been positively identified. The species does not seem to be commercially important, although it was caught in midwater and deep-water bottom trawls in the south.

Diplotaxodon ecclesi Burgess & Axelrod, 1973

This species was described from a single specimen trawled near Domwe Island at the north of the southern arms (USNM 210.696). The type has been examined and measured by Stauffer (Turner & Stauffer, 1998), and excellent colour photographs of the freshly collected fish appear in the original description (Burgess & Axelrod, 1973). The male breeding dress resembles a spent or ripening *D. macrops*. The collecting location is also a major breeding ground of that species, as well as other *Diplotaxodon*, such as *D. apogon*, *D. greenwoodi* and *D.* sp. 'similis'. Turner and Stauffer decided to distinguish *D. macrops* on the grounds that the single specimen of *D. ecclesi* is larger than any of the hundreds of known *D. macrops* and is also rather more slender in build. We have yet to unambiguously identify any individuals of *D. ecclesi* from the field

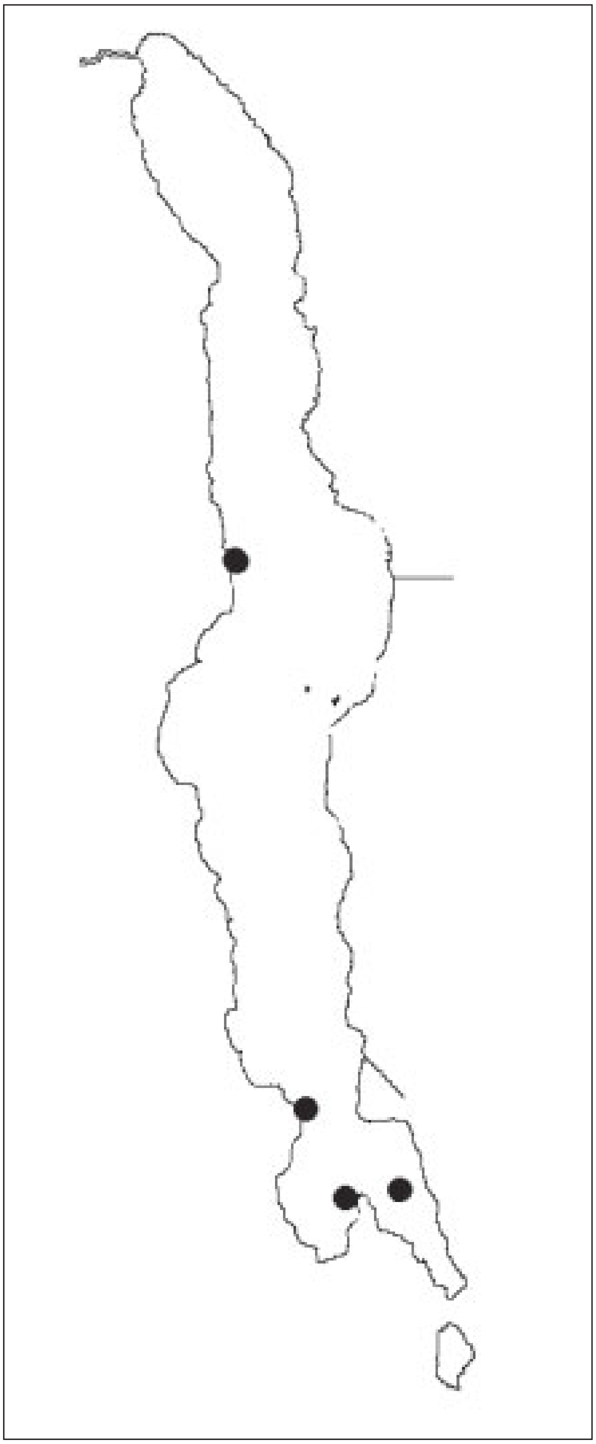

Fig. 39. Distribution records of *Diplotaxodon* sp. 'deep'.

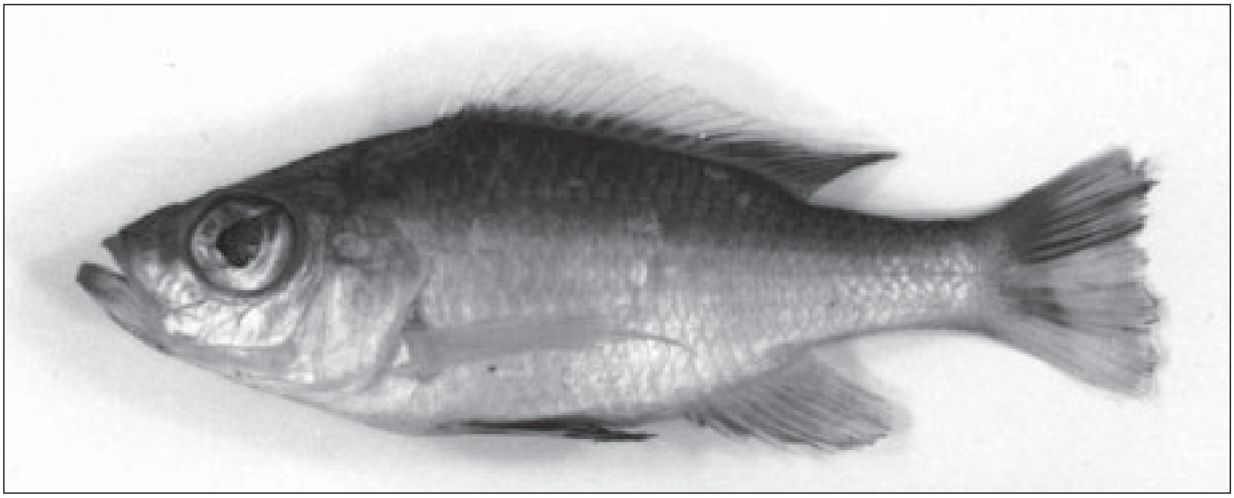

Fig. 40. *Diplotaxodon apogon.* Holotype.

or from other collections we have examined, although some similar-looking specimens have been collected.

Diplotaxodon apogon Turner & Stauffer, 1998 (fig. 40)

Diplotaxodon apogon was described by Turner & Stauffer in 1998, from 22 specimens. Holotype: BMNH 1996.4.30:21. Paratypes: BMNH 1996.4.30: 22-38; PSU 3025 (4). It had previously been illustrated and discussed by Turner (1996) as *Diplotaxodon* 'white belly'.

Distinguishing features: The species has proportionally larger eyes than all *Diplotaxodon* except *D. macrops, D. aeneus and D.* sp. 'offshore'. In comparison to these 3 species, it has a longer lower jaw, a relatively greater predorsal fin distance and shorter dorsal fin base. It also has a longer pectoral fin, which often reaches past the base of the 3rd anal fin spine.

Description: A small, deep-bodied fish with large eyes. The eye diameter is greater than the snout length. The dorsal head profile is straight, apart from the prominent premaxillary pedicel. The lower jaw protrudes slightly, or sometimes clearly, beyond the upper jaw. The mental process is moderately prominent. The pelvic fins are short, often not reaching the vent. Females and non-breeding males are silvery and counter-shaded. Males in breeding dress are darker dorsally with silver flanks and a white belly. They have a broad white border to the dorsal fin. This border tapers from front to back, so that

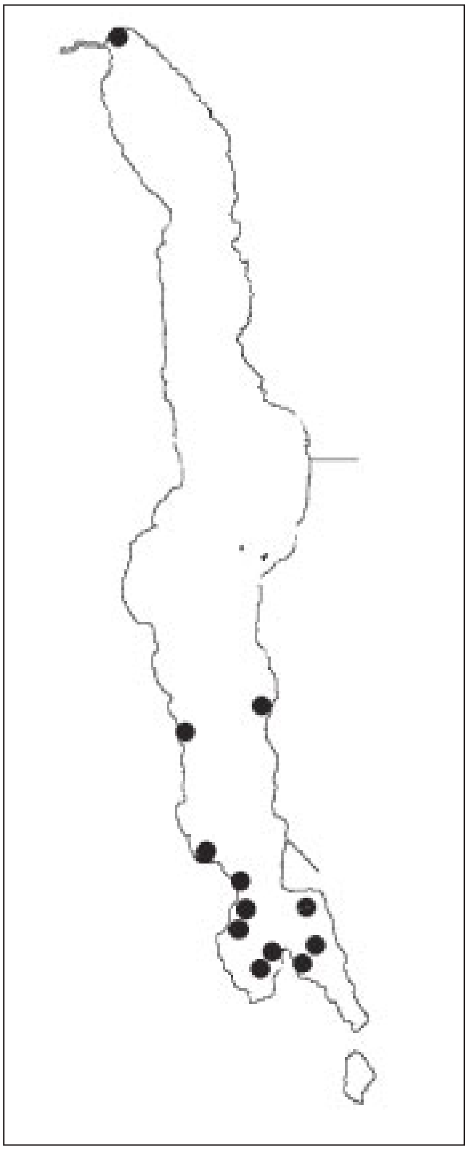

Fig. 41. Distribution records for *Diplotaxodon apogon*.

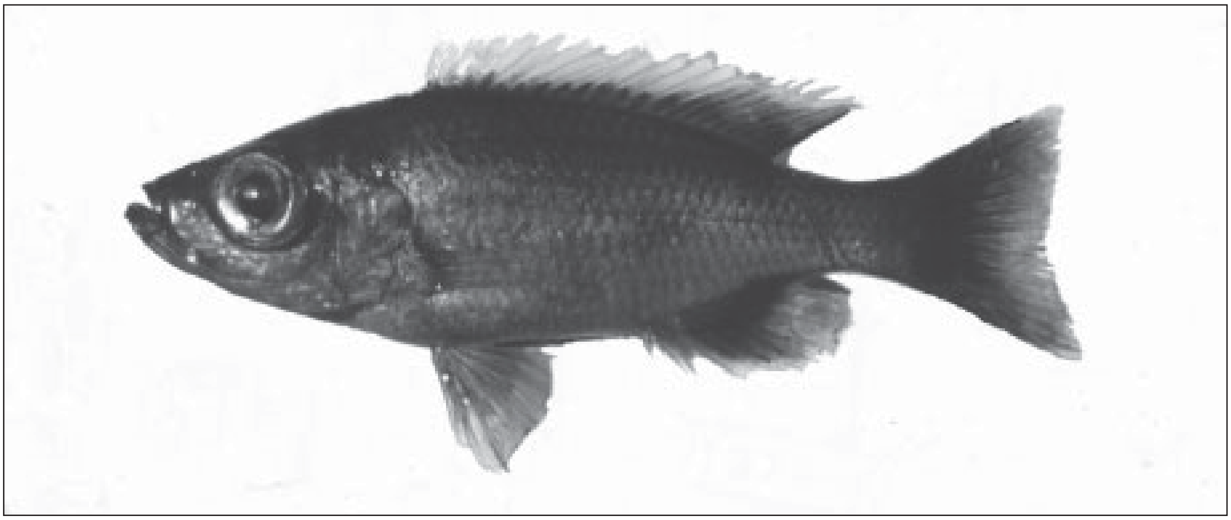

Fig. 42. *Diplotaxodon macrops*. Male in breeding dress. Photo: SADC/GEF Project.

the fin appears white at the front black at the back. The pelvic and anal fins and generally dark. The anal is marked with 1 - 2 large, pale yellow egg-spots. The largest fish we collected was 11.7 cm SL, but Duponchelle *et al.*(2000a) recorded a maximum of 12.5 - 13 cm SL, although very few individuals exceeded 10.5 cm. Females weighed up to 40 g.

Ecology and Distribution: *Diplotaxodon apogon* seems to be a deep water (50 - 200 m) species usually found close to the bottom on shelf areas. We most commonly found the species in the south of the lake (fig. 41), where it can be abundant at around 100 m depth or deeper. A small number of specimens have been collected in the far north, from Wismann Bay in Tanzania. From demersal trawls in the SW Arm in 1998 - 99, Duponchelle *et al.* (2000a) estimated that the species comprised around 3 % of the total biomass at 75 m, 100 m and 125 m. We estimated that the minimum size at maturity of males was 9.5 cm TL and for females 12.5 cm TL. Duponchelle *et al.*(2000a) with a larger sample size, estimated that the smallest ripe females are around 7 cm SL, and 50 % are mature at 8.9 cm SL. The ovaries of ripe females contained an average of 15 - 20 eggs, up to a maximum of ca 35 (Duponchelle *et al.*, 2000a). Eggs were up to 6 mm in diameter, with an average weight to 58 mg. We collected ripe males at depths of 96 - 125 m in June, September, October and December. They were found in all localities where the species was collected except for Wismann Bay. In the SW Arm, Duponchelle *et al.* (2000a) reported that in all months over 60 % of adult males collected were ripe, but ripe females were only recorded from November to April, with a peak from December to March. Small juveniles were found in the southern arms and Wismann Bay at 80 - 98 m depth. Stomach contents consisted of zooplankton**.** The species was of little commercial importance during the 1990s, although it was occasionally seen in deep-water trawl catches in the south.

Diplotaxodon macrops Turner & Stauffer, 1998 (fig. 42)

Described by Turner & Stauffer in 1998, from 21 specimens. Holotype: BMNH 1996.4.30:1. Paratypes: BMNH 1996.4.30.2-1; PSU 3024 (6). The species was previously illustrated and discussed by Turner (1996) as *D.* 'macrops'.

Distinguishing features: The species has relatively larger eyes than all other *Diplotaxodon* except *D. apogon, D.* sp. 'offshore' and *D. aeneus*. Ripe male *D. macrops* are black with a white dorsal fin margin, whereas the ripe males of *D. apogon* and *D.* sp. 'offshore' have pale bellies. Mature male *D. aeneus*, which we believed to be fully ripe, are generally dark and lack the white dorsal fin margin. Compared to *D. apogon*, the dorsal fin base of *D. macrops* is relatively longer, and the lower jaw and distance from snout to dorsal fin proportionally shorter. The smaller head, shallower cheek and proportionally greater interorbital distance distinguish *D. macrops* from *D. aeneus*. We were unable to distinguish consistently females and immature males of *D. macrops* from smaller specimens of *D.* sp. 'offshore'. As a rule, in localities where ripe males of *D. macrops* were not known, but large specimens of *D.* sp. 'offshore' were recorded, all smaller specimens were assigned to the latter species, which may lead to an underestimate of the distribution range of *D. macrops*.

Description: *Diplotaxodon macrops* is a small, deep-bodied fish with a large eye, and a straight dorsal head profile apart from the strongly prominent premaxillary pedicel. The mental process is absent or very slight. The lower jaw protrudes slightly or not at all. Females and non-breeding males are silvery and countershaded. Male breeding dress is black with a coppery iridescence, with a broad white margin to the dorsal fin and up to 2 pale yellow egg-spots on the anal fin. The maximum length recorded was 12.5 cm SL.

Ecology and Distribution: The species was abundant near to the bottom over shelf habitats at depths of 76 - 128 m in the southern arms and at Senga Bay and Domira Bay (fig. 43). In the SW Arm, Duponchelle *et al.* (2000a) reported the species comprising 4 % of benthic trawl biomass at 75 m, 10 % at 100 m and 12 % at 125 m. Ngatunga (pers. comm.) has reported ripe males of this species from Tanzanian waters near Wissman Bay. We recorded males mature at 10.7 cm TL and females at 10.8 cm TL. Duponchelle *et al.* (2000a) reports mean length at maturity as ca 98 mm SL for females. Ripe females have an average of 16 ovarian eggs, with a range of around 10 - 37 eggs. Egg diameter was up to 6 mm and Duponchelle *et al.* (2000a) reported an average ripe egg weight of 56 mg. Ripe males were found in the southern arms, Senga Bay, and Domira Bay at depths of 76 - 125 m, in February, June, July and October. Duponchelle *et al.* (2000a) reported that large aggregations of breeding males, with some ripe females, were found in January to May and in August at 100 - 125 m depth in the SW Arm. Breeding activity was low from October to December. Juveniles were regularly found in the adult habitat.

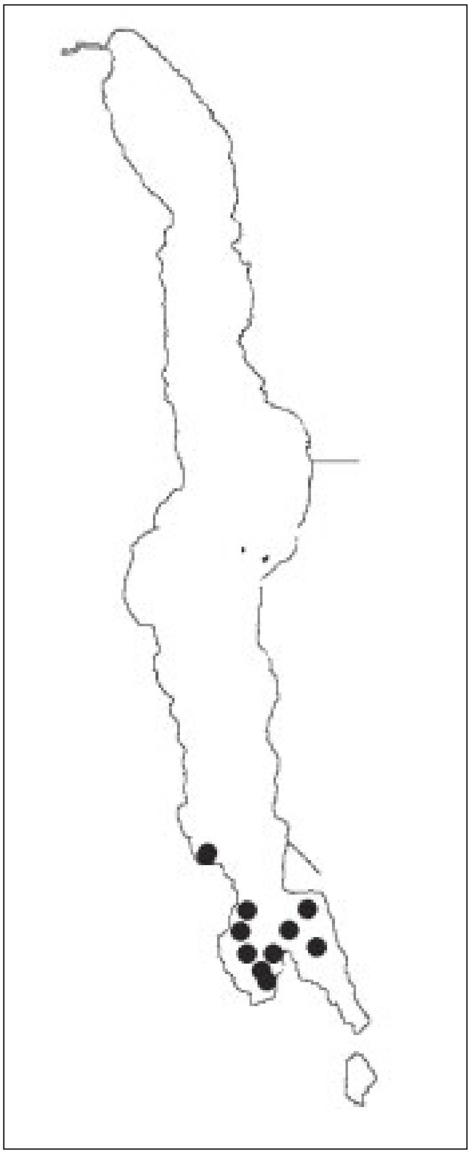

Fig. 43. Distribution records for *Diplotaxodon macrops*, based on specimens examined by the authors. B.P. Ngatunga has also reported the species from the Tanzanian area of the lake.

Diplotaxodon aeneus Turner & Stauffer, 1998 (fig. 44)

Described by Turner & Stauffer in 1998 from 6 preserved specimens, collected previously by the UK/SADC Pelagic Fish Resources Project and seen frozen by Turner. Holotype: BMNH 1996.4.30:16. Paratypes: BMNH 1996.4.30:17-20; PSU 3026 (1).

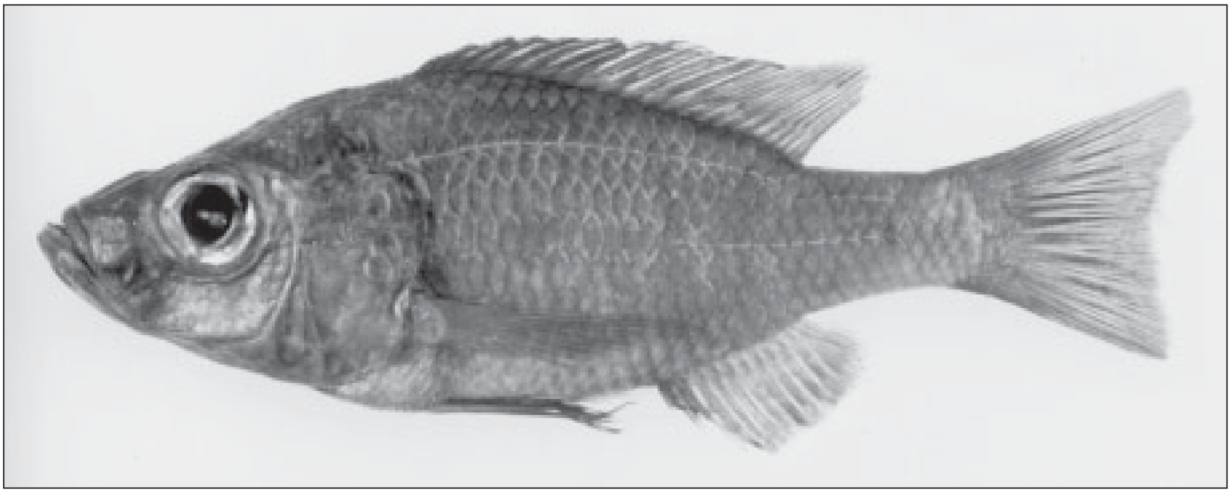

Fig. 44. *Diplotaxodon aeneus.* Holotype.

Distinguishing features: The uniformly dark male breeding colour, including the dorsal fin margin, is distinctive in species where the eye is greater than the snout. In comparison to *D. apogon*, it also has a longer base to the dorsal fin and a greater distance between the snout and the start of dorsal fin. It has a smaller inter-orbital distance than either *D. macrops* or *D.* sp. 'offshore'.

Description: A fairly small fish, with large eye. The head shows a moderate concavity above the eye. The premaxillary pedicel is long and prominent. The tip of the lower jaw protrudes beyond that of the upper. Non-breeding fish are silvery and countershaded. Mature, possibly ripe, males are dark grey to black all over, including the dorsal fin margin. The flanks have a bronze iridescence. There are 1 - 3 pale yellow egg spots on anal fin. The largest known individuals are just over 14 cm SL**.**

Ecology and Distribution: We did not find many individuals of this species, and it is probably uncommon. Most specimens were collected in the centre and north of the lake, though a few were found in Domira Bay (fig. 45). Specimens were found mainly near rocky reefs at depths of 35 - 160 m, although the former may be a recording error. The holotype was collected in open water over the anoxic zone near Nkhata Bay. All known mature males were longer than 12.5 cm SL

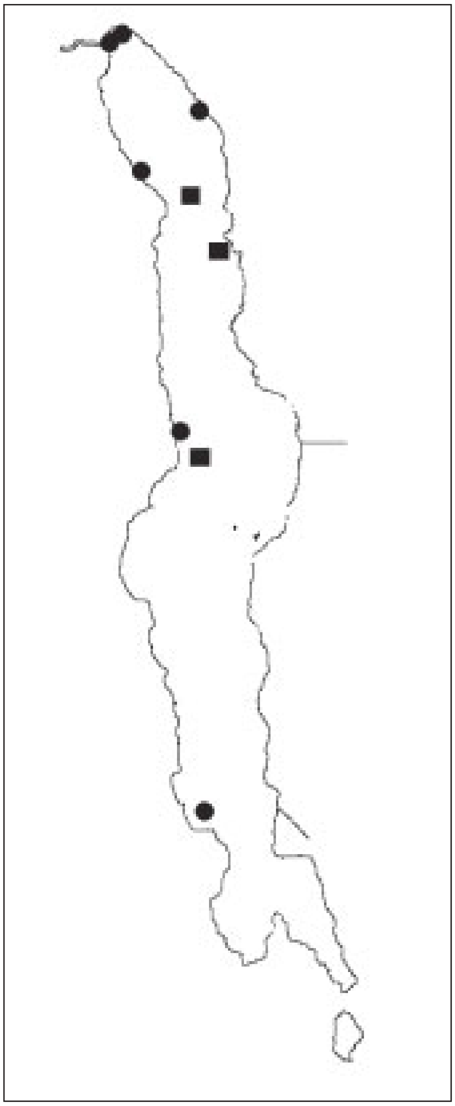

Fig. 45. Distribution records for *Diplotaxodon aeneus*. Square symbols indicate catches from over anoxic bottom, round symbols over oxygenated bottom.

Diplotaxodon sp. 'offshore' (figs 46 & 47)

Diplotaxodon sp. 'offshore' is an undescribed species that seems to comprise the bulk of the offshore-living population previously known as *Diplotaxodon* 'bigeye'.

Distinguishing features: *Diplotaxodon* sp. 'offshore' can be distinguished from *D. macrops* and *D. aeneus* by its male breeding dress. Small individuals which are not in male breeding dress, may be confused with *D. macrops*. However, this species tends to have a shallower cheek and shorter preorbital bone than *D. macrops*. The dorsal fin base is proportionally longer and the lower jaw shorter than in *D. apogon*. Also, the distance from the tip of the snout to the anterior insertion of the dorsal fin is relatively shorter than in *D. apogon*. *Diplotaxodon* sp. 'offshore' has a smaller head, shallower cheek and narrower inter-orbital than *D. aeneus*.

Description: A small, slender to deep-bodied fish with large eyes, a slightly concave dorsal head profile with a long and fairly prominent premaxillary pedicel. The mental process is absent or very slight, and lower jaw protrudes, usually slightly. Females and non-breeding males are silvery and countershaded, usually with a dark bronze cast. Males in breeding dress are dark dorsally, with a pale belly.

Fig. 46. *Diplotaxodon* sp. 'offshore', mature male in breeding dress. Photo: SADC/GEF Project.

Fig. 47. *Diplotaxodon* sp. 'offshore', spent (?) individual. Photo: SADC/GEF Project.

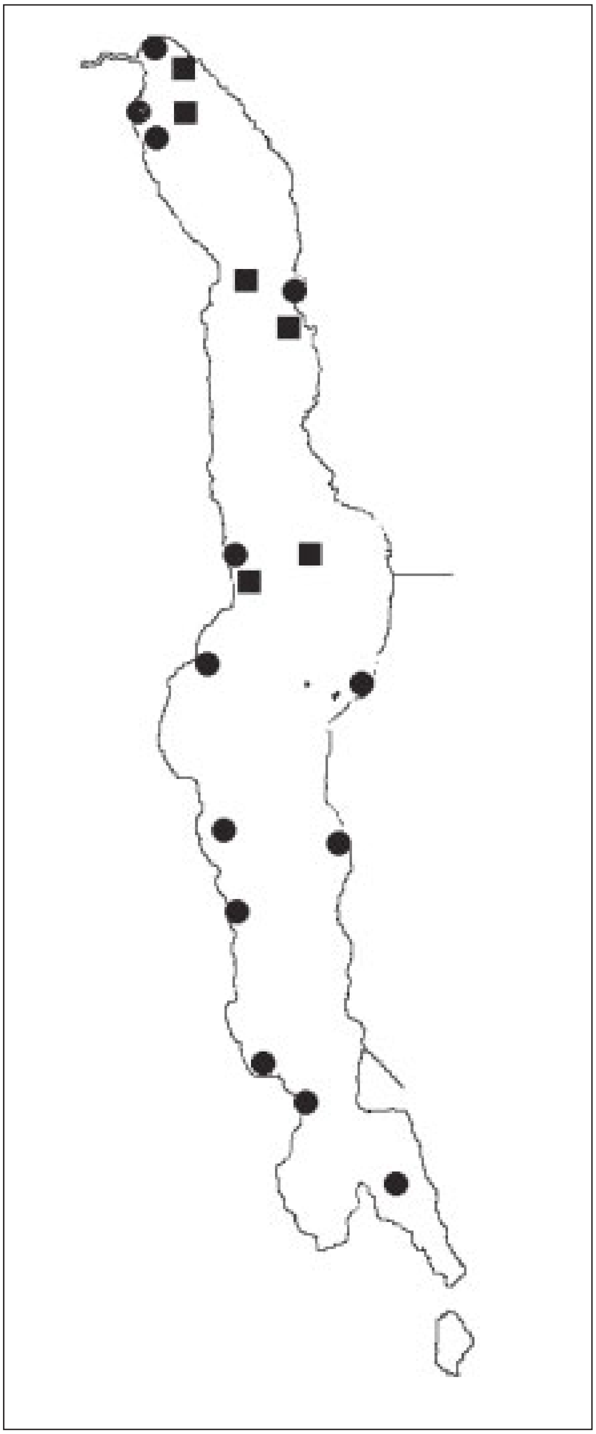

Fig. 48. Distribution records of *Diplotaxodon* sp. 'offshore'. Square symbols indicate catches from over anoxic bottom, round symbols over oxygenated bottom.

The flanks are also usually pale. Pelvic, caudal and anal fins are dark, though the spinous part of the anal fin is pale (probably white in life). The dorsal fin may be completely white or have a dark base covering the lower ¼ anteriorly and lower ¾ to the back of the fin. The largest fish we recorded was around 14 cm TL.

Ecology and Distribution: The species was found throughout the lake in the deep waters over the anoxic zone (fig. 48). It was collected in fairly large numbers from the centre and north of the lake, but was also found rarely at Domira Bay and further south. Most specimens came from depths of 61 - 184 m, though non-breeding fish were also caught between 30 - 50 m by a pelagic trawl off Karonga. Stomach contents were dominated by the pupae and fourth instar larvae of the lakefly, *Chaoborus*, with smaller amounts of crustacean zooplankton and third instar *Chaoborus* larvae (Allison *et al.*, 1995b). Thompson *et al* (1995) found gonadal maturation to begin at around 11 cm TL, and most fish were mature at 13 cm. The same authors reported that ripe fish were collected all year round. We found ripe males from June and September, off Senga Bay, Domira Bay, Nkhotakota, Kande Island and Nkhata Bay at depths of 99 - 184 m. Breeding males were also caught off Karonga in a trawl haul that had fished an 'integrated sample' from 20 - 210 m depth. Small juveniles were observed to be widely distributed in deep water, just like the adults, being collected from Young's Bay, Chilola Bay, Wismann Bay and Domira Bay. Although very abundant, by the late 1990s, the species was probably still not exploited on a large scale, though taken in gillnets in the north of Malawi, in Mozambique and in Tanzania, where it was also reported in chirimila catches (B.P. Ngatunga, pers. comm.).

Discussion: Turner & Stauffer prepared a description of this species for inclusion in what was to become their 1998 paper describing three other 'big-eye' *Diplotaxodon* species. The description was not published due to uncertainties over the distinctness of this species in relation to *D. macrops*. No clearly diagnostic features were found, apart from male breeding dress. The problem was that while the *D. macrops* individuals showed a convincingly conspicuous black breeding dress, the *D.* sp. 'offshore' males exhibited a pale-bellied breeding colour which might possibly have been representative of a ripening or spent individual *D. macrops*. Although we have still not found any clearly diag-

Fig. 49. *Diplotaxodon* sp. 'brevimaxillaris'. Preserved specimen collected from trawl at 90 - 100 m depth off Monkey Bay. 149 mm SL.

nostic counts or measurements (we did find differences on multivariate analysis), we are now reasonably confident of the distinctness of the species following the discovery of specimens collected near Senga Bay by the SADC/GEF project. Several large apparently ripe males were collected simultaneously with males of *D. macrops* (and *D. apogon*). This would seem to rule out the possibility that the two forms are geographic variants of a single species. The *D. macrops* males were much smaller, but of typical size for known populations of that species. Thus, all larger males conforming to the *D. macrops*/ sp. 'offshore' phenotype have so far exhibited the *D.* sp. 'offshore' breeding colour. Within a single location, if all the larger individuals had shown the more intense 'macrops' breeding dress, we might have tentatively concluded that these were territorial, while the smaller pale individuals were floater or ripening fish. However, we found the reverse, which is more consistent with the idea that the two are different species.

Diplotaxodon sp. 'brevimaxillaris' (fig. 49)

Since its collection by T.D. Iles in the 1950s, fisheries recorders in Malawi have known this undescribed species by the manuscript name of 'Diplotaxodon brevimaxillaris'.

Distinguishing features: This species is deeper-bodied than most other members of the genus. It has a proportionally smaller mouth and larger eye than *D. greenwoodi* and usually a less strongly pro-

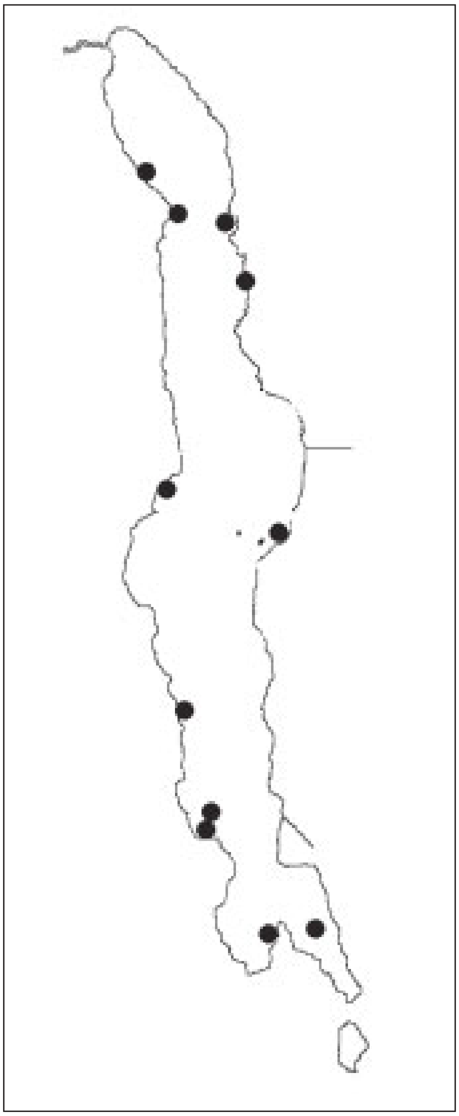

Fig. 50. Distribution records for *Diplotaxodon* sp. 'brevimaxillaris'.

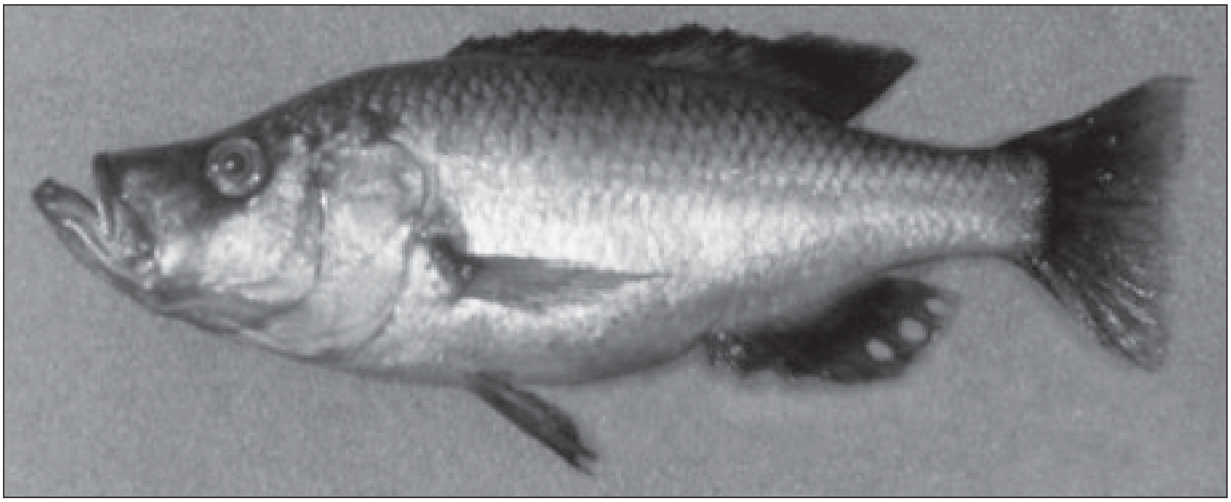

Fig. 51. *Diplotaxodon greenwoodi*. Mature male, approx. 27 cm SL, collected from Nkhata Bay. Ncheni Project # 450.

jecting lower jaw. The smaller eye, stockier body and more upwardly-angled mouth distinguish the species from *D.* sp. 'deep'.

Description: A large, stocky species with a deep body and smallish eye. The mouth is large and steeply angled upwards. Females and non-breeding males are silvery and counter-shaded. Males (possibly ripe or maturing) are darker dorsally, with dark grey dorsal and caudal fins and white dorsal lappets. The maximum length recorded was 21.2 cm SL.

Ecology and Distribution: *Diplotaxodon* sp. 'brevimaxillaris' has never been found in large numbers. It had previously been known only in the southern arms, but recently-collected specimens show a much wider distribution, probably encompassing all suitable habitat in the lake (fig. 50). The preferred habitat is the shelf zone at 50 - 150 m depth. Males showing some development of breeding dress were collected in September 1997, at 114 - 121 m off Chilumba and Nkhotakota. Juveniles have been collected in large numbers in the SW Arm, in same habitat as adults. The species occurs in small numbers in demersal and semi-pelagic trawl catches.

Diplotaxodon greenwoodi Stauffer & McKaye, 1986 (fig. 51)

Stauffer & McKaye (1986) described the species from 4 specimens. Holotype: USNM 270847. Paratypes: USNM 270848 (3).

Distinguishing features: *Diplotaxodon greenwoodi* is the largest known member of the genus. The huge, upwardly angled mouth distinguishes this species from all other *Diplotaxodon*, except *D.* sp. 'brevimaxillaris'. The latter species has a larger eye and wider, more thickset body.

Description: *Diplotaxodon greenwoodi* is a large, laterally compressed fish with a deep body and a relatively small eye. It has a very large, steeply angled, upwardly pointing mouth and usually a markedly projecting lower jaw. Females and non-breeding males are silvery and countershaded. Larger fish tend to have a purplish sheen, while smaller ones are more brownish. The snout is usually grey with a purple sheen. Ripe males have silvery flanks, but the head, snout, dorsum, chin, belly and fins are black. The dorsal lappets are white. There are 3 - 5 pale yellow or white egg-spots in a single row on the anal fin. The maximum length recorded was 24.7 cm SL.

Ecology and Distribution: This species is widespread, and probably found in all suitable habitats — reef and shelf zones at depths of 50 - 148 m — where it is often quite common (fig. 52). Stomach contents indicate a diet of small cichlids (Allison *et al.*, 1995b). It has been reported that this species

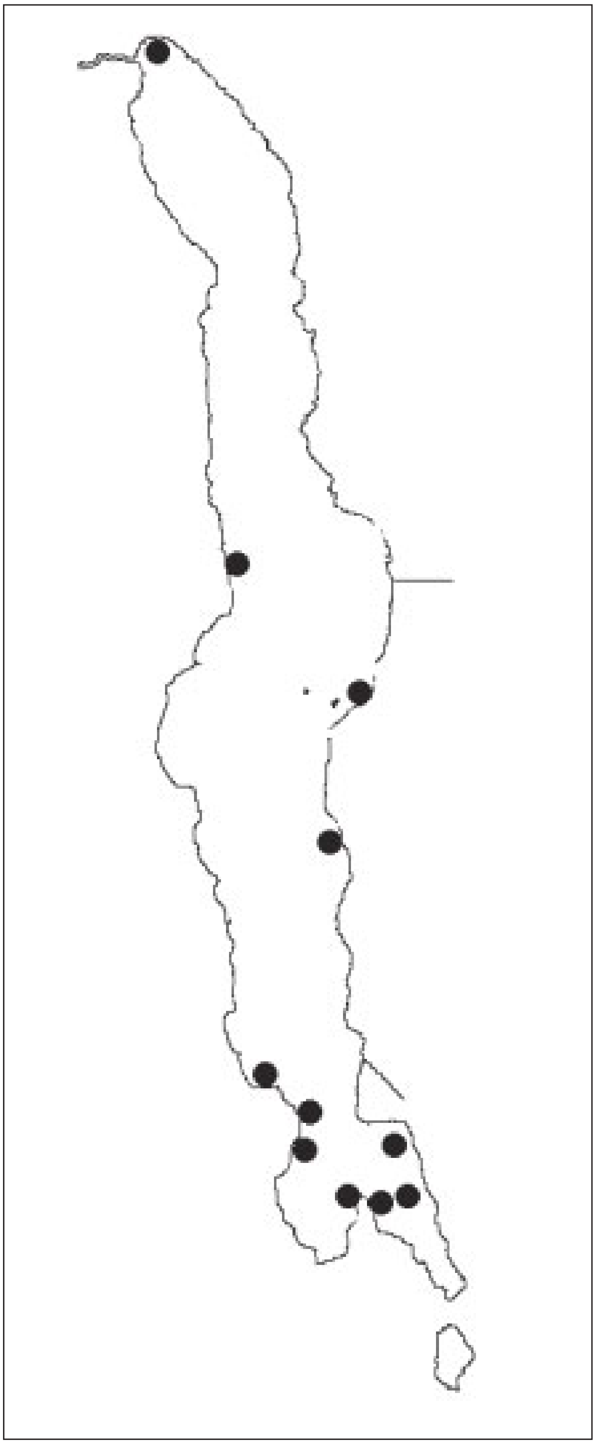

Fig. 52. Distribution records for *Diplotaxodon greenwoodi*.

feeds on eggs and juveniles from the mouths of brooding female cichlids (Stauffer & McKaye, 1986), but this may be opportunistic scavenging of eggs spat out by distressed fish in the trawl in which the specimens were captured. Several large males in breeding dress were caught in a bottom trawl off Domwe Island at 100 m depth, which suggests the presence of a demersal breeding arena. Males in breeding dress were commonly landed at Nkhata Bay and on the shores of the southern arms. A few ripe males were also collected by the SADC/GEF project in Domira Bay at 98 - 100 m depth in June 1997. Juveniles were found in the adult habitat. The species was exploited in small numbers by trawlers in the south of the lake and by artisanal gears (hand-lines and gillnets) throughout the inshore regions of the lake.

Discussion: This is an extremely distinctive species. We have not examined the types, although we have seen several specimens identified in the field by the senior author of the original description (Prof. J. Stauffer).

Specimens of dubious status

In addition to the common or distinctive species discussed above, a number of other forms of *Diplotaxodon* have been collected. We consider that the numbers of specimens collected have been insufficient to definitively define these as distinct species at present.

Diplotaxodon sp. 'large black'
(fig. 53)

A single large specimen of this large laterally compressed form was purchased from an artisanal fisherman just north of Senga Bay. It resembled *D.* sp. 'deep', but has a longer, more acute snout and smaller eye. It is a mature male in uniformly black breeding dress, with white dorsal lappets. Konings (2001) illustrates as *D.* sp. 'brevimaxillaris' a large black male specimen which may be this species. It was collected from Narungu, on the eastern shore, just opposite Senga Bay.

Diplotaxodon sp. 'Ngulube'
(fig. 54)

This forms resembles *D.* sp. 'holochromis' in body shape, but it has a larger eye. Ripe males are dark grey or black, but the entire body surface above upper lateral line is white, as are the dorsal fin, the upper part of the tail and the dorsal surface of the head. Several specimens were collected at Nkhata Bay by Mr. Henry Ngulube.

Fig. 53. *Diplotaxodon* sp. 'large black'. Mature male, Ncheni Project #646, collected near Salima.

Fig. 54. *Diplotaxodon* sp. 'ngulube'. Mature male, collected at Nkhata Bay.

Diplotaxodon sp. 'deep mottled'

This is a fairly deep-bodied fish, with relatively large eyes, a short snout and a fairly large, upturned mouth. It is superficially similar to *D.* sp. 'similis', but has a proportionally shorter snout, larger eye, deeper body, deeper cheek, longer premaxillary pedicel and more upturned mouth. Compared to *D. argenteus*, it has a relatively deeper body, larger eye and wider snout and jaws. Breeding males are dusky, with a pale dorsal 'blaze' like *D. limnothrissa*, with numerous small dark freckles on the pale areas. The form has been collected Likoma Island, Nkhata Bay and further north at depths of 50 - 70 m near rocky shores. It was caught by artisanal gears. Oliver's illustration of 'Diplotaxodon sp. 1' seems to be this form.

Diplotaxodon sp. 'deep white-top'

This form was not recognised until males in breeding dress were examined in the SADC/GEF project collection. It is intermediate in form between *D.* sp. 'holochromis' and *D.* sp. 'deep', and might also be confused with small specimens of *D. argenteus*. The premaxillary pedicel and lower jaw angle are more prominent than those of *D.* sp. 'holochromis'. It is more slender and has a relatively smaller eye than the various forms of *D.* sp. 'deep'. The mouth is proportionally smaller and the body deeper than is typical of *D. argenteus*. Four males in breeding dress were collected by the GEF project from Nkhotakota at depths of 45 - 88 m in September 1997. The dorsal fin was black below and behind a line extending from the lower quarter of the first dorsal spines to the middle of the longest soft dorsal rays. Above this line, the fin was pale, probably white or yellow in life. The dorsal surface of the body was slightly darkened and the flanks pale, and the pelvic, anal and caudal fins are dark. The branchiostegal membranes were also dark. At present, this species cannot be reliably identified except in breeding dress. A specimen of similar body proportions, but not in breeding dress, was collected from 65 - 75 m in the southern arms.

Diplotaxodon sp. 'deep Mozambique'

This relatively large species is characterised by its extremely compressed body; only *D. greenwoodi* is comparable, but that species has a relatively much smaller eye and larger gape. It has huge eyes and a large upwardly directed mouth. All available material is from the Mozambique coast from depths of 73 - 104 m. Four specimens were found in the GEF collection, all from Chiwanga Bay and a fifth was collected from artisanal catches at Ntchepa, near Metangula by J. Halafo for the EU Demersal Ecology Project.

Diplotaxodon sp. 'deep argenteus Tanzania'

This is a fairly deep-bodied fish, resembling *D. argenteus*. Females and non-breeding males are dark grey. In sexually active males, the snout, all fins and the chin region are black. The dorsal lappets are pale, probably white or yellow in life. There were 1 - 2 pale yellow or white egg-spots on the anal fin. The maximum length recorded was 21.5 cm TL. This form has only been found at Nkhata Bay and further north. It has been collected at depths of approximately 100 m depth in Tanzanian waters. It has been collected from artisanal gears including gill nets and night-set chirimilas.

Diplotaxodon sp. 'thick'

This form looks similar to *D.* sp. 'brevimaxillaris', but has a less steeply angled mouth, and generally a smaller eye. It is less laterally compressed than the species of the 'deep' group, but is deeper-bodied than those of the *D. argenteus* complex. Two large specimens could be positively assigned to this form, both from the southern arms, at depths of 75 - 98 m. A specimen of 25.5 cm TL appeared to be a male approaching breeding condition,. It was dark grey, except for a paler belly and pelvic fins and white dorsal lappets. It was collected in October 1997. Also tentatively assigned to this species are 5 smaller specimens: three from Nkhotakota, one from Kande Island and one from Wismann Bay.

Miscellaneous specimens of the *D.* sp. 'deep' complex.

Several smaller specimens were tentatively assigned to this group, although some of them might prove to be members of the *D. argenteus* complex. Four specimens, including one large dusky individual were collected from by the GEF project from Chilola Bay, Mozambique at 51 - 57 m. The premaxillary pedicel was much less prominent than in other individuals of this complex, and the overall appearance resembled a rather large deep-bodied *D.* sp. 'holochromis'. A further unusual specimen was found in a GEF sample from 98 m depth in the SW Arm. This large individual appeared intermediate in form between *D.* sp. 'deep Mozambique' and *D.* sp. 'brevimaxillaris'.

Diplotaxodon sp. 'thick white top'.

A single male in breeding dress was collected by the GEF project from 88 - 91 m at Nkhotakota in September 1997. Superficially, it is very reminiscent of *D.* sp. 'brevimaxillaris', but it is not assigned to this species, on account of its small size at maturity (21 cm TL) and its coloration. The breeding colour is identical to the specimens of *D.* sp. 'deep white top' collected in the same place at the same time, but the latter specimens have more laterally compressed bodies, smaller eyes and less steeply angled mouths. Also similar in colour and again from the same time and place are the two specimens of *D.* sp. 'similis fat'.

Diplotaxodon sp. 'similis fat'.

This was the third morphologically different form with an identical male breeding colour trawled by the GEF project from Nkhotakota in September 1997. For an account of the male colour, see under *D.* sp. 'deep white-top'. These specimens were also from the 5-minute haul at 30 - 45 m. Considerable time was expended in trying to determine if any of the other specimens of *D.* sp. 'similis' could be re-

Fig. 55. *Diplotaxodon* sp. 'black argenteus'. Mature male.

ferred to this form, but in the end it was concluded that they could not. For, example, the 'fat' specimens had ceratobranchial gillraker counts of 22 and 23, while for the clear-cut 'similis' counts ranged from 15 - 19. Three intermediate-looking specimens had counts of 17, 18 and 19, and were tentatively assigned to *D.* sp. 'similis'.

Diplotaxodon sp. 'blackfin'

This is a small fish, with a relatively large mouth and sharply angled lower jaw. Females and non-breeding males are countershaded, grey dorsally. The snout may be brownish-grey and the dorsal fin grey. The ventral fins are dark grey-black. Sexually active males are similar in colour to those of *D. argenteus:* fins, throat and snout are black and the anal fin has 2 - 3 pale yellow egg-spots. This species is dubiously distinct from *D. argenteus*. Male colour and habitat preference are the same and we could find no meristic or morphometric differences between them. However, mature males are clearly smaller and seem proportionately more laterally compressed, although this impression could not be captured as a diagnostic trait by morphometric analysis. *Diplotaxodon* sp. 'blackfin' is known from Likoma Island, Nkhata Bay and SE Arm, at depths of 50 - 70 m.

Diplotaxodon sp. 'black argenteus' (fig. 55)

A small number of specimens were collected from the northern half of the lake which appeared to be mature males of a form similar to *D. argenteus* and *D.* sp. 'similis'. These were uniformly black. There were no clearly diagnostic features for this form and we could not rule out the possibility that it represented one of the more common species in a different motivational state.

Diplotaxodon cf. ecclesi

We have collected several specimens, notably from Domira Bay, which resemble *D. ecclesi* in body shape (fig. 56), but the male breeding dress is slightly different, with a rather paler belly and wider white dorsal fin margin. We have yet to unambiguously identify any individuals of *D. ecclesi* from the field or from other collections we have examined.

Fig. 56. *Diplotaxodon cf. ecclesi.* Mature male, collected in Domira Bay.

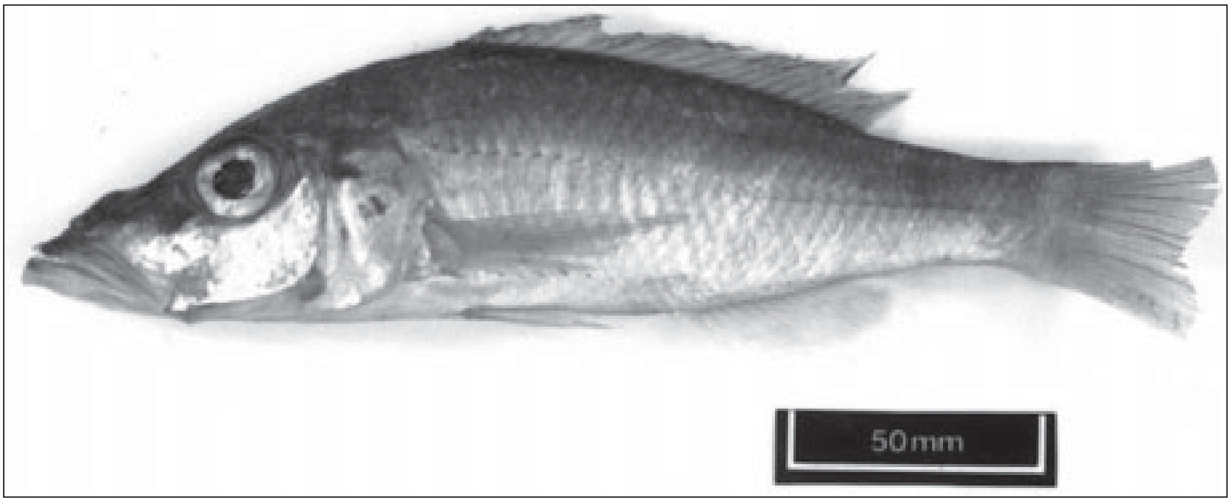

Fig. 57. *Pallidochromis tokolosh.* Holotype.

Pallidochromis Turner, 1994

This is presently a monotypic genus. Analysis of mitochondrial (mt) DNA sequences suggests that *Pallidochromis* is derived from *Diplotaxodon*. If we accept this phylogeny, retention of the genus *Pallidochromis* would render *Diplotaxodon* paraphyletic. If we wished to define genera cladistically, we should propose that *Pallidochromis* is a junior synonym of *Diplotaxodon*. However, to include *Pallidochromis* in *Diplotaxodon* would make it even more difficult to define the latter genus. Furthermore, we are not convinced that mtDNA gene trees are necessarily entirely reliable estimates of species trees, particularly as we cannot rule out the possibility that reticulate evolution has been significant in Malawian cichlids. We believe that there is still only one known species: *Pallidochromis* 'chicken' illustrated by Konings (1995, 2001) is almost certainly *Rhamphochromis* sp. 'grey'. *Pallidochromis* has larger teeth and a more ventrally angled mouth than *Diplotaxodon*, but lacks the enlarged inner series teeth characteristic of those *Rhamphochromis* species with larger widely-spaced teeth. No stripes, bars or spots have ever been observed, and live specimens are only weakly countershaded.

Pallidochromis tokolosh Turner, 1994 (fig. 57)

The species was described by Turner (1994a), who, uncertain of its affinities in relation to *Rhamphochromis* and *Diplotaxodon*, erected a monotypic genus rather than expand the diagnosis of either genus to incorporate this species. The species was previously known to fisheries researchers in Malawi as *Rhamphochromis* 'pallidus' and *Haplochromis* 'leucogaster', and has also been discussed as *Diplotaxodon* 'big head'.

Distinguishing features: The teeth are longer and more widely-spaced than those of any known *Diplotaxodon* species and the mouth is less upwardly-angled. The species has a larger eye and a less streamlined body than most *Rhamphochromis* species. In most *Rhamphochromis*, and certainly all of these with large widely-spaced teeth, there is a group of very large inner-row teeth near the symphysis of the jaws. These are not enlarged in *Pallidochromis*.

Description: A large-mouthed, large-eyed, relatively elongate species with a large mouth and prominent mental process. Non-breeding males and females are pale silvery-white, and only slightly darker dorsally with a brownish cast. A single individual from Chilola Bay, Mozambique, appeared to be a ripe or maturing male. It was dark grey on the dorsum, head and flanks, and on the dorsal and anal fins. The belly and the pelvic and anal fins were pale. This is the only known record of a male in anything approaching breeding dress. The largest specimen recorded (from the Mozambique coast) was 35 cm TL, or approximately 28 cm SL.

Ecology and Distribution: The species seems to have a lake-wide distribution on shelf areas at 75 - 150 m depth, occasionally as shallow as 50 m (fig. 58). We suspect that this species is found near the bottom to great depths. It seems to be fairly common in the southern arms, and Duponchelle *et al.* (2000a) estimated that it comprised 2 % of the demersal trawl fish biomass at 125 m in the SW Arm, and lesser proportions at 75 - 100 m, with occasional individuals at 50 m. It has not been found in the water column over the anoxic zone and appears to be a demersal species. Guts of trawl-landed specimens are usually empty, but two specimens examined by Turner (1994a) contained remains of small benthic cichlids of the genera *Lethrinops* and *Aulonocara*. No known *Diplotaxodon* species has been recorded to feed on benthic organisms. Duponchelle *et al.* (2000a) estimated size at first maturity at around 135 mm SL. Ripe females have been found with up to about 90 eggs in the ovaries (Duponchelle *et al.*, 2000a). Ripe females have been collected from October to February in the SW Arm

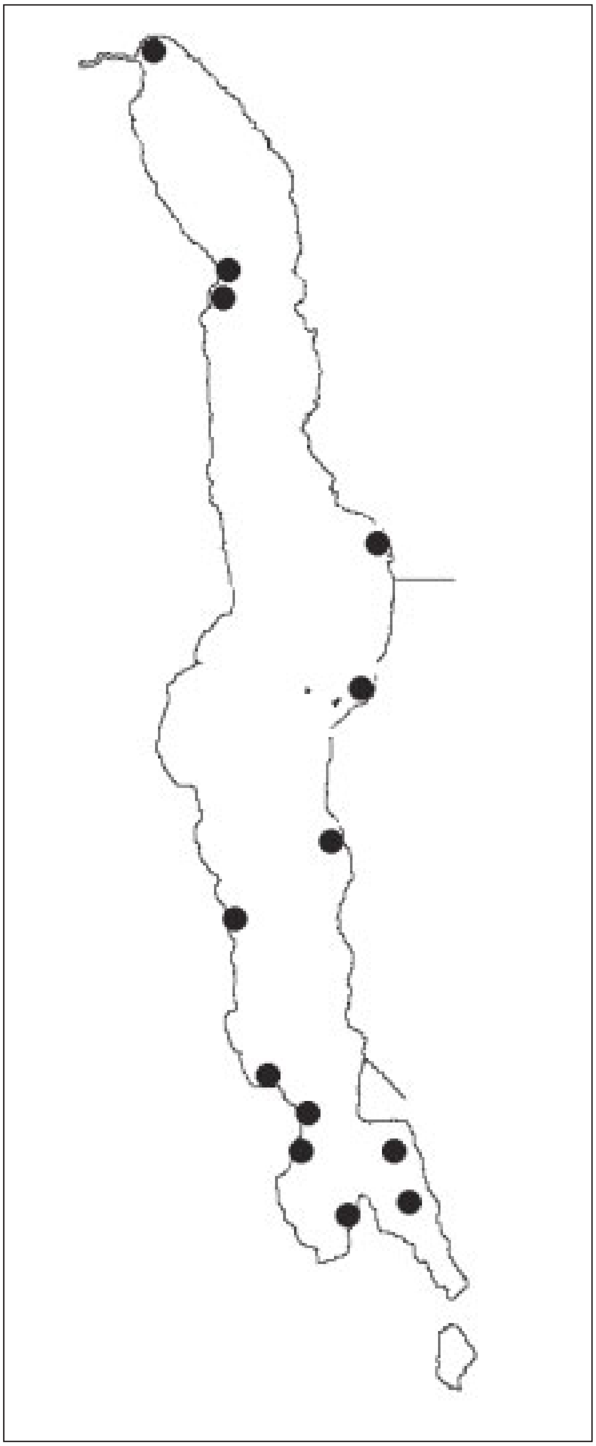

Fig. 58. Distribution records for *Pallidochromis tokolosh*.

(Duponchelle *et al.*, 2000a). A single very large male in (partially-developed?) breeding dress was collected from 148 - 150 m depth in Chilola Bay, suggesting that the breeding grounds are very deep; this was the deepest sample collected on the entire GEF project. No other ripe males have been reported, either by Duponchelle *et al.* (2000a) or ourselves. Juveniles are found in the adult habitat. The species was a minor component of deep-water bottom trawl catches, and it was occasionally caught by artisanal hook and line fishermen.

II. Molecular Studies

Some of our molecular studies of these fishes have been published (Shaw *et al.*, 2000), and so we will not repeat this work in detail, but will instead provide a brief review of the implications of molecular studies for our understanding of the evolutionary relationships of the pelagic cichlids.

Moran *et al.* (1984) assayed a number of Malawian cichlids using restriction fragment length polymorphism analysis of the entire mitochondrial genome. They found that the majority of endemic haplochromines were grouped into two major clades. One clade comprised the mbuna (*Pseudotropheus* and related genera) plus the genera *Aulonocara* and *Alticorpus* and some species of *Lethrinops.* The second major clade consisted of most of the other sandy shore and deep-water benthic cichlids formerly placed in *Haplochromis* (or *Cyrtocara*) and related genera. They also identified four 'oligotypic' lineages: *Rhamphochromis*, *Diplotaxodon*, *Copadichromis mloto* (actually *C.* sp. 'virginalis kajose', J. Snoeks pers. comm.) and *Astatotilapia calliptera* (Günther, 1893). *Rhamphochromis* and *Diplotaxodon* were each represented by a single specimen of unknown species. Interrelationships of these six clades were poorly resolved, but indications were that *Rhamphochromis* lay basal to the rest of the species flock. It had been widely expected that this position would be occupied by *Astatotilapia calliptera*, a species with morphology typical of riverine haplochromines. This species is recorded as occurring not only in Lake Malawi, but also in Lakes Chilwa and Chiuta (which are not presently connected to the Malawi/Shire catchment), the Lower Zambezi, Buzi, Pungwe and Save river systems (van Oijen *et al.*, 1991). Chilwa and Chiuta are not presently connected to the Malawi/Shire catchment, and some of the river systems mentioned flow into the Indian Ocean in Mozambique independently from the Zambezi

We sequenced both the ND2 gene and D-loop of the mitochondrial genomes of a range of Malawian cichlids, including many *Rhamphochromis* and *Diplotaxodon* and specimens of *P. tokolosh*. The six lineages of Moran *et al.* (1984) were again found (fig. 59), but we seem to have had slightly better resolution of their interrelationships. We found that *Rhamphochromis*, *Diplotaxodon* and *Pallidochromis* clustered together to form a 'pelagic/deep-water' clade at the base of the radiation. A second major clade comprised the remaining four clades found by Moran *et al.* The relationships of these clades were unresolved, appearing as a 'starburst'. Within the 'pelagic clade', we found strong support for the monophyly of *Rhamphochromis*. A second, well-supported clade contained all of the *Diplotaxodon* species, plus *Pallidochromis*. *Pallidochromis* was nested within the main *Diplotaxodon* clade, suggesting that (non-cladistically speaking) it is descended from *Diplotaxodon*.

A more detailed analysis was carried out with 40 specimens of *Rhamphochromis* and 73 of *Diplotaxodon* (fig. 60). Again the reciprocal monophyly of the two main 'pelagic' clades was well supported. The deeper relationships within the *Diplotaxodon* clade were poorly resolved. All six specimens of *D. apogon* clustered together with reasonably strong (70 %) bootstrap support, as would be expected if they were members of a single monophyletic species. This species occupied a basal position within the *Diplotaxodon* clade, but this was weakly supported. Within the rest of the *Diplotaxodon* clade, none of the other species were resolved as monophyletic, although 16 of the 22 *D. limnothrissa* specimens formed a clade with 70 % bootstrap support. There was little concordance between morphological species and molecular classification of the other specimens: seven *D.* sp. 'holochromis', eight *D. macrops*, eight *D. argenteus*, six *D.* sp. 'similis', five *D.* sp. 'deep', three *D.* sp. 'brevimaxillaris', eight *D. greenwoodi* and the remaining six *D. limnothrissa.* As the structures of this part of the tree were all weakly supported, we conclude that the molecular data do not provide evidence against our specific designations.

In this study, specimens of *R. longiceps* and *R.* sp. 'slender' were excluded due to the difficulty at that time of identifying individuals. One well-supported (90 % bootstrap value) clade consisted of 12 specimens of *R. esox*. There was no separation between the five individuals classed as 'esox - morphotypes' and the seven 'leptosoma - morphotypes'. This is consistent with our decision to synonymise the species on morphological grounds. It is also consistent

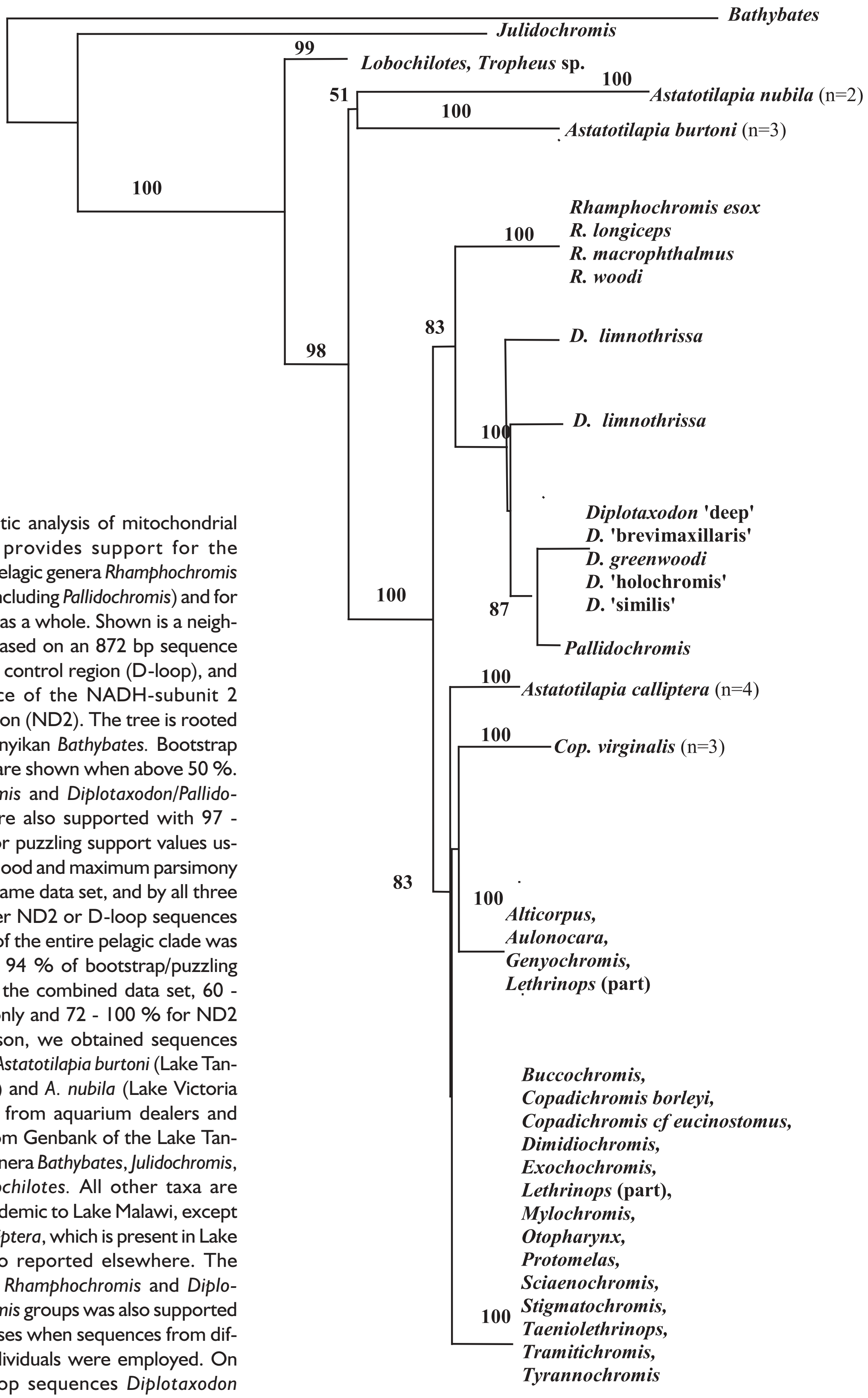

Fig. 59. Phylogenetic analysis of mitochondrial DNA sequences provides support for the monophyly of the pelagic genera *Rhamphochromis* and *Diplotaxodon* (including *Pallidochromis*) and for the pelagic cichlids as a whole. Shown is a neighbour-joining tree based on an 872 bp sequence covering the entire control region (D-loop), and a 981 bp sequence of the NADH-subunit 2 protein-coding region (ND2). The tree is rooted on the Lake Tanganyikan *Bathybates*. Bootstrap support for clades are shown when above 50 %. The *Rhamphochromis* and *Diplotaxodon/Pallidochromis* clades were also supported with 97 - 100 % bootstrap or puzzling support values using maximum likelihood and maximum parsimony analyses using the same data set, and by all three analyses using either ND2 or D-loop sequences alone. Monophyly of the entire pelagic clade was supported by 83 - 94 % of bootstrap/puzzling support values for the combined data set, 60 - 78 % for D-loop only and 72 - 100 % for ND2 only. For comparison, we obtained sequences from specimens of *Astatotilapia burtoni* (Lake Tanganyika catchment) and *A. nubila* (Lake Victoria region) purchased from aquarium dealers and used sequences from Genbank of the Lake Tanganyika endemic genera *Bathybates*, *Julidochromis*, *Tropheus* and *Lobochilotes*. All other taxa are haplochromines endemic to Lake Malawi, except for *Astatotilapia calliptera*, which is present in Lake Malawi, but is also reported elsewhere. The monophyly of the *Rhamphochromis* and *Diplotaxodon/Pallidochromis* groups was also supported in a variety of analyses when sequences from different taxa and individuals were employed. On the basis of D-loop sequences *Diplotaxodon apogon* and *D. argenteus* were also classed within the *Diplotaxodon* clade.

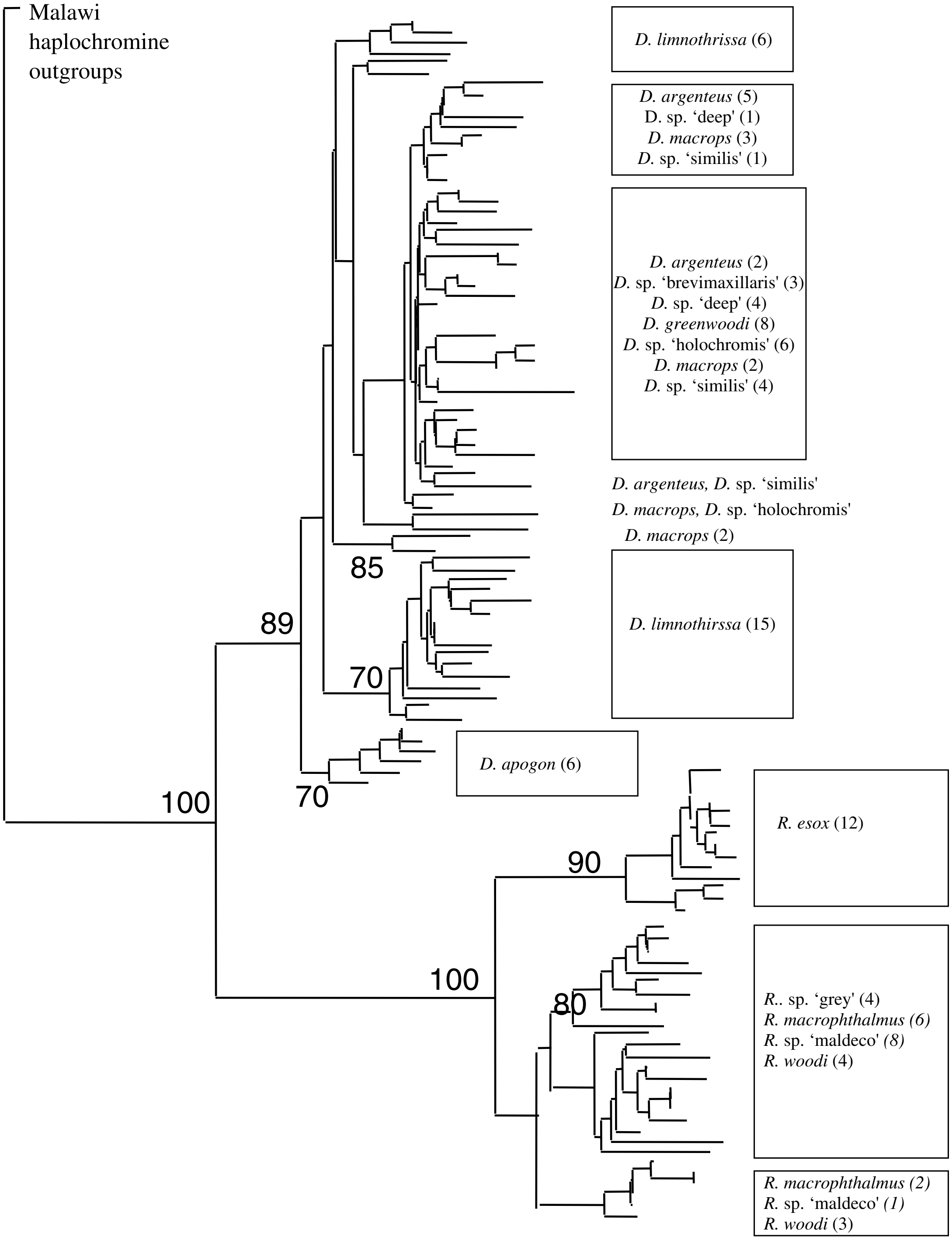

Fig. 60. Neighbour-Joining tree based on K2 distances between control region sequences of L. Malawi pelagic cichlids. Figures above branches are % bootstrap support (1000 replications), of 70 % or above. DARG=*D. argenteus*; DBRE= *D.* sp. 'brevimaxillaris'; DDEP= *D.* sp. 'deep'; DGRN= *D. greenwoodi*; DHOL=*D.* sp. 'holochromis'; DMAC=*D. macrops*; DSIM=*D.* sp. 'similis'; RGRY= *R.* sp. 'grey'; RMAC=*R. macrophthalmus*; RMAL= R. sp. 'maldeco'; RWOO= *R. woodi*

with the poor resolution of the relationships species we found elsewhere in the tree. A second, weakly supported clade was composed of individuals assigned to *R.* sp. 'grey', *R. macrophthalmus, R.* sp. 'maldeco' and *R. woodi*. Within this clade, the mitochondrial tree did not show any concordance with the morphological classification, and we consider it poorly resolved at this level.

A couple of other studies have also looked at the evolutionary relationships of these genera. Takahashi *et al.* (2001) using nuclear SINEs grouped *Rhamphochromis* in the clade with other Malawi cichlids (*Cyrtocara, Fossorochromis, Protomelas, Tyrannochromis* and various mbuna), to the exclusion of *Serranochromis robustus* (Günther, 1864), *Pundamilia nyererei* (Witte-Maas & Witte, 1985), *Astatotilapia burtoni* (Günther, 1893) and various Tanganyikan endemics. This is not very novel, since only one of the species (*S. robustus*, a non-endemic haplochromine present in Lake Malawi) has been suggested as a possible close relative of some Malawian endemic haplochromines (Eccles & Trewavas, 1989). Still, it is useful to have information from nuclear as well as mitochondrial genes, and method has considerable promise. Another promising method is AFLP, which has been employed by Seehausen *et al.* (unpublished) to study the relationships of Malawian and Victorian haplochromines along with a wide range of riverine species. Like our mitochondrial studies, *Rhamphochromis* was placed within the Malawian flock, although it did not appear basal.

Discussion

Assigning species status to samples of Lake Malawi cichlid fishes is not easy. As Snoeks (2001) points out, the species have diverged very recently and cannot be expected to differ in many morphological or genetic traits. Furthermore, Snoeks also makes the important point that most of the 'easy' species have already been described, and we are now left with the hard groups. Having put a lot of effort into these genera, the clearest conclusion we draw from this study is that *Rhamphochromis* and *Diplotaxodon* clearly belong in the 'hard' category.

There have been several major reviews of theoretical and practical species definitions in relation to Malawian cichlid fishes (Ribbink, 1994; Stauffer *et al.*, 1995; Turner, 1999, 2000). We are inclined to believe that the most useful species concepts are those based on genetics, and specifically on interbreeding, such as the classical "biological species concept" (BSC), provided it is not too rigidly defined.

Seehausen (1996) has proposed that a good rule of thumb is to assign species status to two sympatrically occurring forms if they differ in two traits that appear to be unlinked. We interpret this as meaning that traits are not the product of the same genes. For example, length of the lower jaw and length of the upper jaw are often likely to be the influenced by a single gene. We have interpreted the head shape differences between *R. esox* and *R. leptosoma* as falling into this category, and thus synonymised them.

The best-studied group of Malawian cichlids is the mbuna. Within this group, many cases are known where species are found in sympatry with other species that differ clearly in male breeding colour, but are otherwise hardly distinguishable. Studies of assortative courtship and of genetic markers such as allozymes and microsatellites have consistently revealed such colour forms as species (van Oppen *et al.*, 1998 and references therein), except in the few cases where colour morphs seem to be largely female-limited (McKaye *et al.*, 1984). Male colour is thus often diagnostic of species status in mbuna. A difficulty lies in determining whether a difference in male colours reflects a genetic difference or merely an ontogenic stage, perhaps associated with different degrees of sexual maturation or territory control. This is especially difficult in species such as the pelagic and deep-water cichlid where it is not possible to observe adults underwater, at least until someone deploys a submersible or remote operated vehicle (ROV) in the lake.

Diplotaxodon and *Pallidochromis* species.

Bearing Seehausen's principle in mind, we have sought to correlate male colour differences with other traits. For example, Turner & Stauffer (1998) showed that not only did *D. apogon* and *D. macrops* differ in male colour, but they also differed in meristic and morphometric traits, notably gillraker counts and relative lower jaw lengths. In general, most *Diplotaxodon* species comparisons could be resolved in this way, provided we had reasonably large samples of sexually mature males exhibiting breeding dress. Like the mbuna, some pairs of *Diplotaxodon* species (e.g. *D. apogon, D.* sp. 'offshore') seemed to have identical male breeding colours, but differed markedly in several morphometric or meristic traits. These too were assigned to separate species. Other species were morphologically so clearly distinct in several traits that we felt no compunction in assigning species status, even in the absence of information on male breeding dress (e.g. *D.* sp. 'brevimaxillaris', *P. tokolosh*). We feel it is likely that *Diplotaxodon* species follow the same rules as mbuna: morphologically similar species tend to differ clearly in male breeding colours. Unlike mbuna, where brightly coloured males are found throughout year all through the habitat used by the species, *Diplotaxodon* males in breeding colour tended to occur sporadically, although when found they were sometimes numerous. The major difficulties with *Diplotaxodon* lay in cases where morphological characters were not clearly distinctive and we lacked a sufficient number of males in breeding dress to attempt the statistical investigation of more subtle difference in morphometrics or meristics.

Rhamphochromis species

Rhamphochromis species seemed rather different from other Malawi cichlids. Male breeding colours were less easy to discern in most cases. Generally, sexually mature fish developed varying degrees and extent of orange-yellow colour in the ventral area. In some species at least, females as well as males often showed a great deal of bright orange colour. This colour did not persist for long in preserved specimens, so we could say little about coloration for material where we had no live colour photographs or field colour notes. We did not find clear-cut cases of species-specific colour patterns, apart from the generally dark colour of *R.* sp. 'grey' and the prominent horizontal stripes of *R.* sp. 'stripe. Morphometric analyses were of limited use in many cases. It appeared that many species showed a degree of morphological variation unusual in haplochromine cichlids. Some of this variation was size-related, but there was often a great deal of variation between similar-sized individuals too. One possible explanation for this might be that there are many more species than we have been able to identify. We cannot rule this out, but in the absence of correlated colour differences, it has not proved possible to test this to our satisfaction. We think it is unlikely. Another possibility is that there is a good deal of continuous variation or even discrete polymorphism within species.

Molecular Studies.

Our work has probably been the most extensive molecular study yet undertaken of a group of cichlid fishes from the African great lakes. The mitochondrial sequences covered over 800 base-pairs of the highly variable control region and about the same length of the fast-evolving ND2 gene. Sequences were obtained from hundreds of individuals. As a result of this massive effort, we can now be pretty certain that not only are *Rhamphochromis* and *Diplotaxodon* among the 'hard' groups for morphological study, they are no easier to resolve by molecular methods than the notoriously difficult mbuna. Moran *et al.*'s (1984) study suggested to us that these pelagic genera might represent ancient lineages with relatively few species, where we might expect to find clear mitochondrial clades corresponding to morphospecies. In fact, we found the same difficulty in resolving recent branching orders as with mbuna.

Parker & Kornfield (1997) interpreted the problems with resolving mbuna interrelationships from mtDNA as probably resulting from incomplete lineage sorting, which means that polymorphisms are often maintained in mitochondrial sequences right through the entire period between successive speciation events, with different haplotypes fixing later in different lineages, permanently erasing evidence of the true species trees. This process is likely to happen in groups where there are large population sizes and short intervals between speciation events. Another explanation might be a history of frequent introgressive hybridisation events. This is not implausible, as many Malawian cichlids can readily interbreed with each other in captivity, producing viable, fertile hybrids.

Along with the relatively low genetic diversity among the species, Parker & Kornfield's explanations seem to explain why it rarely proved possible to use mtDNA to identify monophyletic species among the *Rhamphochromis* and *Diplotaxodon* specimens we have investigated. However, the deeper relationships seem better resolved. The problem is that incomplete lineage sorting has the potential to produce well supported but false sister group relationships, if mtDNA trees are interpreted as species tree. However, there is no reason to expect that this should aggregate several morphologically similar species into a single clade to the exclusion of dozens of other species. So, we feel pretty confident about the monophyly of the *Rhamphochromis* and *Diplotaxodon/Pallidochromis* clades. However, it is probably appropriate to be more sceptical about the branching order of the clades.

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