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Three new deep water cichlid fishes of the genus *Diplotaxodon* from Lake Malawi, with a redescription of *Diplotaxodon ecclesi*

George F. Turner* and Jay R. Stauffer**

Diplotaxodon macrops, new species, differs from *D. apogon*, new species, in male breeding colour and in the shorter lower jaw. These species occur sympatrically at depths of 90 to at least 120 m in the south of the lake. *Diplotaxodon aeneus*, new species, is known only from the north of the lake, and is distinguished by male breeding colour and morphometrics. The relatively large eyes of all three species distinguish them from other *Diplotaxodon*, except *D. ecclesi*. The holotype of *D. ecclesi* differs from the three new species in its more slender body, from *D. aeneus* and *D. apogon* in male breeding colour, and from *D. macrops* in its longer lower jaw.

Introduction

More than 300 species of endemic haplochromine cichlids have been described from Lake Malawi (Turner, 1996). Currently, efforts at conserving and managing these fishes, both for their scientific and nutritional value, are severely hampered by the inability of field workers to identify the majority of species. Many Malawian cichlids, including some of the most commercially important species, are still undescribed (Turner, 1996). Species of the genus *Diplotaxodon* Trewavas are heavily exploited in the south of the lake (Turner, 1994a-b) and comprise approximately $\frac{3}{4}$ of the biomass of the open-water fish community (Menz, 1995). The purpose of this paper is to describe

three new species of deep-water cichlids of the genus *Diplotaxodon*: *D. macrops*, *D. apogon* and *D. aeneus*.

Since Trewavas's (1935) description of *D. argenteus*, three further species have been described (Burgess & Axelrod, 1973; Stauffer & McKaye, 1986; Turner, 1994a), but little else is known about these fishes. Several authorities have stated that there are several (estimates range from 7 to 20) undescribed species which should be assigned to this genus (Fryer & Iles, 1972; Stauffer & McKaye, 1986; Eccles & Trewavas, 1989). There is circumstantial evidence that some species at least may spawn in open water, posing a problem for hypothesised speciation mechanisms which assume an allopatric mode (Turner, 1994b).

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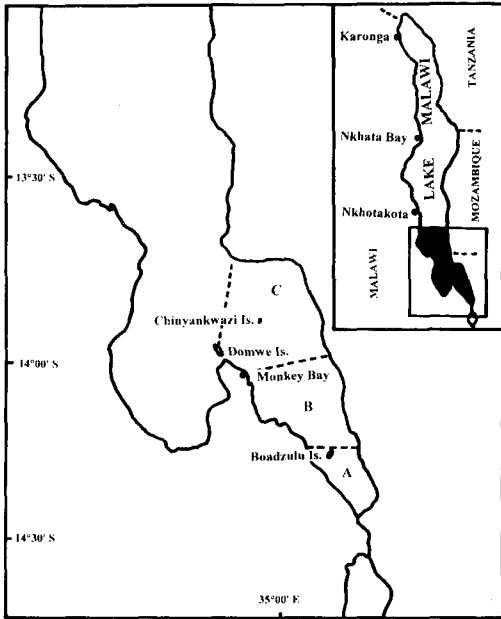


Fig. 1. Map of Lake Malawi, showing collecting locations mentioned in the text. Letters A, B and C indicate commercial fishing areas used for license purposes by the Malawi Government. Broken lines indicate boundaries to fishing areas (large map) or projections of national boundaries on the lake shore (inset map).

Methods

All newly collected specimens were fixed in 10 % formalin and preserved in 70 % ethanol before examination. Additional ecological and distributional data were obtained from fresh specimens. Distribution and abundance of the species were assessed from 36 samples from a commercial semipelagic trawler fishing at depths of 40 to 60 m north of Boadzulu Island (Area B, Fig. 1) from October 1990 and September 1991, 12 samples of commercial demersal trawlers fishing between 50 and 70 m north of Boadzulu Island (Area B) from November 1991 and October 1991, 3 samples of demersal pair-trawlers fishing in water of less than 50 m depth south of Boadzulu Island (Area A, Fig. 1) between October 1991 and February 1992, and from experimental demersal trawls taken throughout the SE Arm of Lake Malawi from 20 to 120 m depth between May 1991 and May 1992 (Turner et al., 1995).

External counts and measurements largely follow Barel et al. (1977); the exceptions are given in Turner (1994a).

Diplotaxodon macrops, new species (Figs. 2-3)

Holotype. BMNH 1996.4.30:1, ripe male, 106.7 mm SL; Malawi: Lake Malawi, bottom trawl at 100 m depth, off of Monkey Bay at 14°03'S 34°56'E; G. F. Turner, 28 February 1991.

Paratypes. All from Malawi, Lake Malawi. BMNH 1996.4.30:2-10, 7 males and 2 females, 89-115 mm SL; collecting data as holotype. – PSU 3024, 3 adult males, 3 immatures, 70-97 mm SL; bottom trawl at 100-105 m depth off Chinyankwazi Island (13°58'S 34°50'E); G. F. Turner & J. R. Stauffer, 31 January 1991. – BMNH 1996.4.30:11-13, 3 immatures, 55-66 mm SL; bottom trawl at 83 m depth off Monkey Bay; G. F. Turner, 23 October 1990. – BMNH 1996.4.30:14, 1 ripe male, 117 mm SL; trawl at 111 m depth between Cape Maclear (northern tip of Domwe Island, 13°58'S 34°49'E) and Chinyankwazi Island, Monkey Bay Fisheries Research Unit, 20 April 1972. – BMNH 1996.4.30:15, immature female (dissected); bottom trawl at 84-94 m depth off Monkey Bay; G. F. Turner, 13 April 1992.

Diagnosis. A small *Diplotaxodon* species, not known to exceed 120 mm SL. The eye diameter is longer than the snout, which distinguishes this species from *D. argenteus*, *D. greenwoodi* and *D. limnothrissa*. It has a deeper body (33.5-37 % SL) than *Diplotaxodon ecclesi* (31.5). The lower jaw is shorter (37-41 % HL) than that of *D. apogon* (42-46). It also generally has higher meristic counts than *D. apogon*: 20-25 vs. 16-20 ceratobranchial gillrakers, 33-35 vs. 31-34 lateral line scales, XIV-XVI vs. XII-XIV dorsal fin spines. It has a smaller head (34-38 % SL), shorter predorsal length (36-39 % SL) and narrower body (40-46 % SL) than *D. aeneus* (38-40, 40-42 and 46-51 % respectively); *D. aeneus* also generally has lower meristic counts: 18-20 ceratobranchial gillrakers and XIII-XV dorsal fin spines. Ripe males are uniformly black, except for a white margin to the dorsal fin and a yellow eggspot on the anal fin. This differs from all of the above species, except *D. ecclesi*.

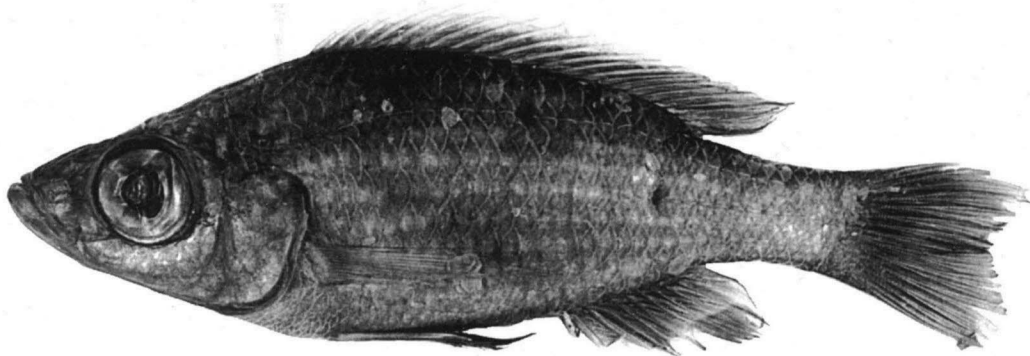


Fig. 2. *Diplotaxodon macrops*, holotype, 106.7 mm SL, male, BMNH 1996.4.30.1.

Description. Principal morphometric ratios are given in Table 1, meristics in Table 2. Body deep, laterally compressed. Head and eyes large. Dorsal head profile straight and 26° to horizontal. Premaxillary pedicel prominent and profile at 30° to horizontal axis. The gape is inclined at 57° to the horizontal axis. All angles are for holotype. Lower jaw slightly protruding. Mental process on lower jaw absent or very slight. Premaxillae very slightly beaked. The posterior end of the maxilla lies just caudally to the nostril, but well in front of the eye. Pectoral fin long, when intact reaching just past the first anal spine. Pelvic fin of females short, not reaching vent. In males longer, reaching posterior to vent but rarely to first anal spine. Caudal emarginate. Dorsal fin XV 11 in holotype, XIV-XVI 11-12 in paratypes. Anal fin III 10 in holotype, III 10-12 in paratypes. Longest rays of dorsal and anal fin not reaching base of the caudal fin.

Scales. Scales ctenoid on flanks both above and below lateral line, with 35 in longitudinal series of holotype, 33-35 in paratypes. The upper lateral line, which may be interrupted posteriorly, often extends to the third to fifth scale caudal to the anteriormost part of the caudal peduncle. The lower lateral line is straight and variable in length: the anteriormost pored scale in some specimens is as much as 3 scales rostral to the first anal spine, in other it lies caudal to the third spine. There are two rows of scales between the upper and lower lateral lines (one on the caudal peduncle). The caudal fin is heavily scaled basally, particularly on the upper- and lowermost rays, where

scales extend along more than half of the length of the rays. Rays as well as inter-radial membranes are scaled. The cheek is fully scaled, with 2-3 scale rows. There is a single row of postorbital scales. The transition between the large flank and small chest scales is gradual.

Gill rakers. The gill rakers are long, slender and slightly thickened towards the tips. There are 6-8 epibranchial, 20-25 ceratobranchial and 1-2 rakers on the angle between the two (7, 21 and 1 respectively in holotype). Both epibranchial and ceratobranchial rakers increase in length towards the articulation and the first two or three rakers on the proximal parts of both epi- and ceratobranchials are often rudimentary.

Dentition. Teeth are numerous, very small, slender, recurved, simple. A total of 2-3 series in both upper and lower jaws.

Osteology. The infraorbital series is reduced. Apart from the preorbital (lacrimal), the bones are represented by a series of slender tubules. Lower pharyngeal bones of dissected paratype (90 mm SL) and intact paratype (95 mm SL) were examined. The bone is slender, long bladed and deeply forked posteriorly. The lower pharyngeal teeth are small, slender, unicuspid and recurved. There are 34-36 teeth on the posterior margin. Lower pharyngeal bone total length 26.1-26.6 % of head length; fork length 87.0-90.0 % of total bone length; total bone width 77.0-77.4 % of pharyngeal bone total length. Vertebrae (from single dissection): 15 abdominal and 16 caudal. The

Table 1. Morphometrics of *Diplotaxodon macrops* (holotype and 19 paratypes), *D. apogon* (holotype and 20 paratypes), *D. aeneus* (holotype and 5 paratypes), and *D. ecclesi* (holotype).

	<i>D. macrops</i>			<i>D. apogon</i>			<i>D. aeneus</i>			<i>D. ecclesi</i>
	holotype	mean \pm SD	min-max	holotype	mean \pm SD	min-max	holotype	mean \pm SD	min-max	holotype
Standard length	106.7	94.5	54.5-117	87.8	91.5	62.5-109	125.2	129.4	125.2-137.3	139.9
As percentage of SL										
Head length	36.1	35.5 \pm 0.9	33.9-37.6	37.2	37.6 \pm 0.9	35.5-39.7	40.5	39.4 \pm 0.9	38.5-40.6	35.5
Maximum depth	35.2	35 \pm 1.0	33.5-36.8	35.9	35.3 \pm 1.3	32.4-37.3	37.1	35.3 \pm 0.9	34.3-37.1	31.6
Maximum width	14.6	15.1 \pm 0.5	14.4-16.5	16.1	16.4 \pm 0.5	15.7-17.6	16.9	16.9 \pm 0.6	16.0-17.9	14.5
Pectoral fin length	33	33.4 \pm 1.6	29.6-37.6	35.1	37.2 \pm 1.6	34.9-40.7	33.6	32.3 \pm 0.9	31.4-34.0	27.8
Pelvic fin length	26	25 \pm 1.8	21.3-28.2	24.9	23.0 \pm 1.2	21.1-25.1	25.4	25.9 \pm 1.5	22.8-27.3	22.9
Dorsal fin base length	48.5	47.6 \pm 1.3	45.1-51.4	43.7	44.2 \pm 0.9	42.9-45.6	43.2	44.6 \pm 1.2	43.2-46.3	48.3
Predorsal length	37.6	37 \pm 0.9	35.5-38.7	39.1	40.4 \pm 1.3	38.2-42.5	40.9	40.8 \pm 0.6	40.2-42.0	36.8
Prepelvic length	42.6	41.2 \pm 1.2	38.4-43.6	43.6	42.8 \pm 1.0	41.1-45.0	44.2	43.1 \pm 1.2	41.1-44.7	39.4
Caudal peduncle length	17	18.3 \pm 1.1	16.3-20.0	19.7	19.0 \pm 1.3	16.5-21.4	18.6	18.1 \pm 0.8	17.1-19.2	18.9
Caudal peduncle depth	12.3	12.7 \pm 0.4	11.9-13.3	12.6	12.4 \pm 0.4	11.6-13.1	12.6	12.5 \pm 0.2	12.3-12.8	11.2
As percentage of head length										
Cheek depth	19.5	22.6 \pm 1.8	19.3-26.5	25.7	25.2 \pm 1.1	23.2-28	26.6	25.8 \pm 1.5	23.2-28.1	31.3
Head depth	81.0	78.7 \pm 2.9	73.0-84.1	74.3	79.4 \pm 2.6	74.3-82.9	76.9	76.7 \pm 1.3	75.5-79.3	78.8
Horizontal eye diameter	34.0	34.7 \pm 1.9	32.6-39.7	32.4	32.6 \pm 1.5	30.5-35.6	30.4	32.1 \pm 1.3	30.4-34.5	32.9
Vertical eye diameter	34.3	33.7 \pm 1.8	30.7-37.5	31.5	31.6 \pm 1.8	28.5-34.8	29.8	31.6 \pm 0.9	29.8-32.5	32.5
Interorbital width	19.2	19.8 \pm 0.8	18.3-21.4	17.4	16.9 \pm 1.0	14.3-18.5	62.7	18.1 \pm 0.8	17.3-19.7	19.2
Lower jaw length	40.5	39.1 \pm 1.0	37.1-40.7	42.2	44.3 \pm 1.0	42.2-46.3	42.6	39.6 \pm 1.4	38.0-42.6	41.7
Premaxillary pedicel length	26.8	26.3 \pm 1.3	24.2-29.3	24.5	24.8 \pm 0.9	23.2-26.3	25.4	25.2 \pm 0.9	23.6-26.1	26.0
Preorbital bone depth	17.4	17.7 \pm 0.8	15.5-19.1	16.5	16.4 \pm 0.9	14.5-19	17.0	17.3 \pm 0.6	16.7-18.6	18.7
Postorbital head length	35.6	36.6 \pm 1.4	33.8-39.3	38.8	37.8 \pm 1.2	35.5-40.3	41.2	39.9 \pm 1.1	37.7-41.2	38.9
Snout length	29.4	28.0 \pm 1.6	24.7-31.8	29.4	28.1 \pm 1.1	26.1-30.5	28.4	28.8 \pm 0.6	27.8-29.9	31.3
As percentage of maximum depth										
Maximum width	41.5	43.3 \pm 1.3	40.2-45.5	44.8	46.6 \pm 1.7	44.2-49.7	45.7	47.9 \pm 1.7	45.7-50.8	45.9
Caudal peduncle length/depth	1.4	1.4 \pm 0.1	1.3-1.6	1.6	1.5 \pm 0.1	1.3-1.8	1.5	1.4 \pm 0.1	1.3-1.5	1.7



Fig. 3. *Diplotaxodon macrops*, freshly collected paratype from Chinyamwezi, 115 mm SL, ripe male, BMNH 1996.4.30:2-10.

inferior apophyses (spondylapophyses) of the third abdominal vertebrae are short and do not meet below the dorsal aorta.

Gonads. A female paratype of 108 mm SL contained 16 mature eggs, all in the right ovary. Maximum egg diameter was 6 mm. In two other preserved specimens not included in the type series, one also had mature eggs only in the right ovary, while in the other the right ovary was much larger than the left.

Coloration. Generally silvery and countershaded-grey dorsally, white ventrally. In immatures, fins hyaline, except dorsal lappets, posterior margin of caudal fin, lower margin of anal fin and tips of pelvic fins which are dark grey or black. In some individuals pelvic fins dusky to base. Adult females darker dorsally, with dusky dorsal fin. Anal and pelvic fins white. Sexually active males black, with a coppery sheen (Fig. 3). Margin of spiny dorsal fin white or whitish yellow. 1-2 large pale yellow eggspots on anal fin.

Table 2. Meristics of *Diplotaxodon macrops*, *D. apogon*, *D. aeneus* and *D. ecclesi*.

	dorsal-fin spines					dorsal-fin rays			anal-fin rays		
	XII	XIII	XIV	XV	XVI	10	11	12	10	11	12
<i>D. macrops</i>			8	11	1		10	10	8	11	1
<i>D. apogon</i>	1	13	7			4	15	2	16	5	
<i>D. aeneus</i>		4	1	1			3	3	1	4	1
<i>D. ecclesi</i>				1				1			1

	lateral line scales					ceratobranchial gill rakers									
	31	32	33	34	35	16	17	18	19	20	21	22	23	24	25
<i>D. macrops</i>			1	11	8					6	8	1	3	1	1
<i>D. apogon</i>	5	4	9	3		4	8	7	1	1					
<i>D. aeneus</i>			1		5			3	2	1					
<i>D. ecclesi</i>		1									1				

Distribution and abundance. Common in trawls from depths of 80 m to at least 130 m in the southern part of Lake Malawi (see Table 3). Range extends at least as far north as Nkhotakota. It may occur in deeper water, but few samples have been taken from below 120 m. At present this species is of little commercial significance.

Diet. Although most stomachs were everted or empty, intestinal contents included fragmentary remains of insect larvae, crustacea and diatoms. The upwardly angled mouth suggests that this material was probably obtained from the plankton, rather than from sediments.

Etymology. Specific name *macrops* (from Greek), a noun in apposition, refers to the large eye.

***Diplotaxodon apogon*, new species**
(Figs. 4-5)

Holotype. BMNH 1996.4.30:21, ripe male, 87.8 mm SL; bottom trawl at 100 m depth, off Monkey Bay, Lake Malawi; G. F. Turner, 28 February 1991.

Paratypes. BMNH 1996.4.30:22-25, 3 males and 1 female, 96-102 mm SL; collecting data as holotype. – BMNH 1996.4.30:26-30, 5 males, 87-103 mm SL; PSU 3025, 4 males, 70-98 mm SL; bottom trawl at 100-105 m depth off Chinyankwazi Island; G. F. Turner & J. R. Stauffer, 31 January 1991. – BMNH 1996.4.30:31, 1 female, 109 mm SL; bottom trawl at 83 m depth off Monkey Bay; G. F. Turner, 22 October 1990. – BMNH

Table 3. Distribution and abundance of *D. apogon* and *D. macrops* in the southeastern arm of Lake Malawi, from experimental bottom trawl surveys. Neither species was recorded from the 59 samples taken at depths shallower than 90 m.

date	trawl station	depth (m)	total numbers		
			all fish	<i>D. macrops</i>	<i>D. apogon</i>
Feb. 1992	Monkey Bay	92	516	1	–
	Chinyankwazi	100	336	–	1
	Chinyankwazi	118	379	7	5
	Domwe	126	373	14	6
May 1992	Monkey Bay	92	686	–	–
	Chinyankwazi	100	490	–	–
	Chinyankwazi	114	457	–	2
	Domwe	126	387	–	9

1996.4.30:32-38, 4 males (one dissected, measurements not included), 2 females and 1 immature, 63-105 mm SL; bottom trawl at 100 m depth off Domwe Island (13°58'S 34°50'E); G. F. Turner & J. R. Stauffer, 31 January 1991.

Diagnosis. A small *Diplotaxodon* species, not known to exceed 110 mm SL. The relatively deeper body (32-37 % SL) and larger eye (30-36 % HL) distinguish this species from most *Diplotaxodon* species. Among known *Diplotaxodon* species in which the eye diameter is greater than the snout length, it is the only one in which ripe males have pale silvery flanks and belly. The lower jaw is relatively longer (42-46 % HL) than that of *D. macrops* (37-41). Body depth (32-37 % SL) is greater than in *D. ecclesi* (32). The dorsal fin spine (12-14) and ceratobranchial gillraker counts (16-20) are lower than those of *D. ecclesi* (15 and 22 respectively) and generally lower than those of *D. macrops* (14-16 and 20-25, respectively).

Description. Principal morphometric ratios are given in Table 1, meristics in Table 2. Body deep, laterally compressed. Head and eyes large. Dorsal head profile straight and 22° to horizontal (all angular measurements for holotype only). Premaxillary pedicel prominent and profile at 31° to horizontal axis. The gape is inclined at 53° to the horizontal axis. Lower jaw slightly protruding. Moderately prominent mental process on lower jaw. Premaxillae very slightly beaked. The posterior end of the maxilla lies well behind the nostril, and just in front of the eye. Pectoral fin long, when intact reaching well past the first anal spine, and often past the third spine. Pelvic fin short, not reaching vent. In mature males it is longer, but only occasionally just reaching the anterior of the genital papilla. Caudal emarginate. Dorsal fin XIII 10 in holotype, XII-XIV 10-12 in paratypes. Anal fin III 10 in holotype, III 10-11 in paratypes. Longest rays of dorsal and anal fin not reaching base of the caudal fin.

Scales. Scales ctenoid on flanks both above and below lateral line, with 33 in longitudinal series of holotype and 31-34 in paratypes. The upper lateral line, which may be interrupted posteriorly, generally extends to the third to fifth scale caudal to the anteriormost part of the caudal peduncle, although in one paratype there are 9 unpored scales caudal to the last pored scale. The lower lateral line is short and straight: the ante-

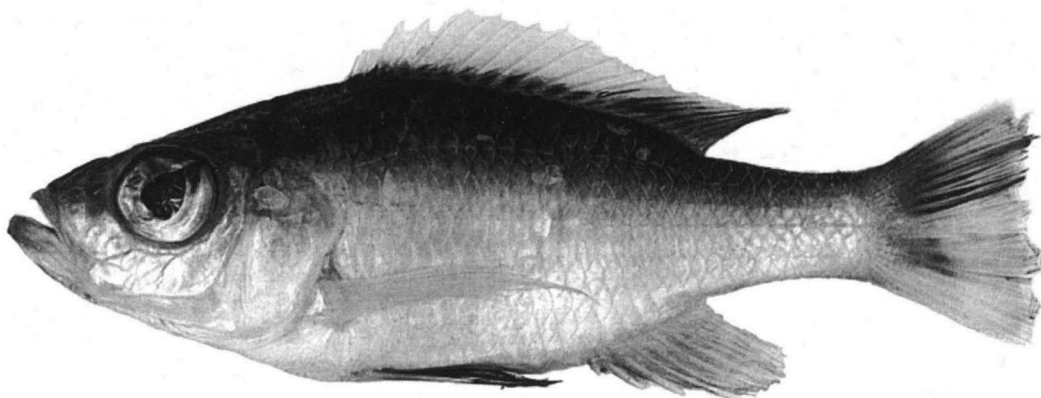


Fig. 4. *Diplotaxodon apogon*, holotype, 87.8 mm SL, male, BMNH 1996.4.30.21.

riormost pored scale generally lies above the spinous portion of the anal fin, although in one paratype it lies one scale row rostral to the first anal spine. There are two rows of scales between the upper and lower lateral lines, except on the caudal peduncle where there is one. The caudal fin is heavily scaled basally, particularly on the upper- and lowermost rays, where scales extend along more than half of the length of the rays. Rays as well as inter-radial membranes are scaled. The cheek is fully scaled, with 3 scale rows. There is a single row of postorbital scales. The transition between the large flank and small chest scales is gradual.

Gill rakers. The gill rakers are long, slender and slightly thickened towards the tips. There are 5-7 epibranchial, 16-20 ceratobranchial and 1-2 gill rakers on the angle between the two (6,18 and 1 respectively in holotype). Both epibranchial and ceratobranchial rakers increase in length towards the articulation and the first two or three rakers on the proximal parts of both epi- and ceratobranchials are often rudimentary.

Dentition. Teeth are numerous, very small, slender, recurved, and simple. A total of 2 series in both upper and lower jaws.

Osteology. The infraorbital series is reduced. Apart from the preorbital (lachrymal), the bones are represented by a series of slender tubules. The single lower pharyngeal bone (of a 103 mm paratype) was examined. It is slender, long-blad-

ed and deeply forked posteriorly. The lower pharyngeal teeth are slender, unicuspid and recurved. There are 26 teeth on the posterior margin. Lower pharyngeal total length was 30.1 % of head length; fork length 93.9 % of total bone length; total bone width 73.7 % of pharyngeal bone total length. Vertebrae (from single dissection): 15 abdominal and 16 caudal. The inferior apophyses (spondylapophyses) of the third abdominal vertebrae are short and do not meet below the dorsal aorta.

Gonads. In the single ripe female examined, a paratype of 102 mm SL, the right ovary contained 17 mature eggs, and the left 4. Maximum egg diameter was 5.6 mm. In unripe females examined, the left ovary is smaller than the right. In ripe males both testes substantially enlarged and presumed functional. Right testis slightly larger in both male specimens opened.

Coloration. Generally silvery and countershaded- grey dorsally, white ventrally. In immature fish fins hyaline, except dorsal lappets, and posterior margin of caudal fin which are often dusky. Adult females darker dorsally, with dusky dorsal fin. Anal and pelvic fins white. Sexually active males more strongly countershaded, with dorsal surface very dark, almost black. The dorsal fin is white anteriorly, black posteriorly. The border between the black and white parts is sharp and runs obliquely (Fig. 5). Pelvic fins black. Caudal fin dusky. Anal fin dark grey to black with 1-2 large pale yellow eggspots.



Fig. 5. *Diplotaxodon apogon*, freshly collected paratypes from Chinyankwazi, probably 103 (upper) and 101 mm SL (lower), BMNH 1996.4.30:26-30.

Distribution and abundance. Common in trawls from depths of 80 m to at least 130 m in the southern part of Lake Malawi (see Table 3). It may occur in deeper water, but few samples have been taken from below 120 m. At present this species is of little commercial significance.

Diet. All specimens examined had empty or everted stomachs. The steeply angled gape and long gill rakers suggest a diet of small midwater animals, perhaps planktonic invertebrates or fish larvae.

Etymology. The specific name refers to the general similarity of body form to some of the cardinalfishes of the genus *Apogon* La Cepède. It strictly means 'lacking barbels' which is true, but not exactly relevant. Treated as a noun in apposition.

Diplotaxodon aeneus, new species
(Fig. 6)

Holotype. BMNH 1996.4.30:16, sexually active male, 125 mm SL; midwater trawling over a lake bed depth of 400 m, offshore at 11°34'S 34°35'E, northeast of Nkhata Bay; ODA/SADC Pelagic Resources Project, 30 November 1993-1 December 1994.

Paratypes: BMNH 1996.4.30:17-20, 4 spec., 126-137 mm SL; PSU 3026, 1 spec., 132 mm SL; collecting data as holotype.

Diagnosis. The uniformly dark male breeding colour, including the dorsal fin, is distinctive among known species where the eye diameter is longer than the snout length. Head longer (38-

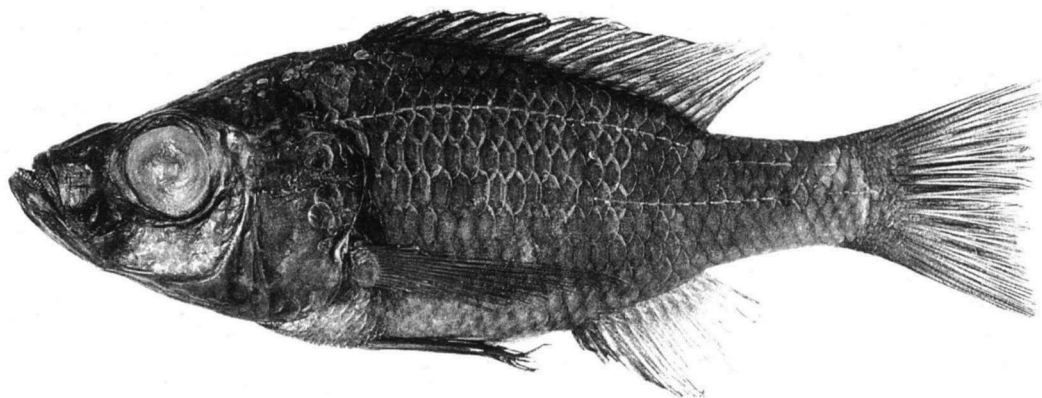


Fig. 6. *Diplotaxodon aeneus*, holotype, 125 mm SL, male, BMNH 1996.4.30:16.

40 % SL), predorsal length greater (40-42 % SL) and body wider (46-51 % of maximum depth) than in *D. macrops* (34-38, 36-39 and 40-46 respectively). Pectoral fin length (30-34 % SL) and lower jaw length (38-43 % HL) shorter than in *D. apogon* (35-41 and 42-46 respectively). Body depth (34-37 % SL) is greater than that of *D. ecclesi* (32).

Description. Principal morphometric ratios are given in Table 1, meristics in Table 2. Body laterally compressed. Head moderately concave in profile above eye. The premaxillary pedicel is long and prominent. The head profile and premaxillary pedicel are both inclined at 30° to the horizontal. The gape is steeply inclined (55° to horizontal). Prognathous, with lower jaw protruding. Mental process absent to moderately prominent. Pelvic fin long, usually reaching to vent, or in ripe males, beyond. Pectoral fin long, normally reaching past first anal spine. Caudal emarginate, heavily scaled basally. Dorsal fin XIII 11 in holotype, XIII-XV 11-12 in paratypes. Anal fin III 11 in holotype, III 10-12 in paratypes. Longest rays of dorsal and anal fin not reaching base of the caudal fin.

Scales. Flank scales ctenoid. Lateral line scales 33 in holotype, 35-36 in paratypes. The upper lateral line, which is sometimes interrupted posteriorly, extends 7-9 scale rows along the caudal peduncle. The lower lateral line is short and straight. There are two rows of scales between the upper and lower lateral line, except on the caudal peduncle, where there is one. Caudal fin heavily

scaled basally. Cheek scales in 3 rows in holotype and most paratypes, 2 in one paratype. There is a single row of postorbital scales and the transition from small chest scales to large flank scales is gradual.

Gill rakers. The gill rakers are similar in appearance to those of *D. macrops* and *D. apogon*. There are 7 epibranchial (6-7 in paratypes), 18 ceratobranchial (18-20 in paratypes) and one gill raker on the angle between the two.

Dentition. Jaw teeth are small, closely packed, simple and erect. There are 2 series of teeth in both upper and lower jaws.

Coloration. Sexually active males (preserved specimens only) are uniformly dark. ODA/SADC project field staff report that fresh males have a coppery sheen on the flanks. Female and immature specimens not included in the type series, but tentatively assigned to this species, are silvery and countershaded.

Distribution. Positively identified specimens of this species are known only from the Nkhata Bay area, but a further, tentatively identified specimen was collected from near 10°5'S 34°10'E, just southeast of Karonga in the far north of Lake Malawi.

Etymology. Aeneus, Latin, meaning bronze, in reference to the bronzy iridescence of ripe male fish. An adjective.

Diplotaxodon ecclesi Axelrod & Burgess

Material examined. USNM 210696, holotype, 139.9 mm SL; trawled from 80 m depth, off Monkey Bay, SE Arm Lake Malawi; H. R. Axelrod.

Diagnosis. Eye diameter greater than snout length. This species is distinguished from the three new species described above by its relatively slender body (maximum depth 32 % SL, vs. 32-37; caudal peduncle depth 11 % SL, vs. 12-13), and from *D. aeneus* and *D. apogon* by male breeding colour, which is dark grey or black with a white dorsal fin margin. The lower jaw is relatively longer (42 % HL) than that of *D. macrops* (37-41).

Description. Principal morphometric ratios are given in Table 1, meristics in Table 2. Body less deep or laterally compressed than other large-eyed congeneric species. Head and eyes large. Dorsal head profile straight and 21° to horizontal. Premaxillary pedicel prominent and profile at 23° to horizontal axis. The gape is inclined at 58° to the horizontal axis. Lower jaw slightly protruding. Moderately prominent mental process on lower jaw. Premaxillae very slightly beaked. Pectoral fin relatively short, not quite reaching the first anal spine. Pelvic fin short, not reaching vent. Caudal emarginate. Dorsal fin XV 12. Anal fin III 11. Longest rays of dorsal and anal fin not reaching base of the caudal fin.

Scales. Lateral line scales 32. Cheek scales in 2 rows.

Gill rakers. There are 6 epibranchial, 22 ceratobranchial and one gillraker on the angle between the two.

Dentition. Jaw teeth are small, closely packed, simple and erect. There are 2 series of teeth in both upper and lower jaws.

Coloration. A colour photograph of the holotype, apparently a ripe male, appears in the original description. The fish is dark grey with a white margin to the dorsal fin, black pelvic fin and two yellowish eggspots on the anal fin. According to the authors, in life it had a bronze sheen.

Distribution. The species is known only from the holotype, trawled from 80 m depth off Monkey Bay. Although we examined many samples from this depth from the vicinity of Monkey Bay, we have not positively identified any further specimens. Distribution records given by Eccles & Trewavas (1989) are probably not reliable, as this species appears to have been confused with *D. macrops* and possibly *D. apogon*.

Discussion

Several authors (Holzberg, 1978; Ribbink et al., 1983; Turner 1994b) have suggested that male coloration is an essential element in the maintenance of reproductive isolation among haplochromine cichlid fishes. Allozyme electrophoresis has indicated that sympatrically occurring male colour forms of the Malawian genus *Petrotilapia* are reproductively isolated, although the females of all forms are virtually indistinguishable (McKaye et al., 1982). This result was obtained from field-collected specimens, and it is possible that reproductive isolation could have been maintained by environmental cues (e.g. reproductive seasonality, spawning habitat choice) rather than by male colours. Seehausen (1996) found that in the laboratory, females of the red and blue sympatric forms of the Victorian '*Haplochromis*' *nyererei* mated exclusively with males of their own form in the laboratory, where no such environmental cues were available. Females were able to make the correct choice even when the males were isolated by a transparent partition, indicating that visual cues alone were decisive. Females of the two forms are virtually indistinguishable, and all were courted by both colours of males. More recently, Seehausen & van Alphen (in press) found that such assortative mating was eliminated when the fish were held in tanks illuminated by orange light which made the two male types appear the same colour. Although these colour forms clearly represent biological species, hybrids are perfectly viable and fertile. Preliminary data from our work with Malawian cichlids (*Pseudotropheus* spp.) is giving a similar pattern.

It has also been shown that haplochromine cichlid females discriminate between conspecific males on the basis of naturally-occurring variation in colour patterns (Hert, 1991) and that mate preferences can be reversed when elements of

the male's colour are experimentally altered (Hert, 1989). This indicates that male colour is under strong sexual selection by female choice, as would be expected in any species where males are larger and brighter than females, and parental care is exclusively by females, leaving males free to be highly polygamous (Turner, 1994b). Females of many haplochromine cichlids are found in several clearly distinct sympatric colour morphs, often with several morphs found at high abundance (>10 % of population). However, polymorphism in males is rare. Where females are polymorphic, a very small proportion of males may exhibit the rarer female patterns, such as the orange-blotched or orange forms of *Pseudotropheus zebra*. Holzberg (1978), who carried out a genetic study of the inheritance of colour morphs in this species, suggests they are a genetic 'accident' and they may never reproduce in nature, although they are perfectly fertile. Male colour polymorphism has not been recorded in any haplochromine species where females are monomorphic.

Generally then, in haplochromine cichlids, one male breeding colour equals one species. Indeed, many workers now believe that divergence in female sexual selection for male courtship traits, especially colour, may often be the actual cause of speciation in haplochromine cichlids (McKaye, 1991; Turner, 1994b). Computer simulation studies have demonstrated that this process is theoretically plausible, even in the absence of geographic isolation (Turner & Burrows, 1995; Payne & Krakauer, 1997). If reproductive isolation is established through female choice of male colours, recently diverged species will not differ in any features except female preference and male colour, although it would be expected that morphological differences would accumulate over a long enough time span once the two gene pools have become isolated. For these reasons, we regard male colours as essential in the definition of morphologically similar haplochromine species.

In the present study, we initially distinguished *D. macrops* and *D. apogon* on the basis of male breeding colours. Morphological differences were not obvious and most were overlapping. The two species had not previously been distinguished despite a history of more than 25 years of intensive taxonomic collections from trawl surveys based at Monkey Bay, less than 2 km from the type locations. Since the fishes were collected by trawls, and not observed underwater, it remained possible that the two male colour

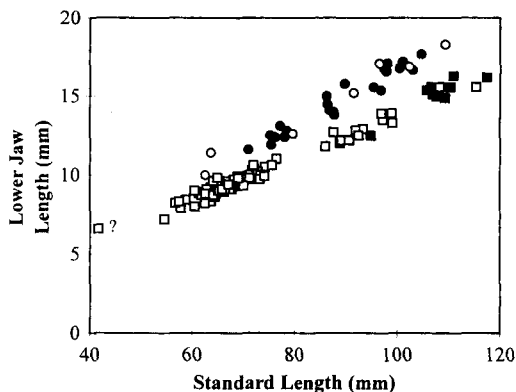


Fig. 7. Plot of lower jaw length on standard length for *Diplotaxodon macrops* (mature males ■, females and immatures □) and *D. apogon* (mature males ●, females and immatures ○) and one tentatively identified specimen? Relative lower jaw length is clearly diagnostic for all specimens above 70 mm SL. Material includes types and additional preserved specimens held at the University of Southampton and not included in the type series.

forms represented fish at different stages of the reproductive cycle, for example territorial and non-territorial ripe males. A number of bivariate scatterplots were constructed for all variables measured against standard length. The most clear-cut separation of the two colour forms was provided by lower jaw length (Fig. 7). Since lower jaw length is not a trait likely to change in the few days between the onset of male ripeness and breeding colours, and the establishment of a territory and the development of full breeding colours, we concluded that the two forms represented separate species. Relative lower jaw length was then used to classify female and immature fish into the two species. Further differences in meristics, morphometric ratios, bivariate plots and multivariate analyses (not shown) confirmed their morphological distinctness. A similar approach was adopted for *D. aeneus*.

We believe that this approach of seeking a concordance of male coloration and morphology is the correct one to adopt with Lake Malawi cichlids, where morphological differences between reproductively isolated sympatric species are often slight. In particular this applies to species which are obtained from depths too great to be surveyed by SCUBA diving. In shallower water, males may be observed on their territories, confirming that their colour is that of fully

territorial fish. Microhabitat differences or differences in male bower form may also be determined for such species. In these cases, male coloration may be sufficient to grant specific status, even in the absence of clear-cut morphological differences.

On the other hand, morphological features including both external body proportions and skeletal structures associated with capture and processing of food are well known to be both geographically variable (Turner & Robinson, 1991) and phenotypically plastic in African cichlids, and many other fish (Kornfield, 1991). Furthermore, such traits are generally under strong directional selection, which, in species with similar genetic and developmental backgrounds, frequently leads to parallel or convergent evolution. For this reason, where male colours are not known, or are identical, caution must be applied to defining species on morphological differences, although specific status could be inferred on morphology alone where such differences were considerable, occurred in a variety of characters which appear to be developmentally uncorrelated, or are at least clearly discontinuous in frequency distribution when a large sample is examined.

Although male colour is of tremendous utility in the hypothesis testing phase of determining if more than one species is present, it is obviously of no value in the identification of female and immature fishes. Thorough morphological analysis is then required, although it must be borne in mind that it is quite possible that there may be no diagnostic differences between species other than male colour. In the present study we were unable to find any character states or meristics which unambiguously diagnosed these species, although morphometric differences were clear-cut and there were also differences in frequency distributions of counts.

The distinctive male colours and morphology of *D. apogon* and *D. aeneus* are convincing evidence that these are separate species. *Diplotaxodon macrops* lives and breeds sympatrically with *D. apogon*. Ripe males of both species are often taken in the same bottom trawl haul, often comprising the majority of specimens of these species, suggesting that they breed colonially and benthically.

The male breeding colour pattern of *D. ecclesi* is very similar to that of *D. macrops* and the reported type localities are in the same area. We initially suspected that they were conspecific, but

now consider them to be different species, not only because of their morphological and meristic differences, which were initially shown by a multivariate analysis (not included in the present paper), but also because none of the hundreds of specimens of *D. macrops* we have examined is larger than 120 mm SL, while the holotype of *D. ecclesi* is 140 mm SL. Some specimens strongly resembling the type of *D. ecclesi*, in shape and size, have been collected from the Domira Bay area, but are paler ventrally. The status of this material is not yet resolved.

The ODA SADC Pelagic Resources Project (Menz, 1995) reported that *Diplotaxodon* 'big-eye' was extremely abundant in the offshore pelagic zone and estimated the standing biomass at 32,700 tonnes, mainly at depths of 150-250 m during the day, although at night they came closer to the surface. We have examined 84 specimens collected by this project. While we were able to distinguish them from the species described above using multivariate analyses, we lack reliable information of male breeding colours. As most of the specimens were collected both further offshore and hundreds of kilometres further north than the types of *D. macrops* and *D. apogon*, their taxonomic status remains unresolved. This has important practical implications, as the inshore bottom trawl fisheries have been greatly expanded since 1993, under the assumption that the exploited stock is replenished by immigration from the unfished deep pelagic zone, where *Diplotaxodon* 'big eye' is the dominant species in terms of biomass. Should this assumption be wrong, rapid overexploitation of stocks is possible.

Two independent mitochondrial DNA studies (Moran et al., 1994; Meyer et al., 1994) have supported the monophyly of the endemic Malawian haplochromines, taken to include *Astatotilapia calliptera* (Günther), a generalised species found in both the main lake and smaller water bodies in its catchment area. The other non-endemic haplochromine found in the lake, *Serranochromis robustus* (Günther), was clearly shown to be not a member of this clade. Both studies also showed the presence of two major sub-clades. One comprised the mbuna (*Pseudotropheus* Regan, *Melanochromis* Trewavas, *Labidochromis* Trewavas, etc) and *Aulonocara* Regan (and in Moran's study *Alticorpus* Stauffer & McKaye and *Lethrinops* Regan which were not examined by Meyer). The other clade comprised all but one of the species examined which had formerly been

placed in *Haplochromis* Hilgendorf by Trewavas (1935), along with a few smaller genera such as *Hemitilapia* Boulenger, *Aristochromis* Trewavas, *Chilotilapia* Boulenger and *Docimodus* Boulenger. Moran et al. provided evidence that the pelagic genera *Rhamphochromis* Regan and *Diplotaxodon* are rather distantly related to each other and to the two major clades containing most of the other Malawian genera. Meyer et al. gave the same picture for *Rhamphochromis*, although *Diplotaxodon* was not included. In neither molecular analysis could the position of *Astatotilapia calliptera* be resolved in relation to the pelagic genera.

All of the Malawian haplochromines examined by Lippitsch (1995), except *Astatotilapia Pellegri*n, but including *Rhamphochromis macrophthalmus* Regan, are united by the possession of a kinked upper lateral line, which results in there being a single row of scales between the upper and lower lines on the caudal peduncle, but two rows anteriorly. *Diplotaxodon* was not examined. We can confirm that the kinked lateral line condition is found in all four species described in the present paper, as well as in *D. limnothrissa* (holotype and non-type material), and in the types of *D. argenteus*, *D. greenwoodi*, *Rhamphochromis lucius* Ahl, *Rhamphochromis esox* (Boulenger), *Rhamphochromis leptosoma* Regan, *Rhamphochromis longiceps* (Günther), *Rhamphochromis ferox* Regan, *Pallidochromis tokolosh* Turner and in a number of specimens of undescribed *Rhamphochromis* and *Diplotaxodon* species. This provides further support for the monophyly of the endemic Lake Malawi haplochromines and indicates the complementary nature of molecular and morphological phylogenetic studies.

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Literature cited

- Barel, C. D. N., M. J. P. van Oijen, F. Witte & E. L. M. Witte-Maas. 1977. An introduction to the taxonomy and morphology of the haplochromine cichlidae from Lake Victoria. *Neth. J. Zool.*, 27: 333-389.
- Burgess, W. E. & H. R. Axelrod. 1973. New cichlids from Lake Malawi. *Trop. Fish Hobby.*, 22 (2): 14, 87-97 & 95-98.
- Eccles, D. H. & E. Trewavas. 1989. Malawian cichlid fishes: a classification of some haplochromine genera. *Lake Fish Movies*, Herten, Germany, 334 pp.
- Fryer, G. & T. D. Iles. 1972. The cichlid fishes of the great lakes of Africa. Oliver & Boyd, Edinburgh, 641pp.
- Hert, E. 1989. The function of egg-spots in an African mouth-brooding cichlid fish. *Anim. Behav.*, 37: 726-732.
- 1991. Female choice based on egg-spots in *Pseudotropheus aurora* Burgess 1976, a rock-dwelling cichlid of Lake Malawi, Africa. *J. Fish Biol.*, 38: 951-953.
- Holzberg, S. 1978. A field and laboratory study of the behaviour and ecology of *Pseudotropheus zebra* (Boulenger), an endemic cichlid of Lake Malawi (Pisces: Cichlidae). *Ztschr. Zool. Syst. Evol. Forsch.*, 16: 171-187.
- Kornfield, I. 1991. Genetics. Pp. 103-128 in: M. H. A. Keenleyside (ed.), *Cichlid fishes: behaviour, ecology and evolution*. Chapman & Hall, London.
- Lippitsch, E. 1995. Scale and squamation character polarity and phyletic assessment in the family Cichlidae. *J. Fish Biol.*, 47: 91-106.
- McKaye, K.R. 1991. Sexual selection and the evolution of the cichlid fishes of Lake Malawi, Africa. Pp. 241-258 in: M. H. A. Keenleyside (ed.), *Cichlid fishes: behaviour, ecology and evolution*. Chapman & Hall, London.
- McKaye, K. R., T. Kocher, P. Reinthal & I. Kornfield. 1982. A sympatric species complex of *Petrotilapia* Trewavas from Lake Malawi analysed by enzyme electrophoresis (Pisces: Cichlidae). *Zool. J. Linn. Soc.*, 76: 91-96.
- Menz, A. (ed). 1995. Fishery potential and ecology of the pelagic zone of Lake Malawi/ Niassa. *Natural Resources Institute*, Chatham, Kent, 386 pp.
- Meyer, A., C. Montero & A. Spreinat. 1994. Evolutionary history of the cichlid fish species flocks of the East Africa great lakes inferred from molecular phylogenetic data. *Arch. Hydrobiol., Beih. Ergebn. Limnol.*, 44: 407-423.

- Moran, P., I. Kornfield & P. N. Reinthal. 1994. Molecular systematics and the radiation of the haplochromine cichlids (Teleostei: Perciformes) of Lake Malawi. *Copeia*, 1994: 274-288.
- Payne, R. J. H. & D. C. Krakauer. 1997. Sexual selection, space, and speciation. *Evolution*, 51: 1-9.
- Ribbink, A. J., B. A. Marsh, A. C. Marsh, A. C. Ribbink & B. J. Sharp. 1983. A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *S. Afr. J. Zool.*, 18: 149-310.
- Seehausen, O. 1996. Lake Victoria rock cichlids. *Verduijn Cichlids*, Zevenhuizen, Netherlands, 304 pp.
- Seehausen, O. & J. J. van Alphen. In press. The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex). *Behav. Ecol. Sociobiol.*
- Stauffer, J. R. & K. R. McKaye. 1986. Description of a paedophagous deep-water cichlid (Teleostei: Cichlidae) from Lake Malawi, Africa. *Proc. Biol. Soc. Washington*, 99: 29-33.
- Trewavas, E. 1935. A synopsis of the cichlid fishes of Lake Nyasa. *Ann. Mag. Nat. Hist.*, Ser. 10, 16: 65-118.
- Turner, G. F. 1994a. Description of a commercially important pelagic species of the genus *Diplotaxodon* (Pisces: Cichlidae) from Lake Malawi, Africa. *J. Fish Biol.*, 44: 799-807.
- 1994b. Speciation mechanisms in Lake Malawi cichlids: a critical review. *Arch. Hydrobiol., Beih. Ergebn. Limnol.*, 44: 139-160.
- 1996. Offshore cichlids of Lake Malawi. *Cichlid Press*, Lauenau, Germany. 240pp.
- Turner, G. F. & M. T. Burrows. 1995. A model of sympatric speciation by sexual selection. *Proc. Roy. Soc. London, Ser. B.*, 260: 287-292.
- Turner, G. F. & R. L. Robinson. 1991. Ecology, morphology and taxonomy of the Lake Malawi *Oreochromis (Nyasalapia)* species flock. *Ann. Mus. Roy. Afr. Centr.*, 262: 23-28.
- Turner, G. F., D. Tweddle & R. D. Makwinja. 1995. Changes in demersal cichlid communities as a result of trawling in southern Lake Malawi. Pp. 397-412 in T. J. Pitcher & P. J. B. Hart (eds), *The impact of species changes in African lakes*. Chapman & Hall, London.

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