

A new genus for *Melanochromis labrosus*, a problematic Lake Malawi cichlid with hypertrophied lips (Teleostei: Cichlidae)

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Melanochromis labrosus is the only one of the 800 or so endemic cichlid species in Lake Malawi whose placement with mbuna or non-mbuna has been disputed on morphological grounds. Here, we redescribe *M. labrosus* using all obtainable specimens collected since its original description. In addition, we extensively survey vertebral counts in the mbuna. To determine if *M. labrosus* belongs with the mbuna, we review the morphological traits often considered to define the mbuna as a natural group, concluding that none is a uniquely shared specialization. Two features of body coloration (a relatively small number of ocellate spots in the anal fin and a possible polychromatism in one population) suggest that *M. labrosus* is best considered a species of mbuna. Although its placement within the mbuna group remains somewhat equivocal, we unambiguously demonstrate that *M. labrosus* is not a *Melanochromis*, since it lacks the synapomorphic striped color pattern typical of that genus. *Melanochromis labrosus* also does not fit within any other described genus. Therefore, we designate it the type species of *Abactochromis*, new genus. *Abactochromis* is unique in the mbuna in having greatly enlarged, lobate lips and several other autapomorphies. Contrary to published opinion, the hypertrophied lips of *A. labrosus* express high densities of taste buds. We review the little that is known about the biology of *A. labrosus* and emphasize its noteworthy distribution within Lake Malawi, on rocky shores lakewide excepting the southern arms. We underscore the importance of including this problematic, and therefore potentially informative, species in future evolutionary genetic and genomic studies of the Lake Malawi cichlid species flock. Finally, we provide a key to the now thirteen genera of mbuna inhabiting Lake Malawi.

Introduction

The mbuna are a speciose assemblage of small, colorful, primarily rocky shore cichlids endemic to Lake Malawi. They have long been regarded as a group distinct from the lake's other endemic haplochromines when characteristics of their morphology, melanin patterning, and col-

oration are considered together (Fryer, 1959; Ribbink et al., 1983; Genner & Turner, 2005). Hundreds of species of mbuna and non-mbuna haplochromine cichlids, together with a single haplochromine species that is not strictly endemic to Lake Malawi proper (*Astatotilapia calliptera*), form an extensive cichlid species flock (Moran et al., 1994; Shaw et al., 2000; Salzburger

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et al., 2005). Molecular clock-based estimates for the time period during which this species flock has radiated evolutionarily range from the last 0.57–4.6 million years (Meyer, 1993; Sturmbauer et al., 2001; Won et al., 2006; Genner et al., 2007).

Regan (1922) described the first two genera now assigned to the mbuna, but Trewavas (1935) erected six more genera (five of which remain in use today) and gave the assemblage unofficial group status by uniting them in a single couplet of her key, remarking that these genera “are more closely related to each other than to any other genus”. One of Trewavas’s original mbuna genera is *Melanochromis*, which she established for five newly described species, with *M. melanopterus* (of which she had 10 specimens) being the type species. The remaining species were *M. vermicorus* (25 specimens), *M. brevis* (2 specimens), *M. perspicax* (1 specimen), and *M. labrosus* (a single juvenile specimen). *Melanochromis labrosus* was – and still remains – unique in the mbuna group in having lips prolonged into median lobes, although this feature is not very pronounced on the holotype (Fig. 1), whose lips may have contracted in the alcohol preservative.

Several hundred additional species of cichlids have been discovered in Lake Malawi since Trewavas’s (1935) synopsis, many of which remain undescribed. Remarkably, it has been possible, based on morphology alone, to allocate every one of these species unambiguously to either the mbuna, as they have been traditionally recognized, or one of the remaining lineages of endemic haplochromine cichlids. The taxonomic position of *Melanochromis labrosus*, in contrast, has been uncertain (Genner & Turner, 2005). Some workers have regarded this species as a definite member of the mbuna (e.g., Fryer, 1959; Fryer & Iles, 1972; Ribbink et al., 1983; Eccles & Trewavas, 1989; Bowers & Stauffer, 1997; Konings, 2004), whereas others have maintained that it is a clear-cut non-mbuna haplochromine (e.g., Eccles, 1973; Burgess, 1976; Oliver, in Loiselle, 1979; Mayland, 1982). The infrequency with which this species has been collected, and its resulting rarity in museum collections, have discouraged its inclusion in morphological and molecular studies.

Here, we redescribe *M. labrosus* based on the holotype and on specimens which one of us (MKO) collected or which were made available by several collections. Additional locality records and data on life coloration were obtained from photographs and field observations. We also

describe aspects of the histology of the hypertrophied lips, and we discuss what is known about the natural history of *M. labrosus*. We call attention to the unusual distribution pattern of this species within Lake Malawi. Because *M. labrosus* lacks the synapomorphic melanin pattern of *Melanochromis* and its vertebral and gill-raker counts are outside the range in that genus, we describe a new monotypic genus for *M. labrosus*. Unique features of the head, jaws, and lips lie outside the range, not just of *Melanochromis*, but of all mbuna genera described to date; furthermore, it does not fit within the definition of any non-mbuna genus having species with hypertrophied lips. Given the unusual suite of characters of this species, we reappraise what constitutes an mbuna and assess what features, if any, support the assignment of “*M.*” *labrosus* to the mbuna. Finally, we provide a key to all currently recognized genera belonging to this distinctive group of Malawi cichlids.

Methods

Measurements were obtained with a digital caliper using reference points described in Oliver (1984); additional measurements follow Snoeks (1994, 2004). Counts are defined in the same sources. In view of the small number of specimens available for study, we made bilateral counts (scales, gill rakers, pectoral fin rays) on both sides of each fish, when possible, to obtain a better understanding of the range of variation. External head angles (Table 1) were measured with an extension-arm protractor on digital photographs taken parallel to the sagittal plane of the fish. These angles were determined relative to the lateral midline, an imaginary straight line passing anteriorly through the premaxillary symphysis and posteriorly through the point where the lower lateral line crosses the caudal fin fold at the posterior edge of the hypurals.

Two specimens of *M. labrosus* (see Material examined) were cleared and counterstained to show bone and cartilage using the method of Dingerkus & Uhler (1977). Lip tissues from two formalin-preserved specimens were embedded in JB-4 plastic (Polysciences, Inc., Warrington, PA, USA), sectioned at 7 μm , stained with toluidine blue, and examined microscopically using the method reported by Arnegard & Snoeks (2001).

We also made vertebral counts in *M. labrosus* and a large number of other mbuna species. These

counts included the element composed of the fused first preural centrum and first ural centrum (counted as one). Vertebral counts were made using radiographs provided by the BMNH or made at the AMNH and ANSP, although cleared and stained material was also used in a limited number of cases.

Institutional abbreviations. AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; BMNH, Natural History Museum, London; CUMV, Cornell University Museum of Vertebrates, Ithaca, New York; FRUMB, Fishery Research Unit collection, Monkey Bay, Malawi; MRAC, Musée Royal de l'Afrique Centrale, Tervuren; USNM, National Museum of Natural History, Washington, D.C.; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Abbreviations used in Material examined and Comparison material sections. c&s, cleared and stained; hist, lip tissue stained and sectioned for histological examination; m, measurements and counts done; r, radiographed; * indicates SL as measured from radiographs.

Abactochromis, new genus

Type species. *Melanochromis labrosus* Trewavas, 1935: 79.

Diagnosis. A putative member of the mbuna group (see Discussion) distinguishable from all other mbuna genera by having strongly hypertrophied, papillose, medially lobate lips, a large head at least 40 % SL in individuals of > 50 mm SL, and premaxillary pedicel (ascending process) > 35 % HL. Several non-mbuna haplochromine species endemic to Lake Malawi resemble *Abactochromis* in having enlarged and often lobate lips, but all can be readily distinguished as follows. *Placidochromis milomo* has 30-31 total vertebrae (vs. 28-29 in *Abactochromis*), 9-10 segmented anal-fin rays (vs. 7-8), four broad black vertical bars below the dorsal-fin base (vs. 6-7 narrow subdorsal bars, when not obscured), and attains at least 190 mm SL (vs. ~120 mm). *Otopharynx pachycheilus* has a longer pectoral fin (38-44 % SL vs. 19-27 in *Abactochromis*), shorter premaxillary pedicel (24-35 % HL vs. 36-46), color pattern of three lateral

spots (vs. vertical bars with no lateral spots), and known depth range of 78 to 135 m (vs. 0 to 30 m). *Cheilochromis euchilus* has 30-31 total vertebrae (vs. 28-29), head and jaws not laterally compressed (vs. distinctly compressed), and color pattern of 2-3 horizontal stripes (vs. narrow bars with no horizontal stripes). *Chilotilapia rhoadesii* has 31 total vertebrae (vs. 28-29), thickened lips lacking median lobes (vs. strongly lobate medially), adult oral teeth specialized for crushing gastropod mollusks by being robust and with crowns shaped like grains of wheat, blunt, recurved, and grooved on their outer surface (vs. oral dentition not similarly specialized), head and jaws not laterally compressed (vs. compressed), and color pattern with 2-3 horizontal stripes (vs. narrow bars with no horizontal stripes). *Electochromis* spp. have 30 total vertebrae (vs. 28-29), 10-11 segmented dorsal-fin rays (vs. 7-9), thickened lips lacking median lobes (vs. with prominent median lobes), some submolariform posteromedian pharyngeal teeth (vs. posteromedian teeth slightly enlarged but their crowns laterally compressed), and color pattern of vertical bars alternating with dark spots along dorsum (vs. bars only). *Lichnochromis acuticeps* has 32 total vertebrae (vs. 28-29), thickened lips lacking median lobes (vs. with prominent median lobes), and color pattern with oblique stripe from nape to base of caudal fin (vs. no oblique stripe). (Data on genera other than *Abactochromis* are from Eccles & Trewavas, 1989 and Arnegard & Snoeks, 2001, supplemented by our own observations; see Comparison material.)

See also Comparisons with other mbuna genera (in Discussion, below).

Etymology. From the Latin “abactus”, driven away, banished, expelled; and “chromis” (widely used as a root in generic names of cichlids, especially haplochromines). The name alludes both to the solitary, wandering, apparently nonterritorial habits of living individuals, and to our removal of this species from the genus in which it was originally described, where it has mistakenly remained for 75 years. Gender masculine.

Twelve indigenous names have been recorded for this species (Ambali et al., 2001), of which the most frequent is Nyamlepetu (in the Tonga language). The same name is among those collected for *Placidochromis milomo* and *P. johnstoni*.

Description. See species description (below).

Abactochromis labrosus (Trewavas)

(Figs. 1-2)

Melanochromis labrosus Trewavas, 1935: 79*Haplochromis labrosus*: Loiselle, 1978; Merritt, 1978;
Adler, 1979*Cyrtocara labrosa*: Mayland, 1982: 39, 47, 152

Material examined. 12, 42.0-115.0 mm SL. BMNH 1935.6.14:321, holotype, 1 (m, r), 42.0 mm SL; Deep Bay [now Chilumba], Lake Nyasa; C. Christy, 1925. – YPM 15188, 2 (m, r), 54.8-82.0 mm SL; Malawi: Nkhata Bay, tip of peninsula between N and S bays, 15-27 m depth; M. K. Oliver, K. R. McKaye, T. D. Kocher, 23 Jul 1980. – YPM 15189, 1 (m, r), 115.0 mm SL; Malawi: Nkhata Bay, off S edge of S bay, 6-45 m depth; M. K. Oliver, K. R. McKaye, T. D. Kocher, 24-25 Jul 1980. – YPM 21603, 2 (m), 77.1-84.4 mm SL; Malawi: Nkhata Bay, mid S bay near edge drop-off, 8-12 m depth; M. K. Oliver, K. R. McKaye, T. D. Kocher, 25 Jul 1980. – YPM 21602, 1 (m, r), 78.0 mm SL; Malawi: Likoma Island; T. E. Davies, Aug 1973. – AMNH 221548, 1 (m, c&s), 75.3 mm SL; Malawi: Nkhata Bay, north bay along peninsula 15 m from tip, 5-15 m depth; M. K. Oliver, K. R. McKaye, T. D. Kocher, D. S. C. Lewis, 21 Jul 1980. – MRAC 99-041-P-1364,



Fig. 1. *Abactochromis labrosus*, BMNH 1935.6.14:321, holotype, 42.0 mm SL; as photographed by MKO in 1972. Scale bar 10 mm.

1 (m, hist, r), 83.2 mm SL; Mozambique: Likwanje Reef, bay S of Luaice River, 4.9-5 m depth, 13°14.33' S 34° 48.89' E; "G. B. M.", 28 May 1998. – MRAC 164900, 1 (m, r), 90.4 mm SL; Mozambique: Nyassa district, vicinity of Vila Cabral; M. Costa, Feb 1956. – MRAC 99-041-P-1323, 1 (m, hist, c&s), 114.0 mm SL; Mozambique: Tchulutcha Reef, in front of Metangula, 34-29 m depth, 12°42.19' S 34°47.46' E; "G. B. M.", 25 May 1998. – BMNH unregistered when seen in 1972, 1 (r), 92.0 mm SL*; country unknown: Lake Malawi.

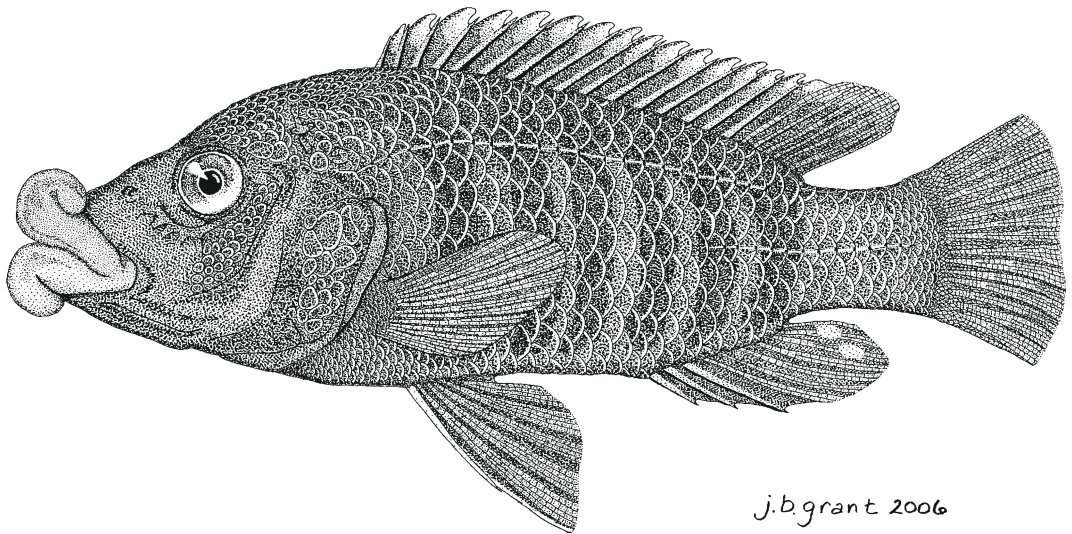
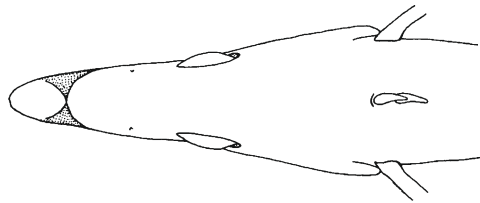


Fig. 2. *Abactochromis labrosus*, YPM 21602, male, 78.0 mm SL (Likoma Island). Inset: head in dorsal view. Scale bar 20 mm.

Diagnosis. As for genus.

Original description. Trewavas (1935) gave only the following brief description of her new species *Melanochromis labrosus*, which was contained in a couplet of her synoptic key: "Lips produced into pointed lobes; diameter of eye $3\frac{1}{3}$ in length of head; 13 gill rakers on lower part of anterior arch; maxillary not extending to below eye; lower jaw $2\frac{2}{7}$ in length of head." She noted that the single [holotype] specimen "of 54 mm." [total length] was in the collection made by Cuthbert Christy in 1925 and was from Deep Bay, a locality now known as Chilumba ($10^{\circ}27' S$ $34^{\circ}16' E$) in Malawi (Fig. 3). No illustration was provided.

The holotype, at 42.0 mm SL, remains even today the smallest known individual of the species. When examined by MKO in 1972 (Fig. 1), its coloration was uniform light brown except for dark brown lip lobes. It was missing the first gill arch on the left side, the lower pharyngeal bone, several upper jaw teeth, and a number of anterior scales on the upper part of the lateral line on the left side.

Description. Morphometric and meristic data are given in Tables 1 and 2.

Body rather deep (its depth at least 33 % SL); body and head laterally compressed (head width ~34-42 % head length). Head large, its length 40-43 % SL in all specimens >50 mm SL. Mouth large, terminal. Jaws long, lower jaw 45-55 % HL; lower jaw usually projecting slightly. Snout and jaws laterally compressed, head wedge-shaped when seen from above (Fig. 2).

Lips conspicuously hypertrophied, each with a prominent, recurved, median lobe (Fig. 2). Lips containing numerous simple, Type III taste buds (Reutter et al., 1974); 84-136 taste buds per mm^2 (in the two specimens examined histologically) in the anterior-lateral to medial portions of the upper and lower lips (Fig. 4).

Outer jaw teeth small, slender, slightly incurved, buried to tips of crowns in thickened oral mucosa; larger anterior teeth gradually grading in size to smaller ones laterally and posteriorly; posterior teeth not enlarged relative to lateral teeth (Fig. 5); anterior teeth erect, not procumbent, with intermixed unicuspid and very unequally bicuspid crowns (bicuspid less frequent in larger specimens) (see Figs. 6a-b); lateral and posterior teeth nearly all unicuspid. Inner tooth rows separated by distinct space from outer teeth;

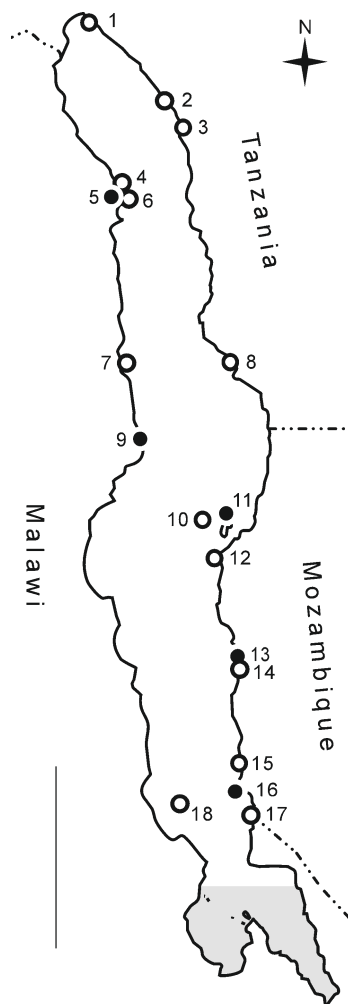
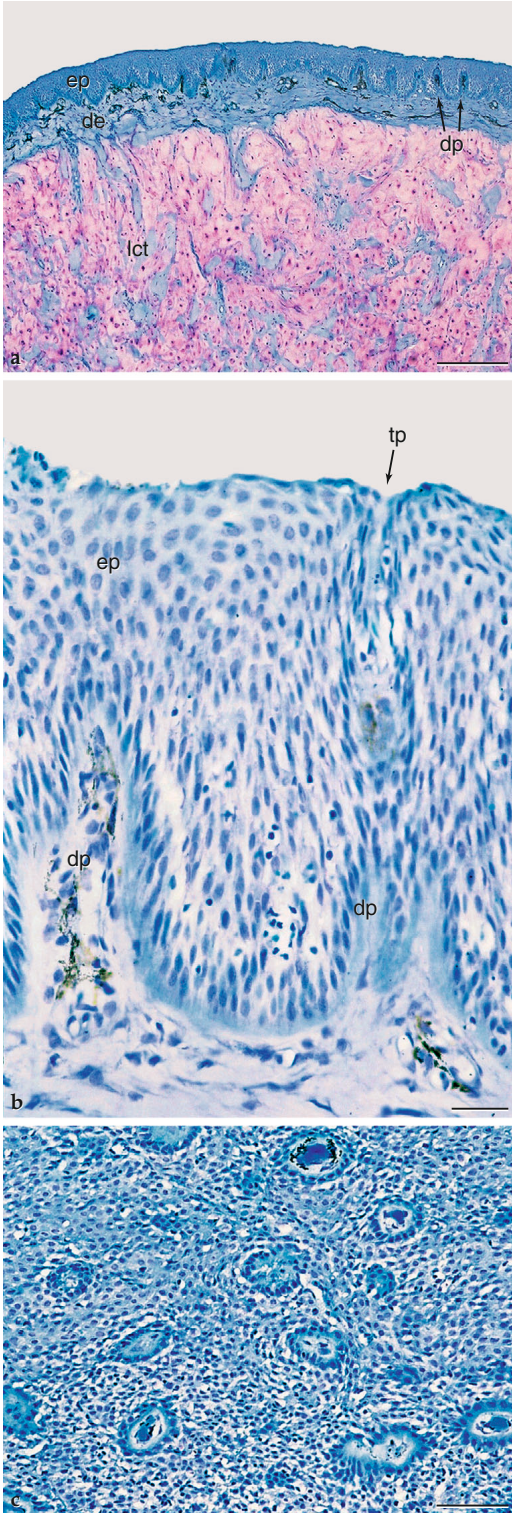


Fig. 3. Lake Malawi showing localities where *Abactochromis labrosus* has been observed. Gray area indicates shallow southern arms in which *A. labrosus* is absent. ● specimens examined; ○ published underwater photographs (Konings, 2001b), except as noted. 1, Ikombe (underwater photograph, A. Konings, in litt., 14 Nov 2005); 2, Makonde (underwater photograph, DeMason, 1995); 3, Lupingu (underwater photograph, Spreinat, 1995); 4, Chitande Island; 5, Chilumba (=Deep Bay, type locality); 6, Katala Island; 7, Mara Rocks; 8, estimated locality "just north of Mbamba Bay" (underwater photograph, A. Spreinat, in litt., 31 May 2007); 9, Nkhata Bay; 10, Linganjala Reef and Mkanila Bay, Chisumulu Island (underwater photographs, A. Konings, in litt., 14 Nov 2005); 11, Likoma Island; 12, Nkwichi Lodge (underwater observations, G. F. Turner, in litt., 16 Jun 2004); 13, Chilucha (or Tchulutch) Reef; 14, N'kolongwe; 15, Likwanje Reef, Chilolo (or Tchilouelo); 16, estimated locality of MRAC 164900; 17, Gome; 18, Mbenji Island. Scale bar 100 km.



inner teeth very small, tricuspid with middle cusp longest; arranged in 2-4 irregular rows in upper, 1-3 in lower jaw. Lower pharyngeal bone (Fig. 7) Y-shaped, rather lightly built. Lateral edges of dentigerous surface concave. About five postero-medial teeth (2-3 on each side) somewhat enlarged relative to others, but laterally compressed and cuspidate, not molariform.

Gill rakers of outer gill arch (Fig. 6c) slender and of moderate length except for short rakers ventrally on ceratobranchial. Rakers unbranched with occasional exceptions that may be anvil-shaped, shallowly or deeply bifurcated, or (several ceratobranchial rakers near angle with epi-branchial in 114.0 mm SL specimen) roughly quadrate and with as many as six points. Rakers lightly pigmented with scattered melanophores.

Scales ctenoid on flanks and caudal peduncle. Lateral line discontinuous, two sections separated by 2 scale rows on posterior body, upper section not kinked downward posteriorly. Sixteen scales around caudal peduncle. Squamation extending onto caudal fin along fin rays, covering basal 40-75 % of middle rays and basal 60-100 % of upper and lower lobes. Scale coverage on caudal fin increasing with fish length, covering fin membrane and markedly stiffening caudal fin in large individuals.

Cranium with ethmovomerine block angled $\sim 40^\circ$ relative to parasphenoid in single specimen examined (Fig. 8). Rostral tip of vomer not swollen. Supraoccipital crest high. Suspensorium deep; endopterygoid suturally united with metapterygoid (Fig. 5). Premaxillary ascending process (i.e., pedicel) long, $\sim 25\%$ longer than alveolar process (Fig. 5). Preoperculum with 7, anguloarticular with 2, and dentary with 5 lateralis foramina (Fig. 5). Infraorbital bones consisting of lachrymal with 5 lateralis foramina (4 neuromasts); infraorbitals 2 through 6 tubular, each with 2 foramina

◁ **Fig. 4.** *Abactochromis labrosus*, MRAC 99-041-P-1323, 114.0 mm SL; internal lip anatomy. **a**, Sagittal section showing numerous taste buds subtended by dermal papillae; scale bar 0.25 mm. **b**, Magnified sagittal section through a taste bud (on the right), showing its dermal papilla and taste pore; scale bar 25 μm . **c**, Section tangential to surface of lip showing spacing and distribution of dermal papillae; scale bar 50 μm . All sections from left side of lower lip (anterior-lateral region exposed to outside environment). Abbreviations: **de**, dermis; **ep**, epidermis; **dp**, dermal papilla; **lct**, loose connective tissue; **tp**, taste pore.

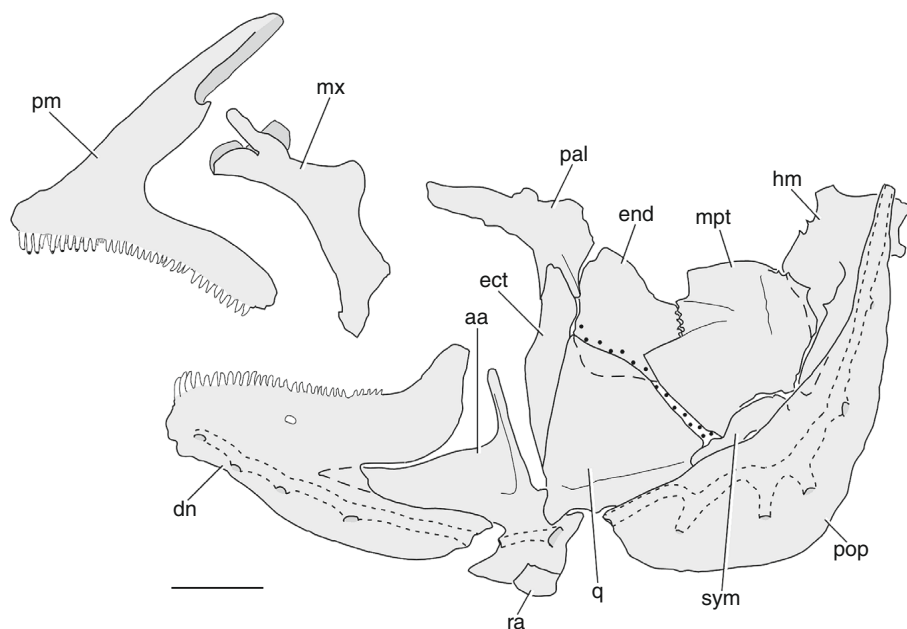


Fig. 5. *Abactochromis labrosus*, MRAC 99-041-P-1323, 114.0 mm SL (right side reversed); suspensorium and jaws; upper part of hyomandibula drawn from AMNH 221548, 75.3 mm SL. Abbreviations: **aa**, anguloarticular; **dn**, dentary; **ect**, ectopterygoid; **end**, endopterygoid; **hm**, hyomandibula; **mpt**, metapterygoid; **mx**, maxilla; **pal**, palatine; **pm**, premaxilla; **pop**, preopercular; **q**, quadrate; **ra**, retroarticular; **sym**, symplectic. Heavy dots indicate cartilage. Scale bar 5 mm.

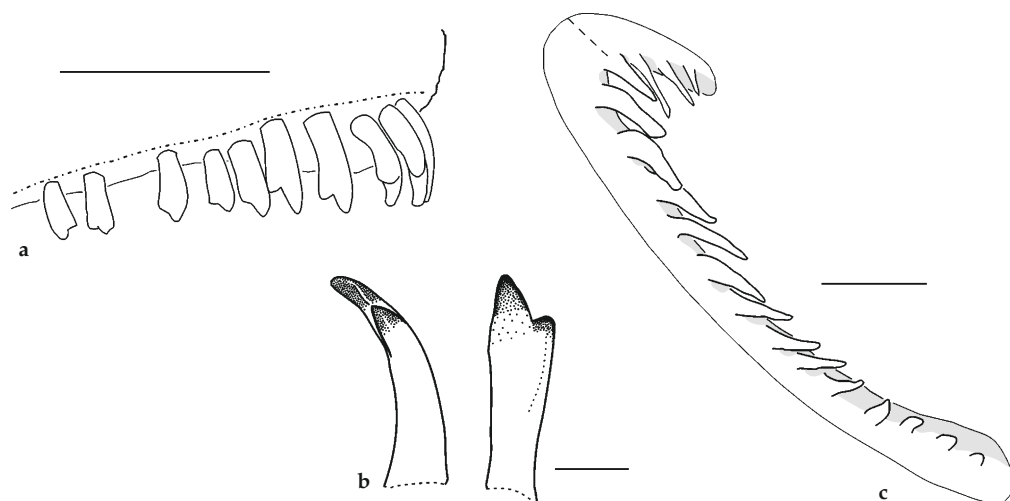


Fig. 6. *Abactochromis labrosus*, BMNH 1935.6.14:321, holotype, 42.0 mm SL; **a**, anterior outer teeth of right side of upper jaw in lateral view; scale bar 1 mm; **b**, anteriormost outer tooth of right side of lower jaw in right lateral (left) and lingual (right) views; scale bar 0.5 mm; **c**, gill rakers of right outer arch; scale bar 1 mm.

and 1 neuromast; infraorbitals 3+4 fused unilaterally in one specimen. One supraneural (predorsal) bone.

Modal vertebral count of 29 is lowest of any mbuna genus (Table 3).

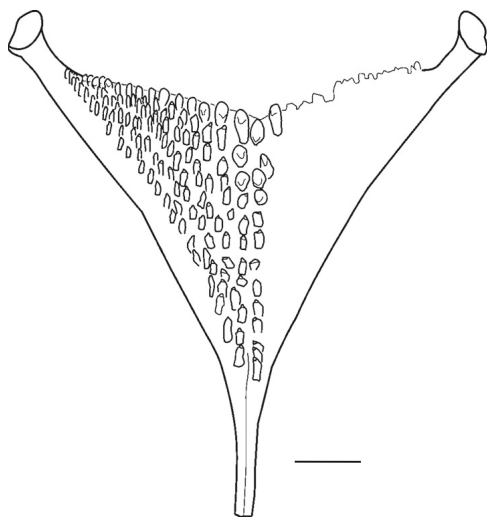


Fig. 7. *Abactochromis labrosus*, YPM 21602, 78.0 mm SL; lower pharyngeal bone. Teeth of right side and along midline are shown. Scale bar 1 mm.

Coloration in life. In females and nonbreeding males, body and fins (except pectoral) with variable, dark, muted ground coloration in life (usually dusky brown or gray, sometimes virtually black, rarely dull orange). Bars below dorsal fin or on caudal peduncle, or both, may be indistinct in living specimens (see Fig. 2). Males may be suffused with reddish or purplish flush over body. Pectoral fins with rays same color as body, membranes hyaline. Lips often palest part of fish. Dorsal fin lappets yellow to dull orange; margin of soft dorsal colored same as lappets, or distinctly brighter orange. Blackish submarginal band may be evident in dorsal fin, particularly obvious when viewed in front of a light background (Fig. 9a). Sexually active males (Fig. 9b) bluish-gray to purplish-gray on lips, upper head surfaces, and body; dark vertical bars strongly contrasting in such individuals; unpaired fins blackish brown except for margins; dorsal fin lappets pale blue-white, margin of soft dorsal pale blue with narrow orange edge; caudal and anal fins colored like soft dorsal; anal fin with two to four posteriorly placed, small, yolk-yellow to deep orange eggspots (Fig. 9c). A single individual of indeterminate sex with overall yellow-orange coloration was photographed at Chitande Island by A. Konings (Fig. 9d; see Discussion).

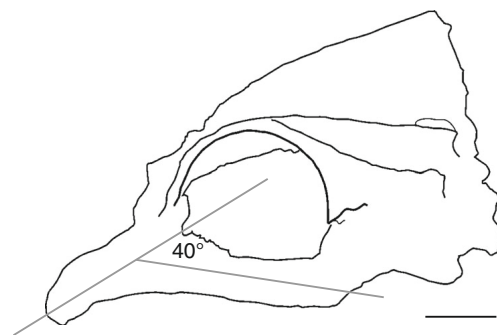


Fig. 8. *Abactochromis labrosus*, MRAC 99-041-P-1323, 114.0 mm SL; outline of neurocranium in lateral view. Superimposed gray lines show estimated angle of ethmovomerine block relative to parasphenoid. Scale bar 5 mm.

Coloration in preservative. Head, body, and fins are essentially uniform brown, ranging from darkish tan to deep chocolate. Melanin pattern composed of narrow vertical bars not wider than eye diameter, but often masked by dark ground coloration. Nuchal region with either one bar or none; 6 or 7 bars below dorsal-fin base; 1 or 2 on caudal peduncle. No horizontal stripes on body. Dark opercular spot and lachrymal stripe evident in some individuals.

Discussion

Autapomorphies of *Abactochromis*. Ultimately, the validity of any genus can only be tested with reference to a phylogeny. The lack of a corroborated phylogeny of the mbuna precludes resolution of sister-group relationships of *Abactochromis* with other mbuna at this time. It is possible nonetheless to identify apparent autapomorphies of this genus. Comparison of *Abactochromis* with all other mbuna genera and *Astatotilapia calliptera* (a non-endemic haplochromine considered closely related to the stem of the Lake Malawi flock; e.g., Trewavas, 1949; Fryer & Iles, 1972; Moran et al., 1994; Loh et al., 2008) leads us to postulate that the following characters (among others) are autapomorphies of *Abactochromis*:

1. endopterygoid and metapterygoid suturally united (Fig. 5);
2. premaxillary pedicel (ascending process) long relative to head length, >35 % HL (Table 1);
3. head enlarged (Fig. 2), at least 40 % SL in fish >50 mm SL (Table 1);

4. lips hypertrophied and produced into prominent median lobes (Fig. 2).

Most or all of these characters occur in other cichlids, but none is found, to our knowledge, in any other mbuna.

Comparisons with other mbuna genera. *Abactochromis* is easily distinguished from *Melanochromis* by the plesiomorphic melanic color pattern of vertical bars (vs. sexually dimorphic horizontal stripes synapomorphic for *Melanochromis* spp.; Meyer & Foerster, 1984; Trewavas, 1984; but see Hale et al., 1998 for an exception and Tawil, 2002 for a contrasting opinion), as well

as by the hypertrophied, lobate lips (vs. lips normal in *Melanochromis*) and the strongly compressed head and beaklike jaws with long premaxillary pedicel (vs. head not laterally compressed, jaws not beaklike, premaxillary pedicel shorter than alveolar process in *Melanochromis*). As noted below, with available information, vertebral counts are non-overlapping in the two genera (28-29 vs. 30-33 in *Melanochromis*).

Abactochromis most closely resembles *Labidochromis* among genera of mbuna (see also Loisel, 1978). Species in both genera have a narrow snout and narrow, pointed jaws (as viewed from above). In *Labidochromis*, however, the mouth is much

Table 1. Morphometric characters of *Abactochromis labrosus*. N, number of non-type specimens measured; S.D., standard deviation.

	holotype	non-types			
		N	mean	S.D.	range
Standard length (mm)	42.0	10	85.4	17.9	54.8-115.0
Head length (mm)	15.1	10	35.6	7.7	23.0-48.9
In percent of standard length					
Head length	36.0	10	41.6	8.8	40.0-42.9
Body depth	33.3	10	35.7	12.7	33.7-37.6
Dorsal fin base length	53.6	10	50.2	16.4	48.2-53.7
Predorsal length	38.1	10	43.3	14.5	42.1-46.7
Prepectoral length	36.9	9	42.6	11.7	40.9-44.0
Prepelvic length	–	9	48.4	16.7	46.0-50.7
Preanal length	–	8	73.1	13.2	71.1-75.1
Belly length	–	9	26.9	10.0	25.0-28.2
Anal fin base length	–	9	17.0	9.1	15.8-18.5
Caudal peduncle length	14.0	10	12.7	9.7	11.1-14.6
Caudal peduncle depth	13.1	10	13.1	5.3	12.5-13.9
Pectoral fin length	25.2	10	24.2	22.5	19.5-26.8
Pelvic fin length	24.5	10	26.7	16.7	23.3-28.9
In percent of head length					
Head width	39.1	10	36.8	23.7	34.5-42.1
Interorbital width	17.2	10	18.0	11.6	16.1-19.3
Snout length	29.8	10	43.0	21.9	39.6-46.8
Snout width	25.2	10	25.3	16.6	23.5-28.6
Lower jaw length	46.4	10	49.2	27.1	44.8-54.9
Lower jaw width	23.8	10	25.8	40.4	20.1-30.8
Premaxillary pedicel length	35.8	10	40.7	26.1	36.3-45.6
Upper jaw length	31.8	10	36.5	28.8	32.2-40.9
Cheek depth	20.5	10	21.5	26.4	18.1-25.8
Orbit length	31.1	10	21.4	21.4	18.4-25.2
Vertical eye diameter	–	8	19.9	19.1	16.7-22.2
Preorbital (lacrimal) depth	17.2	10	20.0	11.8	17.4-21.5
Postorbital head length	41.1	10	37.9	12.7	35.0-39.9
Angular measurements (degrees)					
Premaxillary pedicel	–	10	31.9	3.0	27-36
Interorbital	30	10	35.9	8.9	22-49
Nape	–	10	14.7	3.6	8-21
Lower jaw (lower edge)	40	10	30.0	3.7	24-35

smaller, with premaxillary pedicel much shorter relative to head length [20.8-35.7 % HL in the 16 species with proportional measurements (here converted to percentages) reported in Lewis (1982), with means for each species of 26.3-31.3 %, vs. premaxillary pedicel 35.8-45.6, mean 40.7 % HL in *Abactochromis* individuals > 50 mm SL]; the jaws are shorter [lower jaw 19.6-35.7 % HL, with means for each species of 25.6-31.3 % (Lewis, 1982), vs. lower jaw 44.8-54.9, mean 49.2 % HL in *Abactochromis*]; the anterior upper jaw teeth in *Labidochromis* are markedly enlarged relative to lateral teeth and often procumbent, vs. anterior

teeth neither enlarged nor procumbent in *Abactochromis* (Figs. 5, 6a); and the outer teeth of the upper jaw are less numerous [11-21 on each side (Lewis, 1982), vs. 18-30 in *Abactochromis*]. Gill rakers 7-11 in *Labidochromis* spp., vs. 11-14 (median 14) in *Abactochromis* (this median gill raker count is the highest of any mbuna genus except, perhaps, *Cynotilapia*). In discussing the possible "affinities" of *Labidochromis*, Lewis (1982: 257-259) made no mention of "*Melanochromis labrosus*".

Abactochromis shares two characters with *Labidochromis* and no other mbuna genus: the premaxillary pedicel is longer than the premaxil-

Table 2. Meristic characters of *Abactochromis labrosus*. N, when not enclosed in brackets, indicates number of specimens counted (for counts made on one side); square brackets enclose total number of sides counted for bilateral structures if more than one side was counted on some specimens.

	holotype	nontypes			
		N	median	1 st -3 rd quartiles	range
Scales					
Lateral line scales	29	[17]	31	30-31	30-32
Upper lateral line scales	21	[17]	21	20-22	18-22
Lower lateral line scales	7	[17]	10	8-11	7-12
Lateral line scales on caudal fin	2	[17]	2	1-2	0-3
Upper transverse line scales	–	[12]	6	5.5-7	5-8
Lower transverse line scales	–	[12]	8	7-9	6-10
Predorsal scales	–	9	19	18-20	15-21
Prepelvic scales	–	8	23.5	22-25	21-29
Belly scales	–	7	25	25-27	21-30
Cheek scales	5	[14]	4	4-5	3-6
Scales between pectoral and pelvic fin bases	6-7	[11]	8	7-9	7-9
Fins					
Dorsal spines	16	11	16	16-16	15-17
Dorsal segmented rays	8	11	9	8-9	7-9
Dorsal total elements	24	11	25	24-25	23-25
Anal spines	3	11	3	3-3	3-3
Anal segmented rays	7	11	7	7-7	7-8
Pectoral rays	–	[17]	14	14-15	14-15
Gill rakers					
Epibranchial	3	[20]	4	4-5	3-6
Angle	1	[20]	1	1-1	1-1
Ceratobranchial	13	[20]	14	12.5-14	11-14
Total	17	[20]	19	18-20	15-21
Teeth					
Outer upper jaw teeth one side	–	[20]	24	22.5-27	18-30
Number inner rows upper jaw	2	10	3	2-4	2-4
Number inner rows lower jaw	2	9	3	2-3	1-3
Lower pharyngeal teeth posterior edge	–	3	34	31-38	31-38
Lower pharyngeal teeth median column	–	[6]	11	11-12	10-13
Lower pharyngeal teeth oblique count	–	[4]	7	7-7.5	7-8
Vertebrae					
Abdominal	13	9	13	13-14	13-14
Caudal	16	9	16	15-16	15-16
Total	29	9	29	29-29	28-29

lary alveolar process (Fig. 5), and the alveolar processes of both the premaxilla and the dentary have reduced lateral curvature, giving an acute angle to the symphysis of the left and right sides of the upper (Fig. 2 inset) and lower jaws. It is unclear if these resemblances are due to homoplasy (so that these characters are autapomorphies of both genera), or to homology (in which case these characters are synapomorphies of the two genera suggesting they are sister groups).

Although the lips of *Abactochromis labrosus* are hypertrophied and lobate, similar specializations have occurred many times in cichlids, and this is not our primary reason for proposing a new genus (even though these specialized lips are diagnostically valuable within the mbuna). With its large, compressed head, long, beaklike jaws, characteristic vertebral and gill raker counts, and unusual ecology, *Abactochromis* is much more distinctive than some other genera of Lake Malawi cichlids such as *Maylandia* (Meyer & Foerster, 1984) and *Mchenga* (Stauffer & Konings, 2006). Indeed, over a quarter century ago, Lewis (in Ribbink et al. 1983: 209) already considered that *Melanochromis labrosus* warranted the creation of a new genus, although he has never published one; Konings (1998) also opined that this species requires its own genus.

Vertebral counts. Eccles & Trewavas (1989: 21) state that mbuna have 30 or 31 vertebrae. We surveyed the number of vertebrae in the mbuna (272 individuals representing all genera) and found considerably more variation than this, with total counts ranging from 28 to 33 (Table 3). The two mbuna individuals we found with 28 vertebrae (13 abdominal and 15 caudal) were a *Labidochromis pallidus* (AMNH uncat.) and an *A. labrosus* (BMNH uncat.). The modal (and maximum) count in *A. labrosus* is 29 (13+16 or 14+15), the lowest modal total count of any mbuna species we examined (excepting only *Pseudotropheus minutus*, of which we saw only one specimen, also with 29 vertebrae). By contrast, in the six species of *Melanochromis* we examined, total counts range from 30 to 33 (Table 3). In the non-endemic haplochromine *Astatotilapia calliptera*, considered phylogenetically close to the stem of the Lake Malawi haplochromine flock (including mbuna), we found 29 vertebrae in 2 specimens (13+16) and 30 in 4 (13+17 in 3, 14+16 in 1). Therefore, the low counts in *Abactochromis* appear plesiomorphic relative to the higher modal counts



Fig. 9. Aspects of melanin patterning and coloration of *Abactochromis labrosus*; **a**, dorsal fin (YPM 15189, live male, 115.0 mm SL, Nkhata Bay; photo by MKO), showing dark submarginal band, photographed against a light-colored background; **b**, male in breeding coloration (Mara Rocks; photo by A. Konings); **c**, anal fin of a male, showing hyaline (i. e., de-pigmented) ring around each ocellate spot (aquarium trade specimen; photo by A. Spreinat); **d**, putative orange morph (Chitande Island; sex undetermined; photo by A. Konings).

in all other mbuna genera, suggesting the possibility that *Abactochromis* might be a basal mbuna.

Distribution and natural history. Although *A. labrosus* occurs widely in Lake Malawi, it appears to be rare at any reported locality. It is seldom encountered by observers diving with

SCUBA on its preferred habitat: rocky shoreline. During general collecting of small rocky shore fishes for export to the aquarium trade, only five to ten *A. labrosus* (out of ~75,000 cichlids) are encountered per year (S. Grant, pers. comm., June 1999).

The documented depth range of *A. labrosus* extends from the surface to roughly 30 m. G. F. Turner (pers. comm.) observed two individuals on the Mozambique shore at Nkwichi Lodge beach, just south of Cobue and Mara Point (see Fig. 3 for this location and all other reported sites of observation or collection). One, a large black individual, was in extremely shallow water (<30 cm) near a small patch of reeds; it rapidly disappeared under rocks (in litt., 16 Jun 2004). Ribbink et al. (1983: 208, fig. 54, table 29) found

A. labrosus (as *Melanochromis labrosus*) to occur only to a depth of 8 m at Likoma Island and shallower than that at Mbenji Island. These authors noted that “[i]t usually remains hidden among the rocks and appears to be rare. However, a rotenone sample at Maingano [on Likoma Island] revealed that there are more *M. labrosus* among the rocks than indicated by transects and by observation”, although they did not elaborate upon this finding. Consideration of these remarks together with results of previous rotenone collections by one of us (MKO) indicates that densities of *A. labrosus* may be, in general, significantly underestimated in rocky habitats on the basis of observation and SCUBA-assisted nettings. At Nkhata Bay in 1980, MKO and party did not observe this species during several diurnal dives

Table 3. Vertebral counts in representative species of mbuna genera, showing number of individuals with each count.

		abdominal				caudal				total					
		13	14	15	16	15	16	17	18	28	29	30	31	32	33
<i>Abactochromis</i>	<i>labrosus</i>	7	3	–	–	4	6	–	–	1	9	–	–	–	–
<i>Cyathochromis</i>	<i>obliquidens</i>	4	6	–	–	–	7	2	1	–	2	6	2	–	–
<i>Cynotilapia</i>	<i>afra</i>	–	3	3	–	4	2	–	–	–	1	5	–	–	–
<i>Genyochromis</i>	<i>mento</i>	1	9	–	–	–	–	9	1	–	–	1	8	1	–
<i>Gephyrochromis</i>	<i>lawsii</i>	–	1	–	–	–	–	1	–	–	–	–	1	–	–
	<i>moorii</i>	–	3	–	–	–	–	2	1	–	–	–	2	1	–
<i>Iodotropheus</i>	<i>sprengeriae</i>	–	5	–	–	1	4	–	–	–	1	4	–	–	–
<i>Labeotropheus</i>	<i>fuellborni</i>	–	9	6	–	–	2	3	–	–	–	6	9	–	–
	<i>trewavasae</i>	–	–	2	1	–	–	3	–	–	–	–	–	2	1
<i>Labidochromis</i>	<i>caeruleus</i>	–	1	–	–	–	1	–	–	–	–	1	–	–	–
	<i>freibergi</i>	1	–	–	–	–	–	1	–	–	–	1	–	–	–
	<i>pallidus</i>	39	16	–	–	1	35	19	–	1	19	35	–	–	–
	<i>shiranus</i>	1	–	–	–	–	–	1	–	–	–	1	–	–	–
	<i>textilis</i>	–	2	–	–	–	1	1	–	–	–	1	1	–	–
	<i>vellicans</i>	8	22	–	–	2	22	6	–	–	6	22	2	–	–
<i>Maylandia</i>	<i>elegans</i>	–	3	–	–	–	1	1	1	–	–	1	1	1	–
	<i>livingstonii</i>	–	3	1	–	–	2	2	–	–	–	2	2	–	–
	<i>zebra sensu lato</i>	–	–	7	2	4	5	–	–	–	–	3	5	1	–
<i>Melanochromis</i>	<i>auratus</i>	–	2	3	–	–	3	2	–	–	–	–	5	–	–
	<i>joanjohnsonae</i>	1	–	–	–	–	–	1	–	–	–	1	–	–	–
	<i>johannii</i>	–	19	18	–	2	18	17	–	–	–	7	27	3	–
	<i>melanopterus</i>	–	4	21	1	–	10	16	–	–	–	–	14	11	1
	<i>simulans</i>	–	–	1	–	–	1	–	–	–	–	–	1	–	–
	<i>vermivoorus</i>	–	1	1	–	–	1	1	–	–	–	–	2	–	–
<i>Petrotilapia</i>	sp.	–	6	3	–	–	8	1	–	–	–	2	7	–	–
<i>Pseudotropheus</i>	<i>elongatus</i>	–	–	4	1	–	2	3	–	–	–	–	1	4	–
	<i>lucerna</i>	–	1	–	–	–	–	–	1	–	–	–	–	1	–
	<i>minutus</i>	–	1	–	–	1	–	–	–	–	1	–	–	–	–
<i>Tropheops</i>	<i>tropheops</i>	–	–	15	–	3	11	1	–	–	–	3	11	1	–

and transects swum on rocky shores. During the same collecting trip to Nkhata Bay, however, emulsified rotenone was set on rocky shore while diving at three collection stations (recorded depths of application: approx. 9 m; < 15 m; and 17-20 m), resulting in the capture of five *A. labrosus* specimens, with at least one from each station (respectively: YPM 21603, AMNH 221548, and YPM 15188). Thus, this species is found to a depth of at least 17 m at Nkhata Bay. The deepest record for *A. labrosus* that we know of is from 29-34 m at Tchulutcha Reef, Mozambique (MRAC 99-041-P-1323, see Material examined). Given how infrequently it is seen and collected, the species might also occur deeper than this.

Although *A. labrosus* has been collected or seen by divers at numerous locations in Lake Malawi, it has never been documented in the two southern arms of the lake (Fig. 3). This is a striking observation – the southern part of the lake has been the focus of extensive collecting and diving efforts for half a century. For example, rotenone collections by MKO and colleagues (1980) on apparently suitable rocky shores at Mumbo Island (two stations), Domwe Island (two stations), and Thumbi Island West (one station) did not produce any specimens of *A. labrosus*. This species is not reported from this area by Ribbink et al. (1983), nor included in a guide to the fishes of Lake Malawi National Park (Lewis et al., 1986). It is possible that *A. labrosus* formerly occurred on suitable rocky habitat patches in this Cape Maclear region of the lake and further south before an apparent, recent drop in lake level (estimated to have occurred approximately 18,000-10,700 years ago) shifted the south shore to a position north of today's two southern arms (reviewed in Sturmbauer et al., 2001). If so, *A. labrosus* may disperse less frequently across intervening habitats lying between rocky patches than two noteworthy rock-dwelling species (*Labeotropheus fuelleborni* and *Genyochromis mento*) with cosmopolitan distributions including the lake's southern arms (Arnegard et al., 1999). However, given its habit of wandering laterally along rocky shorelines, as described below, *A. labrosus* individuals may be more vagile within stretches of rocky shoreline than many other mbuna (Knight et al., 1999).

Assuming *Abactochromis* should best be placed operationally among the mbuna (as we will argue), *A. labrosus* is an unusual member of this

group in several respects. Males of many mbuna species defend conspicuous and stable territories which are clustered on rocky habitats (Holzberg, 1978; Marsh & Ribbink, 1985; Hert, 1992; Genner et al., 1999; Markert & Arnegard, 2007). In contrast, males of *A. labrosus* apparently do not defend fixed territories for feeding or breeding in any habitats visible to divers (Konings, 2001a). Rather, *A. labrosus* “appears to be a solitary fish” (Ribbink et al., 1983). Inevitably, only single individuals are rarely seen swimming slowly along the rocks, wandering from crack to crack (A. Konings, pers. comm.). An affinity for small crevices has also been noted from observations of aquarium specimens (Merritt, 1978). Spawning by *A. labrosus* has never been observed in the wild.

According to Konings (2001a), the laterally compressed body enables *A. labrosus* to enter narrow spaces between rocks in search of prey species (purportedly small mbuna and crustaceans), and the hypertrophied lips are used to seal off cracks in the rocks from which these prey are, thereby, more efficiently removed by suction. This speculated feeding mode was also reported by Ribbink et al. (1983). However, the lips of *A. labrosus* may be too delicate for this function in our opinion, and the biomechanics of feeding has yet to be studied in this species. Earlier, Fryer (1959) speculated that the soft lips of *A. labrosus*, in addition to those of *C. euchilus*, mediate the tactile detection of insect prey. In contrast, Loiselle reported that “preliminary studies ... disclosed no sensory tissue in the lips of *Haplochromis labrosus*” (in Merritt, 1978: 12).

Among haplochromine cichlids, internal lip anatomy has only been examined in detail in *O. pachycheilus* and now *A. labrosus*. Both species express rather high densities of taste buds in their lips (see Arnegard & Snoeks, 2001), suggesting the possession of an enhanced gustatory sense. Much like catfish barbels (Bardach et al., 1969; Atema, 1971), hypertrophied lips may allow these cichlid species not only to express higher densities of taste receptors but also to express them over a larger peri-oral field than would be possible with reduced lips. An enhanced gustatory system would likely facilitate prey detection by *A. labrosus* in dark cracks, crevices, and caves (cf. Schemmel, 1967). This hypothesized function of enlarged lips awaits functional and behavioral study in cichlid species expressing this trait.

What are the mbuna, and is *Abactochromis* a member of this group? Since being popularized by Fryer (1959), use of the term “mbuna” in the literature is often followed by its characterization as a group or assemblage (sometimes guild) of hundreds of species of largely herbivorous, often colorful, cichlids of relatively small size that dominate littoral rocky habitats in Lake Malawi. Although the feeding habits of *A. labrosus* remain to be formally investigated, this species certainly seems to prefer rocky habitats. However, mbuna co-occur on rocky shores with many non-mbuna, including species of *Protomelas*, *Aulonocara*, and *Otopharynx* in particular (Ribbink et al., 1983; Grant et al., 1987; Eccles & Trewavas, 1989; Konings, 2001a). In addition, not all mbuna are herbivores that feed on aufwuchs. One of the most notable exceptions, *Genyochromis mento*, is a morphologically specialized fin and scale eater (Ribbink et al., 1983). Moreover, *Cyathochromis obliquidens* lives exclusively in weedy environments away from rocks, while several other mbuna species strictly inhabit open sand (Ribbink et al., 1983; Turner, 1996).

To determine if the mbuna constitute a natural group it is necessary to ask: What, if any, are its unique phenotypic or genetic synapomorphies? Although Fryer & Iles (1972: 493) asserted “There is ample evidence to show that the Mbuna comprise a monophyletic group”, they adduced no specific characters in support of this view. Several phenotypic traits have been proposed by various authors as characteristic of this putative group vis-à-vis other haplochromine cichlids restricted in their distribution to Lake Malawi (and, in some cases, Lake Malombe and the upper Shire River). The proposed suite of traits includes: (1) small/minute scales on the chest and belly, transitioning abruptly to larger scales on the flank; (2) an asymmetry in ovary size (with the left ovary typically atrophied, presumably due to the reduced clutch sizes of mbuna); (3) a melanic submarginal band in the dorsal fin; (4) presence of certain polychromatic phenotypes; and (5) a relatively small number of true ocelli (versus a larger number of simple spots) in the anal fin (Trewavas, 1935; Fryer, 1959; Ribbink et al., 1983; Oliver, 1984; Konings, 2004). We review this morphological evidence below, and then consider (6) the few relevant molecular data that are available.

(1) In their key to the genera of Lake Malawi cichlids, Eccles & Trewavas (1989: 31) lump all

mbuna under the following description within a single couplet: “dentition usually specialised; chest scales small, with sharp transition in size between pectoral and pelvic fins”. Consistent with the inclusion of *A. labrosus* in the mbuna, we find that the size of its thoracic scales does appear abruptly smaller than those in neighboring body regions (Fig. 2). Among Lake Malawi cichlids, however, the transition in scale size in this body region can be difficult to categorize as abrupt or not, and we suspect that relative thoracic scale size is too variable to be systematically informative. Squamation patterns fitting the description by Eccles & Trewavas are also present in lineages of African cichlids outside Lake Malawi (Greenwood, 1979; Seehausen, 1996).

(2) We have not examined the ovaries of *A. labrosus* because of the rarity of specimens in collections. However, two pelagic genera of non-mbuna haplochromines from Lake Malawi (i. e., *Diplotaxodon* and *Rhamphochromis*) and an assemblage of colorful, herbivorous, rock-dwelling cichlids from Lake Victoria (the mbipi) are also reported to exhibit asymmetries in ovary size (Genner & Turner, 2005). Thus, it remains possible that ovarian size asymmetry is either a plesiomorphic trait for the mbuna, providing no morphological evidence for the monophyly of this group, or may have evolved convergently multiple times.

(3) Among Lake Malawi cichlids, a melanic submarginal band in the dorsal fin is, in general, most strongly developed in the mbuna, yet not all mbuna species exhibit a submarginal band. *Abactochromis labrosus* appears to exhibit a moderately well-developed submarginal band when this character is not obscured by overall dorsal fin coloration (Fig. 9a). Extensive photographic documentation of variation in living coloration and melanin patterns of Lake Malawi cichlids has demonstrated that several non-mbuna species (e. g., *Lethrinops auritus*, *Lethrinops* “aulonocara type”, *Mylochromis* “mollis gallireya”, *Otopharynx* “decorus mbuyu”) show more robust submarginal bands, at least in males, than does *A. labrosus* (Konings, 1990, 2001a-b, and in litt., 2 May 2010). Thus, presence of a submarginal band in the dorsal fin of *A. labrosus* is uninformative with respect to the affinity of this species to the mbuna.

(4) A polychromatism is a discrete, genetically based color polymorphism that is maintained within populations, rather than simply a by-product of general sexual dimorphism or age-

dependent phenotypic variation (Huxley, 1955; Roulin, 2004). A well-known polychromatism in cichlids involves a sex-linked color phenotype known as orange blotch (OB), occurring more frequently (but not exclusively) in females (Fryer, 1959; Fryer & Iles, 1972; Holzberg, 1978; Arnegard et al., 1999; Seehausen et al., 1999; Streebman et al., 2003; Konings, 2004; Roberts et al., 2009). OB morphs typically express dark blotches in a piebald (i. e., mottled) pattern on a body ground color that can range from a light, drab brown to orange, white, or (in males of some species) light blue. The “normal morph” (i. e., counterpart to the OB morph in the same population) lacks blotching. Depending on the species and population, normal (N) morphs can range from strongly barred to nearly lacking in bars. A second polychromatism involving orange (O) morphs without bars (or blotching) has also been distinguished in several cichlid lineages (Ribbink et al., 1983; Konings, 2004). Although similar in appearance to rare xanthochromatic (also called xanthistic) mutants in other fishes (e. g., Waschkewitz & Wirtz, 1990), O phenotypes in cichlids are thought of as “morphs” because they appear to be maintained in populations at higher frequencies than expected for xanthochromatic mutants, perhaps due to selective trade-offs like those hypothesized by Roberts et al. (2009). The same genetic mechanism that causes the pigmentation difference between OB and N also accounts for the difference between O and N (Roberts et al., 2009), yet the genetic basis underlying degree of blotchiness (e. g., OB vs. O) is not yet understood. Possible similarities between OB and O phenotypes in terms of genetic and developmental mechanisms have not yet been examined.

Within Lake Malawi, a xanthochromatic individual of a tilapiine cichlid, *Oreochromis karongae*, is shown by Turner (1996: 49), although we are aware of no definitive examples of xanthochromatic mutants published for the lake’s haplochromine species flock. Among members of the Malawi haplochromine cichlid radiation, both kinds of polychromatism (OB/N and O/N) appear to be restricted to the mbuna (Ribbink et al., 1983; Konings, 1990, 2001a-b, 2004). Nevertheless, such polychromatic phenotypes are notably absent in three speciose mbuna genera: *Petrotilapia*, *Labidochromis* and *Melanochromis*. Konings (2001a, 2004) discovered an apparent O morph of *A. labrosus* at Chitande Island (Fig. 9d). This individual’s yellow-orange coloration resembles that

of other mbuna previously described as O morphs, and its color appears richer than that of the xanthochromatic *O. karongae* photographed by Turner (1996). In addition, the extremely small number of *A. labrosus* ever observed at this site, or elsewhere in the wild, suggests that this single case of a yellow-orange individual may actually reflect a phenotype that is maintained in the Chitande population at a higher frequency than one might expect for recurrent xanthochromatic mutants. While additional study of color variation is needed to understand the origin, frequency, and selective consequences of the orange phenotype in *A. labrosus*, we tentatively interpret Konings’s finding as a persistent polychromatism. On the basis of this observation, *A. labrosus* may have a closer phylogenetic relationship to one of the mbuna lineages exhibiting polychromatism than to any of Lake Malawi’s non-mbuna haplochromines.

(5) Males of many mouth-brooding cichlids express prominent anal fin spots that are thought to facilitate, or guide, buccal fertilization (Wickler, 1962). When each of these spots is bordered by translucent patches, a complete depigmented (i. e., hyaline) ring, or (in some opinions) a darkly pigmented ring, they are referred to as “true ocelli” or “ocellate spots” (Oliver, 1984; Genner & Turner, 2005). To human observers, the depigmented (or darkly pigmented) surrounding ring gives ocelli the appearance of three-dimensional relief. Some haplochromine cichlids possess many, simple anal fin spots, whereas others express a smaller number of ocellate spots in the anal fin (Fig. 10). Although a complete survey is needed, it appears that primarily the mbuna and *Astatotilapia calliptera* exhibit true ocelli in their anal fins within the Lake Malawi cichlid species flock (Oliver, 1984). However, mbuna differ from *A. calliptera* in having ocelli irregularly positioned in the posterior half of the anal fin, whereas ocelli are arranged into a longer and more regular row (i. e., nearly linearly) in the anal fin of *A. calliptera* (Fig. 10). Based on the best available photographic evidence (Fig. 9c and all other examples we examined), males of *A. labrosus* possess a rather small number of ocellate spots arranged irregularly in the posterior half of the anal fin. Thus, given the apparent presence of O/N polychromatism and mbuna-like ocelli, we suggest that *A. labrosus* is more closely allied with the mbuna than with one of the lineages of non-mbuna haplochromine cichlids endemic to Lake

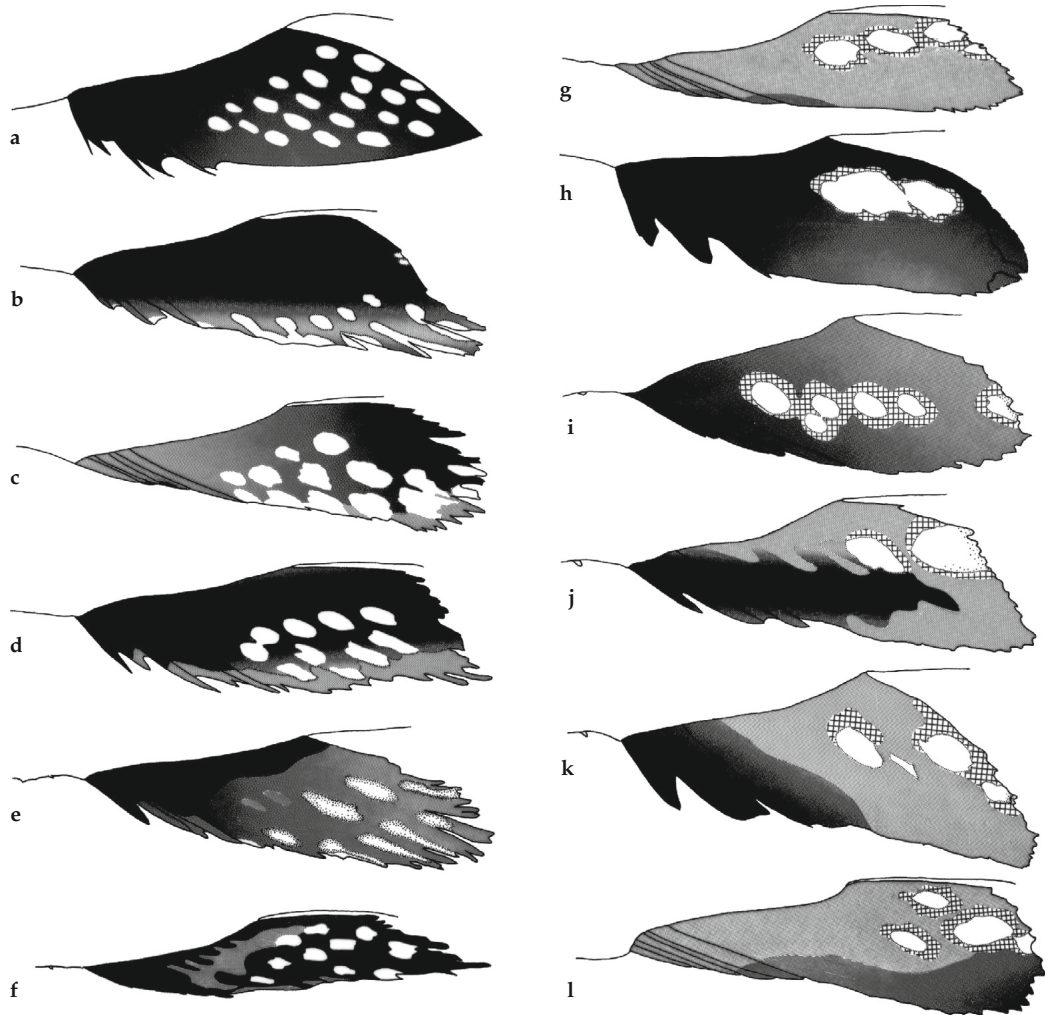


Fig. 10. Anal fins of some adult male haplochromines, from Oliver (1984). Transparent, lightly pigmented areas of fin membrane indicated by crosshatching (only present in species in right column). All except (a) traced from color transparencies of live fishes in aquaria, most photographed soon after capture. Each fin drawn from a single fish. Not drawn to scale. Non-ocellate fin spots are shown in a-f; ocellate spots in g-l. Species are from Lake Malawi, except as noted. **a**, *Serranochromis longimanus*, Okavango and Upper Zambesi rivers (redrawn from Trewavas, 1964: fig. 9); **b**, *Nimbochromis* cf. *polystigma*, aquarium specimen; **c**, *Protomelas spilopterus*; **d**, *Otopharynx tetrastigma*; **e**, *Mylochromis lateristriga*; **f**, *Lethrinops* cf. *argentea*; **g**, *Harpagochromis squamipinnis*, Lake George, Uganda; **h**, *Astatotilapia schubotziella*, Lake George, Uganda; **i**, *Astatotilapia calliptera*; **j-k**, two individuals of *Cyathochromis obliquidens*; **l**, *Iodotropheus sprengerae*. Compare with *Abactochromis labrosus* (see Fig. 9c).

Malawi. However, we emphasize that none of the traits discussed above has been rigorously demonstrated to be a synapomorphy of the mbuna.

(6) Some of the more taxonomically inclusive molecular phylogenetic studies that have been conducted to date have suggested that the mbuna sensu Fryer (1959) may not be monophyletic to the exclusion of all non-mbuna within the

haplochromine species flock of Lake Malawi. Instead, the weight of molecular evidence has indicated the existence of a highly speciose clade composed almost exclusively of mbuna (plus perhaps a small number of *Alticorpus*, *Lethrinops*, and/or *Aulonocara* species and perhaps other non-mbuna species), outside of which no (or at most extremely few) species regarded as mbuna

are thought to have arisen (Moran et al., 1994; Meyer et al., 1996; Albertson et al., 1999; Shaw et al., 2000; Salzburger et al., 2005; Won et al., 2006; Hulsey et al., 2010). Some of these authors refer to a clade they explicitly label “mbuna” (or Group B), in addition to one or more non-mbuna clades. Consistent with past controversies regarding the taxonomic status of *A. labrosus*, Meyer et al. (1996) – in the only molecular phylogenetic study to date that has included this species – provided weak evidence (itself consistent with our suggestive evidence from vertebral counts) of a basal, sister-group relationship between this enigmatic species and a clade uniting the rest of the Group B (mbuna) species they investigated.

Very recently, however, Sylvester et al. (2010) identified a single nucleotide polymorphism, located in a transcription factor affecting forebrain development (*irx1b*), that is alternatively fixed between large samples of mbuna and non-mbuna species. The mbuna allele appears to be the derived one – a possible mbuna synapomorphy – and, tantalizingly, it has also been found in some, but not all, individuals of the *Astatotilapia calliptera* complex (J. T. Streebman, in litt., 7 Jun 2010). The set of mbuna examined by Sylvester and colleagues included 25 species representing ten mbuna genera (but unfortunately not *A. labrosus*). The even larger set of non-mbuna species included two *Aulonocara* and three *Lethrinops* species. This intriguing result demands continued examination of the possibility that the mbuna (together with a subset of *A. calliptera*) may, in fact, represent a monophyletic group within the Malawi species flock. Further evolutionary genetic study of Malawi cichlids should benefit greatly from the inclusion of *A. labrosus*, as this unusual species may help shed light on the origin and radiation of the mbuna clade within Lake Malawi’s extraordinary cichlid species flock.

Recommendation. Because it remains controversial whether the mbuna, as they are currently recognized phenotypically, compose a strictly monophyletic group to the exclusion of all non-mbuna (e.g., *Alticorpus*, *Aulonocara*, *Lethrinops*), we support the following two usages of this term until definitive evidence indicates that their distinction is unnecessary. In the context of phylogenetics and systematics, it should only be given as “mbuna clade”, referring to the smallest monophyletic group that includes all (or at least the vast majority) of mbuna species (e.g., with the

possible exception of *L. caeruleus* [Won et al., 2006], although the phylogenetic hypothesis shown in that study certainly warrants additional testing with multiple nuclear markers and newly collected material). *Abactochromis labrosus* appears to belong to this “mbuna clade” based on its phenotypic similarities to members of this group and the genetic result of Meyer et al. (1996). However, the enduring popularity of the term “mbuna” also reflects its continued importance in the scientific literature for succinctly describing a speciose and ecologically important assemblage (or guild) of phenotypically recognizable Malawi cichlids. Therefore, we also endorse unmodified use of this term in ecological and behavioral contexts when reference is made to the now thirteen genera recognized as mbuna (see key, below).

Key to the thirteen genera of the mbuna group of Lake Malawi cichlids

- 1 – Upper jaw narrow at symphysis (joint) between left and right halves, Λ -shaped when head viewed from above; premaxillary pedicel (ascending process) longer than alveolar (tooth-bearing) process; color pattern not dominated by horizontal stripes.2
- Upper jaw broader at symphysis, Ω -shaped to Γ -shaped as viewed from above, or not visible from above; premaxillary pedicel not longer than alveolar process; if upper jaw somewhat Λ -shaped then color pattern with prominent horizontal stripes.3
- 2 – Lips normal, not conspicuously thickened, nor with median lobes; mouth small, lower jaw length 20-36 % of head length, premaxillary pedicel 21-36 % of head length; 3-5 anterior teeth of each premaxilla much longer and stouter than lateral and posterior teeth; head smaller, 27-36 % SL; gill rakers on lower limb (ceratobranchial) of outer arch, excluding 1 in angle, 6-11 (rarely 11) including all rudiments. *Labidochromis*
- Lips conspicuously hypertrophied, each with prominent, fleshy median lobe; mouth large, lower jaw length 45-55 % of head length, premaxillary pedicel 36-46 % of head length; anterior premaxillary teeth not much

enlarged compared to lateral and posterior teeth; head larger, 36-43 % SL; gill rakers on lower limb 11-14 (rarely 11).

.....*Abactochromis*

- 3 – Mouth inferior, not visible when head viewed from above, hidden by fleshy pad at front of snout; dental arcade of upper jaw —-shaped; anterior teeth of outer row in each jaw subequally tricuspid, crowns not markedly recurved, shafts not extremely slender.

.....*Labeotropheus*

- Mouth terminal to subterminal, at least upper jaw visible from above; dental arcade of upper jaw typically ∩-shaped, rarely —-shaped; outer jaw teeth usually not subequally tricuspid; if tricuspid then crowns recurved and shafts extremely slender.

.....4

- 4 – Lower jaw heavy, wide, strongly projecting forward beyond upper jaw; outer and inner tooth rows (dental arcade) of lower jaw predominantly transverse as viewed from above; lower jaw with outer teeth stout, unequally bicuspid; body elongate, its depth at most 25-30 % SL.

.....*Genyochromis*

- Lower jaw not as described; if prognathous, not strongly so; dental arcade of lower jaw rounded as viewed from above, not strongly transverse; dentition of lower jaw various; body usually deeper, its depth more than 30 % SL, if body elongate then lower jaw not heavy, wide, or strongly projecting.

.....5

- 5 – Teeth of both jaws unequally tricuspid, crowns abruptly recurved, shafts long and narrow (tooth length from attachment to tip ~16-20× shaft width); teeth movably implanted in jaws, forming brushlike surface; mouth terminal, lower jaw decurved anteriorly in adults, making multiple rows of teeth visible even when mouth closed; adult size large, commonly >110 mm SL, some species attaining 165 mm SL.

.....*Petrotilapia*

- Teeth not as described, their shafts much less slender; lower jaw usually not decurved anteriorly, rarely showing more than out-

ermost row of teeth when mouth closed; adult fishes usually <110 mm SL.

.....6

- 6 – Outer teeth of both jaws with crowns recurved, compressed, spoonlike, markedly angled obliquely toward jaw symphysis, crown edge rounded with very small lateral cusp, shaft narrow (tooth length ~12 × minimum shaft width); inner teeth very unequally tricuspid, middle cusp often semicircular in outline; habitat intermediate zone (i.e., preferred substrate typically composed of a mixture of sand, rocks, aquatic vegetation, and sometimes gravel), often feeding on epiphytic aufwuchs growing on *Vallisneria* and *Potamogeton*.

.....*Cyathochromis*

- Teeth with crowns not as described, not markedly angled obliquely toward symphysis; inner teeth, if tricuspid, lacking semicircular middle cusp; habitat most often rocky shores and reefs, in some cases open sand, rarely intermediate zone.

.....7

- 7 – Color pattern on flanks (unless obscured by general dark pigment in some preserved specimens) dominated by two horizontal stripes that are either dark on pale ground color (females and immature fishes), or pale on dark ground color (almost always males); usually one stripe midlateral in position and other stripe along or near upper lateral line; stripes shifted downward in a few species; vertical bars present in addition to stripes in a few species sometimes assigned to this genus.

.....*Melanochromis*

- Color pattern lacking prominent, sexually dimorphic horizontal stripes.

.....8

- 8 – Outer teeth of both jaws numerous, closely spaced, long, slender, with small crowns, unicuspid or unequally bi- or tricuspid, those of upper jaw recurved, those of lower jaw markedly procumbent (implanted so tooth shafts are directed forward); lower jaw scooplike, somewhat flattened dorsoventrally; habitat usually intermediate zone, open sand, or soft bottom.

.....*Gephyrochromis*

- Teeth not as described, those of lower jaw not directed strongly forward; lower jaw not flattened; habitat usually rocky shore.9
- 9 – Anterior outer teeth of jaws unicuspid, stout, the cusp conical, acute, recurved, teeth not closely spaced. *Cynotilapia*
- Anterior outer jaw teeth not as described, typically bicuspid.10
- 10 – Upper lip usually connected medially to skin of snout by a frenum; mouth small, terminal; outer teeth of both jaws unequally bicuspid, loosely spaced, shafts inclined slightly toward jaw symphysis; anterior teeth of upper jaw much longer and stouter than lateral and posterior teeth; coloration of body golden brown to rusty reddish brown in life; distribution restricted to islands of Boadzulu, Chinyankwazi, and Chinyamwezi, Makokola Reef, and southeastern shore of lake from Chilolo (Mozambique) to Nsinje R. (Malawi). *Iodotropheus*
- Upper lip free, lacking a frenum; mouth small, subterminal or larger, terminal; dentition various, but outer teeth closely spaced, shafts not inclined toward symphysis; anterior teeth of upper jaw not much longer than lateral and posterior teeth; coloration of body various, rarely golden brown or rust-colored in life; distribution not necessarily restricted to above areas.11
- 11 – Mouth small, subterminal; upper jaw overhanging lower jaw anteriorly; posterior teeth of upper jaw conical, incurved, often distinctly enlarged in diameter relative to anterior teeth, which are subequally bicuspid; profile of snout (and ethmovomerine area of skull, seen by dissection or radiograph) steeply inclined, curved downward, giving many individuals a blunt-headed appearance. *Tropheops*
- Mouth larger, terminal; lower jaw equal with upper jaw anteriorly, or lower jaw projecting somewhat; posterior teeth of upper jaw often conical but not markedly larger than anterior teeth; snout profile and ethmovomerine angle various, front of head usually not steeply inclined.12
- 12 – Lower jaw of closed mouth sloping at ~45° angle to horizontal midline of fish; ethmovomerine area of skull (seen by dissection or radiograph) moderately sloping, its anterior surface ~65° to horizontal (Fig. 8 illustrates measurement of ethmovomerine angle); vomer subquadrate in lateral view, its rostral tip swollen, bluntly rounded. *Maylandia*
- Lower jaw roughly parallel to midline of fish (in *P. williamsi* complex, i. e., *Pseudotropheus sensu stricto*); or ethmovomerine angle steeply sloping, ~80° to horizontal, vomer wedge-shaped in lateral view, its rostral tip not swollen (in *P. elongatus* complex); or characters various (in *P. “aggressive”* and *P. “miscellaneous”* complexes, see Note 4 below). *Pseudotropheus*

Notes on key. (1) We follow recent workers in recognizing at full generic rank the taxa *Tropheops* (Konings 2001a; Stauffer et al., 2002; Allender et al., 2003; Kocher, 2004; Won et al., 2005; Konings & Stauffer, 2006; Albertson, 2008; Martin & Genner, 2009; Sylvester et al., 2010) and *Maylandia* (Allender et al., 2003; Clabaut, 2005; Kassam et al., 2005; Tobler, 2006; Loh et al., 2008; Sylvester et al., 2010), both initially proposed as subgenera of *Pseudotropheus*.

(2) We recognize that there is not universal agreement about which genus-group name is valid for the former *Pseudotropheus zebra* species group. Despite the revised diagnosis of *Metriaclima* given by Konings & Stauffer (2006), our understanding is that the prior name *Maylandia* was validly published and available, and thus has priority over *Metriaclima* and is unambiguously the correct name for this assemblage (Eschmeyer, 1990; Condé & Géry, 1999).

(3) We wish to emphasize the inadequacy of current definitions of the genera *Tropheops*, *Pseudotropheus*, and *Maylandia*. We include the three in our key mainly on the basis of characterizations in other literature, and call attention to the need for more rigorous descriptive and phylogenetic work in those speciose assemblages.

(4) The *Pseudotropheus* “aggressive” and

P. “miscellaneous” species-groups were characterized by Ribbink et al. (1983) as categories of convenience, and it was explicitly stated they were unlikely to be natural groups. *Pseudotropheus* “aggressive” members are “strongly territorial fishes which live among small and medium-sized rocks in shallow water. [Their] territories ... are so aggressively defended that they develop algal gardens ... It is usual for both sexes to practice territoriality” (Ribbink et al., 1983: 190). *Pseudotropheus* “miscellaneous” species “are morphologically and behaviourally diverse and the group is undoubtedly polyphyletic” (Ribbink et al., 1983: 194). The names of both these complexes have been employed occasionally by subsequent workers, so we refer to them in the key even though they are ill-defined.

Comparison material. *Astatotilapia calliptera*: USNM 330613, 6 (r), 68.6-78.9 mm SL*; Malawi: Chikwawa, ponds at fish farm.

Cheilochromis euchilus: BMNH 1935.6.14:1016-1017, lectotype and paralectotype, 2 (r), 78.0-96.0 mm SL; Malawi: Chilumba. – AMNH 222094, 3 (r), 55.0-79.3 mm SL*; Malawi: ENE shore Maleri Island. – AMNH 98210, 1, 73.2 mm SL; Malawi: W. shore Domwe Island.

Chilotilapia rhoadesii: AMNH 31860, 2 (r), 102.8-106.8 mm SL*; Malawi: trawled in 15 fathoms ~6 miles from southernmost extremity of L. Malawi. – AMNH 31861, 1 (r), 165.0 mm SL*; Malawi: Monkey Bay off Bweyawayami.

Cyathochromis obliquidens: AMNH 31887, 7 (r), 61.3-75.8 mm SL*; Malawi: Koko Bay near Monkey Bay. – AMNH 233482, 2 (r), 81.0-86.8 mm SL*; Malawi: Monkey Bay. – Uncat MKO68-7-31, 1 (c&s), 92.5 mm SL; Malawi: Monkey Bay.

Cynotilapia afra: AMNH 31892, 4 (r), 64.5-70.7 mm SL*; Malawi: Nkata Bay. – Uncat MKO80-70, 2 (c&s), 62.0-62.5 mm SL; Malawi: Nkhata Bay, south bay S of peninsula tip.

Ectochromis festivus: BMNH 1935.6.14:1013, holotype, 70.0 mm SL; Malawi: “Nyasa, Nkudzi”. *E. lobocheilus*: BMNH 1935.6.14:1015, holotype, 83.0 mm SL; Malawi: “Deep Bay, L. Nyassa”. *E. ornatus*: BMNH 1921.9.6:112, holotype, 115.0 mm SL; “Nyassa”. – BMNH 1935.6.14:1014, 1, 132.0 mm SL; “Nyassa”.

Genyochromis mento: AMNH 31903, 1 (r), 73.0 mm SL; Malawi: Monkey Bay. – AMNH 220337, 1 (r), 92.0 mm SL; Malawi: Jalo Reef [near Nkhotakota]. – AMNH 233496, 6 (r), 64.2-78.0 mm SL*; Malawi: Maleri Island, pebble/cobble beach ENE side. – Uncat MKO80-70, 2 (c&s), 70.5-72.0 mm SL; Malawi: Nkhata Bay, south bay S of peninsula tip.

Gephyrochromis lausi: AMNH 31863, 1 (r), 101 mm SL; Malawi: Nkhata Bay, fringe of rocky shore. *G. moorii*: Uncat MKO80-40, 3 (c&s), 70.5-86.5 mm SL; Malawi: Mazinzi Bay, trawled in 9-10 m.

Iodotropheus sprengerae: USNM 207012-207015, 4 (paratypes, r), 62.0-82.8 mm SL; Malawi: Boadzulu Island (?). – Uncat MKO, 1 (c&s), 62.0 mm SL; country unknown: Lake Malawi.

Labeotropheus fuelleborni: AMNH 19128, 7 (r), 84.2+ mm SL*; Malawi: Deep Bay. – AMNH 31894, 4 (r), 86.1-93.9 mm SL*; Malawi: Monkey Bay. – AMNH 31906, 4 (r), 27.5-39.1 mm SL*; Malawi: Monkey Bay. *L. trewavasae*: AMNH 31890, 1 (r); Malawi: Nkhata Bay. – AMNH 31893, 1 (r); Malawi: Nkhata Bay. – AMNH 31899, 1 (r), 52.0 mm SL*; Malawi: Nkhata Bay.

Labidochromis caeruleus: FRUMB uncat., 1 (r), 55.4 mm SL*; Lake Malawi. *L. freibergeri*: AMNH 33466, 1 (holotype, r), 63.3 mm SL*; Lake Malawi, off Likoma Island. *L. pallidus*: AMNH 222087, 13 (r), 32.4-49.8 mm SL*; Malawi: Maleri Island E shore. – Uncat, 42 (r, 4 c&s), 30.9-61.8 mm SL*; L. Malawi. *L. shiranus*: BMNH 1935.6.14: 335, 1 (syntype of *L. vellicans*, redetermined by Lewis, 1982; r), 82.0 mm SL*; Malawi: Nkudzi Bay. – *L. textilis*: BMNH 1975.5.27: 9, 1 (holotype, r), 76.5 mm SL; Lake Malawi. – AMNH 33465, 1 paratype of *L. joanjohnsonae* (r), 68 mm SL; Mozambique: Lake Malawi, probably east central coast. *L. vellicans*: BMNH 1935.6.14: 326-335, 6 (syntypes, r), 32.6-53.8*; Malawi: Nkudzi Bay. – BMNH 1965.10.26: 14-21, 8 (r), 37.6-53.2 mm SL*; Malawi: Nkhata Bay. – Uncat MKO71-V-2, 16 (r), 39.4-63.8 mm SL*; Malawi: Maleri Island.

Maylandia elegans: AMNH 233548, 1 (r), 116.0 mm SL; Malawi: Mazinzi Bay. – AMNH 226057, 2 (r), 107.0-111.6 mm SL*; P. E. A. [Portuguese East Africa, i.e., Mozambique]: Mtengula. *M. livingstonii*: AMNH 221238, 4 (r), 55.0-77.0 mm SL; Malawi: Crocodile Rocks. *M. zebra*: AMNH 19127, 3 (r), 78.4-90.0 mm SL*; Malawi: Deep Bay. – AMNH 31891, 1 (r), 88.5 mm SL*; Malawi: Monkey Bay. – AMNH 31907, 1 (r), 62.2 mm SL*; “Lake Malawi”. – Uncat MKO80-93, 4 BB morph (c&s), 68.0-88.0 mm SL; Malawi: W shore Domwe Island 40 m from N tip.

Melanochromis auratus: AMNH 31901, 2 (r), 42.2-55.0 mm SL*; “Lake Malawi”. – AMNH 31904, 1 (r), 57.9 mm SL*; Malawi: Monkey Bay. – Uncat MKO80-93, 2 (c&s), 65.0-73.0 mm SL; Malawi: W shore Domwe Island 40 m from N tip. *M. joanjohnsonae*: AMNH 33464, holotype of *Labidochromis joanjohnsonae* (r), 60.2 mm SL*; Malawi: off Likoma Island. *M. johannii*: USNM 210702, holotype (r), 67.9 mm SL*; USNM 210701, 1 paratype (r), 67.7 mm SL*; Malawi: rocky coast S of Cape Ngambo on E coast about 20 mi. N. of Monkey Bay, 13°45' S 34°50' E. – AMNH 215563, 35 (r), 35.3-80.0 mm SL*; country unknown: E shore of L. Malawi near Malawi/Mozambique border. *M. melanopterus*: Uncat MKO80-93, 3 (c&s), 57.0-74.0 mm SL; Malawi: W shore Domwe Island 40 m from N tip. – MRAC 99-41-P-1345-353, 2 (r), 68.0-80.0 mm SL; Mozambique: Tchilouelo Point, just N of Luaice River; SADC/GEF project, 1998. – AMNH 31889, 3 (r), 56.5-123.0 mm SL*; Malawi: Nkhata Bay, off rocks in S bay. – AMNH 226068, 2 (r), 73.6-95.6 mm SL*; Malawi: Lake Malawi. – BMNH 1935.6.14:302, 1 (r); Malawi: Monkey Bay. – BMNH 1935.6.14:304-306, 8 (r);

Literature cited

- Malawi: Monkey Bay. – BMNH 1956.9.4:12, 1 (r); Malawi: Nkhata Bay. – BMNH 1971.9.13:32-36, 5 (r); Malawi: Nkhata Bay. – BMNH 1956.9.4:15, 1 (r); Malawi: Nkhata Bay. *M. simulans*: USNM 210700, holotype (r), 67.2 mm SL*; Malawi: rocky coast S of Cape Ngambo on E coast about 20 mi. N. of Monkey Bay, 13°45' S 34°50' E. *M. vermivorus*: AMNH 31896, 2 (r), 55.0-60.5 mm SL; Malawi: Monkey Bay, Tumbi Island E.
- Petrotilapia* sp.: AMNH 19131, 1 (r), 75.0 mm SL*; Malawi: Deep Bay. – AMNH 31888, 1 (r), 93.6 mm SL*; Malawi: Monkey Bay. – AMNH 31895, 1 (r), 137.0 mm SL*; Malawi: Monkey Bay. – AMNH 31905, 1 (r), 48.2 mm SL*; Malawi: Monkey Bay, Tumbi Island East. – Uncat MKO71-V-2, 5 (c&s), 48.8-68.0 mm SL; Malawi: Maleri Island.
- Placidochromis milomo*: AMNH 92694, 3 (r); Malawi: Mitande. – USNM 265487, 1 (r); Malawi: Thumbi Island [West], Cape Maclear.
- Pseudotropheus elongatus*: AMNH 31897, 2 (r); Malawi: Monkey Bay, Tumbi I. East. – Uncat MKO80-93, 3 (c&s), 59.0-75.0 mm SL; Malawi: W shore Domwe Island 40 m from N tip. *P. lucerna*: AMNH 31898, 1 (r), 53.3 mm SL*; Malawi: Nkhata Bay, Makoka. *P. minutus*: AMNH 31900, 1 (r), 46.0 mm SL*; Malawi: Nkhata Bay.
- Tropheops tropheops*: CUMV 89948, 16 (r, 15 with vertebrae countable), 69.4-92.8 mm SL*; Malawi: Monkey Bay: Harbour Island.
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- Adler, W. 1979. Cichliden von A-Z. *Haplochromis labrosus* (Trewavas, 1935). DCG (Deutsche Cichliden Gesellschaft) Informationen, 10: 1-2.
- Albertson, R. C. 2008. Morphological divergence predicts habitat partitioning in a Lake Malawi cichlid species complex. *Copeia*, 2008: 689-698.
- Albertson, R. C., J. A. Markert, P. D. Danley & T. D. Kocher. 1999. Phylogeny of a rapidly evolving clade: the cichlid fishes of Lake Malawi, east Africa. *Proceedings of the National Academy of Sciences (USA)*, 96: 5107-5110.
- Allender, C. J., O. Seehausen, M. E. Knight, G. F. Turner & N. Maclean. 2003. Divergent selection during speciation of Lake Malawi cichlid fishes inferred from parallel radiations in nuptial coloration. *Proceedings of the National Academy of Sciences (USA)*, 100: 14074-14079.
- Ambali, A., H. Kabwazi, L. Malekano, G. Mwale, D. Chimwaza, J. Ingainga, N. Makimoto, S. Nakayama, M. Yuma & Y. Kada. 2001. Relationship between local and scientific names of fishes in Lake Malawi/Nyasa. *African Study Monographs*, 22: 123-154.
- Arnegard M. E., J. A. Markert, P. D. Danley, J. R. Stauffer, A. J. Ambali & T. D. Kocher. 1999. Population structure and colour variation of the cichlid fish *Labeotropheus fuelleborni* Ahl along a recently formed archipelago of rocky habitat patches in southern Lake Malawi. *Proceedings of the Royal Society B*, 266: 119-130.
- Arnegard, M. E. & J. Snoeks. 2001. New three-spotted cichlid species with hypertrophied lips (Teleostei: Cichlidae) from the deep waters of Lake Malawi/Nyasa, Africa. *Copeia*, 2001: 705-717.
- Atema, J. 1971. Structures and functions of the sense of taste in the catfish (*Ictalurus natalis*). *Brain, Behavior and Evolution*, 4: 273-294.
- Bardach, J. E., G. H. Johnson & J. H. Todd. 1969. Orientation by bulk messenger sensors in aquatic vertebrates. *Annals of the New York Academy of Sciences*, 163: 227-235.
- Bowers, N. J. & J. R. Stauffer. 1997. Eight new species of rock-dwelling cichlids of the genus *Melanochromis* (Teleostei: Cichlidae) from Lake Malawi, Africa. *Ichthyological Exploration of Freshwaters*, 8: 49-70.
- Burgess, W. E. 1976. Studies on the family Cichlidae: 3. A new *Melanochromis* from Lake Malawi, with comments on the genus. *Tropical Fish Hobbyist*, 24: 61-65.
- Clabaut, C. 2005. Morphometric, molecular phylogenetic and gene expression approaches towards the understanding of the adaptive radiations of the East African cichlids. Unpubl. Ph.D. dissertation, University of Konstanz, 122 pp.
- Condé, B. & J. Géry. 1999. *Maylandia* Meyer et Foerster, 1984, un nom générique disponible (Teleostei, Perciformes, Cichlidae). *Revue Française d'Aquariologie Herpétologie*, 26: 21-22.

- DeMason, L. 1995. A guide to the Tanzanian cichlids of Lake Malawi. National Art Publishing, Ft. Myers, 102 pp.
- Dingerkus, G. & L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology*, 52: 229-232.
- Eccles, D. H. 1973. Two new species of cichlid fishes from Lake Malawi (formerly known as Lake Nyasa). *Arnoldia*, 6: 1-7.
- Eccles, D. H. & E. Trewavas. 1989. Malawian cichlid fishes. The classification of some Haplochromine genera. *Lake Fish Movies*, Hertel, 335 pp.
- Eschmeyer, W. N. 1990. Catalog of the genera of Recent fishes. California Academy of Sciences, San Francisco, vi+697 pp.
- Fryer, G. 1959. The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with especial reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. *Proceedings of the Zoological Society of London*, 132: 153-281.
- Fryer, G. & T. D. Iles. 1972. The cichlid fishes of the Great Lakes of Africa. Oliver & Boyd, Edinburgh & TFH Publications, Neptune City, 641 pp.
- Genner, M. J., O. Seehausen, D. H. Lunt, D. A. Joyce, P. W. Shaw, G. R. Carvalho & G. F. Turner. 2007. Age of cichlids: new dates for ancient lake fish radiations. *Molecular Biology and Evolution*, 24: 1269-1282.
- Genner, M. J. & G. F. Turner. 2005. The mbuna cichlids of Lake Malawi: a model for rapid speciation and adaptive radiation. *Fish and Fisheries*, 6: 1-34.
- Genner, M. J., G. F. Turner & S. J. Hawkins. 1999. Resource control by territorial male cichlid fish in Lake Malawi. *Journal of Animal Ecology*, 68: 522-529.
- Grant, S. M., H. W. Dieckhoff, H. J. Mayland & M. M. Meyer. 1987. Ecology of *Aulonocara* REGAN, 1922 in Lake Malawi. Contributions to the knowledge of the cichlid fishes of the genus *Aulonocara* of Lake Malawi (East-Africa). *Courier Forschungsinstitut Senckenberg*, 94: 131-139.
- Greenwood, P. H. 1979. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part I. *Bulletin of the British Museum (Natural History)*, *Zoology*, 35: 265-322.
- Hale, A. E., J. R. Stauffer & M. D. Mahaffy. 1998. Exceptions to color being a sexually dimorphic character in *Melanochromis auratus* (Teleostei: Cichlidae). *Ichthyological Exploration of Freshwaters*, 9: 263-266.
- Hertel, E. 1992. Homing and home-site fidelity in rock-dwelling cichlids (Pisces: Teleostei) of Lake Malawi, Africa. *Environmental Biology of Fishes*, 33: 229-237.
- 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). *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, 16: 171-187.
- Hulsey, C. D., M. C. Mims, N. F. Parnell & J. T. Streebman. 2010. Comparative rates of lower jaw diversification in cichlid adaptive radiations. *Journal of Evolutionary Biology*, 23: 1456-1467.
- Huxley, J. S. 1955. Morphism in birds. *Acta 11th International Ornithological Congress, Basel 1954*: 309-328.
- Kassam, D., S. Seki, B. Rusuwa, A. J. D. Ambali & K. Yamaoka. 2005. Genetic diversity within the genus *Cynotilapia* and its phylogenetic position among Lake Malawi's mbuna cichlids. *African Journal of Biotechnology*, 4: 1195-1202.
- Knight, M. E., M. J. H. van Oppen, H. L. Smith, C. Rico, G. M. Hewitt & G. F. Turner. 1999. Evidence for male-biased dispersal in Lake Malawi cichlids from microsatellites. *Molecular Ecology*, 8: 1521-1527.
- Kocher, T. D. 2004. Adaptive evolution and explosive speciation: the cichlid fish model. *Nature Reviews Genetics*, 5: 288-298.
- Konings, A. 1990. Cichlids and all the other fishes of Lake Malawi. T.F.H. Publications, Neptune City, 495 pp.
- 1998. Comments on the classification of species of the genus *Melanochromis*. *Cichlid News*, 7: 6, 8-10, 12, 14-16.
- 2001a. Malawi cichlids in their natural habitat. 3rd edition. Cichlid Press, El Paso, 352 pp.
- 2001b. The cichlids of Lake Malawi. CD-ROM. Cichlid Press, El Paso.
- 2004. Orange-blotch polychromatism in cichlids. *Tropical Fish Hobbyist*, 52: 80-88.
- Konings, A. F. & J. R. Stauffer. 2006. Revised diagnosis of *Metriaclima* (Teleostei: Cichlidae) with description of a new species from Lake Malawi National Park, Africa. *Ichthyological Exploration of Freshwaters*, 17: 233-246.
- Lewis, D. S. C. 1982. A revision of the genus *Labidochromis* (Teleostei: Cichlidae) from Lake Malawi. *Zoological Journal of the Linnean Society*, 75: 189-265.
- Lewis, D., P. Reinthal & J. Trendall. 1986. A guide to the fishes of Lake Malawi National Park. *World Wildlife Fund, Gland*, 71 pp.
- Loh, Y. H. E., L. S. Katz, M. C. Mims, T. D. Kocher, S. Yi & J. T. Streebman. 2008. Comparative analysis reveals signatures of differentiation amid genomic polymorphism in Lake Malawi cichlids. *Genome Biology*, 9: R113.
- Loiselle, P. V. 1978. Reflections on the generic placement of *Haplochromis labrosus*. *Buntbarsche Bulletin*, 67: 16-18.
- 1979. *Melanochromis* the beautiful baddies from Lake Malawi. *Freshwater and Marine Aquarium Magazine*, December: 17-23.
- Markert, J. A. & M. E. Arnegard. 2007. Size-dependent use of territorial space by a rock-dwelling cichlid fish. *Oecologia*, 154: 611-621.
- Marsh, A. C. & A. J. Ribbink. 1985. Feeding-site utilization in three sympatric species of *Petrotilapia* (Pisces:

- Cichlidae) from Lake Malawi. *Biological Journal of the Linnean Society*, 25: 331-338.
- Martin, C. H. & M. J. Genner. 2009. High niche overlap between two successfully coexisting pairs of Lake Malawi cichlid fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 579-588.
- Mayland, H. J. 1982. *Der Malawi-See und seine Fische*. Landbuch-Verlag, Hannover, 336 pp.
- Merritt, M. 1978. Further notes concerning the species *Haplochromis labrosus*. *Buntbarsche Bulletin*, 67: 11-16.
- Meyer, A. 1993. Phylogenetic relationships and evolutionary processes in East African cichlid fishes. *Trends in Ecology and Evolution*, 8: 279-284.
- Meyer, A., C. M. Montero & A. Spreinat. 1996. Molecular phylogenetic inferences about the evolutionary history of the East African cichlid fish radiations. Pp. 303-323 in: T. C. Johnson, E. O. Odada & K. T. Whittaker (eds.), *The limnology, climatology and paleoclimatology of the East African lakes*. Gordon and Breach Scientific Publishers, Toronto.
- Meyer, M. K. & W. Foerster. 1984. Un nouveau *Pseudotropheus* du lac Malawi avec des remarques sur le complexe *Pseudotropheus-Melanochromis* (Pisces, Perciformes, Cichlidae). *Revue Française d'Aquariologie Herpétologie*, 10: 107-112.
- Moran, P., I. Kornfield & P. Reinthal. 1994. Molecular systematics and radiation of the haplochromine cichlids (Teleostei: Perciformes) of Lake Malawi. *Copeia*, 1994: 274-288.
- Oliver, M. K. 1984. Systematics of African cichlid fishes: determination of the most primitive taxon, and studies on the haplochromines of Lake Malawi (Teleostei: Cichlidae). Unpubl. Ph.D. dissertation, Yale University, New Haven, ix + 326 pp.
- Regan, C. T. 1922. The cichlid fishes of Lake Nyassa. *Proceedings of the Zoological Society of London*, 1921: 675-727.
- Reutter, K., W. Breipohl & G. J. Bijvank. 1974. Taste bud types in fishes. II. Scanning electron microscopical investigations on *Xiphophorus helleri* Heckel (Poeciliidae, Cyprinodontiformes, Teleostei). *Cell and Tissue Research*, 153: 151-165.
- 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. *South African Journal of Zoology*, 18: 149-310.
- Roberts, R. B., J. R. Ser & T. D. Kocher. 2009. Sexual conflict resolved by invasion of a novel sex determiner in Lake Malawi cichlid fishes. *Science* 326: 998-1001.
- Roulin, A. 2004. The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biological Reviews*, 79: 815-848.
- Salzburger, W., T. Mack, E. Verheyen & A. Meyer. 2005. Out of Tanganyika: genesis, explosive speciation, key-innovations and phylogeography of the haplochromine cichlid fishes. *BMC Evolutionary Biology*, 5: 17.
- Schemmel, C. 1967. Vergleichende untersuchungen an den Hautsinnesorganen ober- und unterirdisch lebender *Astyanax*-Formen: ein Beitrag zur Evolution der Cavernicolen. *Zeitschrift für Morphologie der Tiere*, 61: 255-316.
- Seehausen, O. 1996. Lake Victoria rock cichlids: taxonomy, ecology, and distribution. *Verduijn Cichlids*, Zevenhuizen, 304 pp.
- Seehausen, O., J. J. M. van Alphen & R. Lande. 1999. Color polymorphism and sex ratio distortion in a cichlid fish as an incipient stage in sympatric speciation by sexual selection. *Ecology Letters*, 2: 367-378.
- Shaw, P. W., G. F. Turner, M. R. Idid, R. L. Robinson & G. R. Carvalho. 2000. Genetic population structure indicates sympatric speciation of Lake Malawi pelagic cichlids. *Proceedings of the Royal Society B*, 267: 2273-2280.
- Snoeks, J. 1994. The haplochromines (Teleostei, Cichlidae) of Lake Kivu (East Africa): a taxonomic revision with notes on their ecology. *Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques*, 270: 1-221.
- Snoeks, J. (ed.). 2004. *The cichlid diversity of Lake Malawi/Nyasa/Niassa: identification, distribution and taxonomy*. Cichlid Press, El Paso, 360 pp.
- Spreinat, A. 1995. Lake Malawi cichlids from Tanzania. *Verduijn Cichlids*, Zevenhuizen-Moerkapelle, 316 pp.
- Stauffer, J. R. & A. F. Konings. 2006. Review of *Copadichromis* (Teleostei: Cichlidae) with the description of a new genus and six new species. *Ichthyological Exploration of Freshwaters*, 17: 9-42.
- Stauffer, J. R., K. R. McKaye & A. F. Konings. 2002. Behaviour: an important diagnostic tool for Lake Malawi cichlids. *Fish and Fisheries*, 3: 213-224.
- Streelman, J. T., R. C. Albertson & T. D. Kocher. 2003. Genome mapping of the orange blotch colour pattern in cichlid fishes. *Molecular Ecology*, 12: 2465-2471.
- Sturmbauer, C., S. Baric, W. Salzburger, L. Rüber & E. Verheyen. 2001. Lake level fluctuations synchronize genetic divergences of cichlid fishes in African lakes. *Molecular Biology and Evolution*, 18: 144-154.
- Sylvester, J. B., C. A. Rich, Y. H. Loh, M. J. van Staaden, G. J. Fraser & J. T. Streelman. 2010. Brain diversity evolves via differences in patterning. *Proceedings of the National Academy of Sciences (USA)*, 107: 9718-9723.
- Tawil, P. 2002. Notes sur le genre *Melanochromis* et l'appartenance générique de *Pseudotropheus johannii* Eccles, 1973, et espèces apparentées. *L'An Cichlidé*, 2: 61-68. Association France Cichlid, Solliés-Ville.
- Tobler, M. 2006. The eggspots of cichlids: evolution through sensory exploitation? *Zeitschrift für Fischkunde*, 8: 39-46.
- Trewavas, E. 1935. A synopsis of the cichlid fishes of Lake Nyasa. *Annals and Magazine of Natural History*, Series 10, 16: 65-118.

- 1949. The origin and evolution of the cichlid fishes [sic] of the Great African Lakes, with special reference to Lake Nyasa. 13th International Congress of Zoology, 365-368.
- 1964. A revision of the genus *Serranochromis* Regan (Pisces, Cichlidae). Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques, 125: 1-58.
- 1984. Nouvel examen des genres et sous-genres du complexe *Pseudotropheus-Melanochromis* du lac Malawi (Pisces, Perciformes, Cichlidae). Revue Française d'Aquariologie Herpétologie, 10: 97-106.
- Turner, G. J. 1996. Offshore cichlids of Lake Malawi. Cichlid Press, Lauenau, 240 pp.
- Waschkewitz, R. & P. Wirtz. 1990. Annual migration and return to the same site by an individual grouper, *Epinephelus alexandrinus* (Pisces, Serranidae). Journal of Fish Biology, 36: 781-782.
- Wickler, W. 1962. Egg-dummies as natural releasers in mouth-brooding cichlids. Nature, 194: 1092-1093.
- Won, Y.-J., A. Sivasundar, Y. Wang & J. Hey. 2005. On the origin of Lake Malawi cichlid species: a population genetic analysis of divergence. Proceedings of the National Academy of Sciences (USA), 102 (Suppl. 1): 6581-6586.
- Won, Y.-J., Y. Wang, A. Sivasundar, J. Raincrow & J. Hey. 2006. Nuclear gene variation and molecular dating of the cichlid species flock of Lake Malawi. Molecular Biology and Evolution, 23: 828-837.

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