Systematics of Tanganyikan cichlid fishes (Teleostei: Perciformes)

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Abstract The relationships among 53 genera of Tanganyikan cichlid fishes were analyzed based on internal and external morphological features. Comparison of the morphological cladistic tree with a previously proposed classification showed 5 of 12 tribes to be nonmonophyletic. Sixteen tribes were recognized, the changes in classification being that Trematocarini was treated as a junior synonym of Bathybatini; 5 new tribes were established for each of the following genera, *Benthochromis*, *Boulengerochromis*, "*Ctenochromis*" *benthicola*, *Cyphotilapia*, and *Greenwoodochromis*; "*Ctenochromis*" *horei* was transferred from Haplochromini to Tropheini; and "*Gnathochromis*" *pfefferi* was transferred from Limnochromini to Tropheini. The revised classification was supported by previously proposed molecular trees.

Key words Cichlidae · Lake Tanganyika · Tribe · Systematics · Morphology

The ancient great lakes in the East African Rift Valley harbor an extraordinarily rich fauna of cichlid fishes, almost all being endemic to their respective lakes. Lake Tanganyika, the oldest of the Rift lakes, has existed in various forms for about 14 million years (Coulter, 1991, 1994). Although it contains fewer cichlid species (250) than the numbers estimated for Lakes Victoria (500) and Malawi (800, including Lake Nyasa species) (Snoeks, 2000), those of Lake Tanganyika exhibit the greatest morphological diversity of the three Lakes (Coulter, 1991).

Taxonomic investigations of the cichlid fishes of Lake Tanganyika began in the late 19th century. In a series of publications, Boulenger (1898, 1899, 1915) contributed greatly to the acknowledge of the unique ichthyofauna, describing many new species, as did Poll (1942, 1946, 1956). About 70% of the Tanganyikan cichlid fishes presently known were described by these two authors, although new species are still being discovered in the lake (Büscher, 1995; Nakaya and Gashagaza, 1995; Takahashi et al., 1997, 2002).

Using an osteological approach to classify the Tanganyikan cichlid fishes, Regan (1920) recognized three types of pharyngeal apophysis (a posteroventral part of the neurocranium), referred to as the *Tylochromis*, *Tilapia*, and *Haplochromis* types. Subsequently, Greenwood (1978) separated the *Tropheus* type from Regan's *Tilapia* type, describing the four pharyngeal apophysis types in detail. Trewavas (1983) redescribed the *Tilapia* type apophysis and tentatively recognized the tribe Tilapiini for the African and Levantine assemblage, including *Tilapia* and related ten genera. She also proposed tribe Haplochromini on the basis of apophysis structure, although the limits of included genera were not defined. Based on Greenwood's (1978) pharyngeal apophysis types and external morphological features, Poll (1986) classified Tanganyikan cichlid fishes into 12 tribes (Table 1). However, he did not give a clear definition for some tribes.

In morphological phylogenetic studies, several synapomorphies have been proposed for seven tribes, each being suggested as representing a monophyletic group (Table 1). Stiassny (1981) examined the phylogenetic relationships between Bathybatini and Trematocarini, and indicated that the former was paraphyletic unless the latter was included. Stiassny (1997), therefore, modified Poll's tribal classification with the incorporation of Trematocarini into an expanded Bathybatini. Lippitsch (1998) indicated that *Gnathochromis pfefferi* and *Cyphotilapia* should be excluded from Limnochromini and Tropheini, respectively, and doubted the monophyly of these tribes.

Based on genetic analyses, four of Poll's tribes were each indicated as monophyletic with high probability—viz., >90% bootstrap value or insertion of short interspersed repetitive elements (SINEs) (Table 1). Two tribes, however, were suggested as being a nonmonophyletic group.

Among Poll's tribes, Tylochromini has been strongly suggested as the oldest lineage, on the basis of both morphological (Stiassny, 1990, 1991; Lippitsch, 1995) and molecular (Salzburger et al., 2002) evidence. The present study was undertaken to clarify the comprehensive relationships of Tanganyikan cichlid fishes on the basis of internal and external morphological characters, using Tylochromini as outgroup. A new classification system reflecting their relationships is proposed.

Materials and Methods

Ingroups comprised 52 genera (67 species) representing 11 of Poll's (1986) tribes, including all 46 genera endemic to

Table 1. Comparison between Poll's (1986) tribal classification of Tanganyikan cichlid fishes and morphological and molecular phylogenetic studies

Poll's (1986) tribe	Morphological phylogeny		Molecular phylogeny	
	Monophyly	Reference	Monophyly[a]	Reference
Bathybatini	Yes	Lippitsch, 1998	—	—
	No	Stiassny, 1981		
Cyprichromini	Yes	Lippitsch, 1998	—	—
Ectodini	Yes	Greenwood, 1983; Lippitsch, 1998; Takahashi, 2003a, b	Yes	Sturmbauer and Meyer, 1993; Takahashi et al., 1998; Salzburger et al., 2002
Eretmodini	Yes	Liem, 1979; Lippitsch, 1998	Yes	Salzburger et al., 2002
Haplochromini	—	—	—	—
Lamprologini	Yes	Stiassny, 1997; Lippitsch, 1998	Yes	Takahashi et al., 1998; Salzburger et al., 2002
Limnochromini	No	Lippitsch, 1998	No	Kocher et al., 1995; Salzburger et al., 2002
Perissodini	—	—	Yes	Takahashi et al., 1998; Salzburger et al., 2002
Tilapiini	—	—	—	—
Trematocarini	Yes	Stiassny, 1981; Lippitsch, 1998; Takahashi, 2002, 2003b	—	—
Tropheini	No	Lippitsch, 1998	No	Kocher et al., 1995; Salzburger et al., 2002
Tylochromini	Yes	Stiassny, 1989	—	—

[a] Supported by high bootstrap value (>90%) or insertion of short interspersed repetitive elements (SINEs)

Lake Tanganyika. The outgroup comprised Tylochromini, represented by five *Tylochromis* species. A single specimen of each species was dissected. In undissected specimens, external characters 6–9, 19, 20, 22, 31–35, and 37 and an internal character 36 were determined, the latter being discernible from radiographs. Dissections and drawings of specimens were done using a binocular microscope (Nikon SMZ-1000 and Leica MZ12). Osteological characters were examined in specimens stained with Alizarin Red-S in 75% ethyl alcohol or 50% 2-propanol. Osteological and myological terminologies followed Johnson et al. (1996) and Winterbottom (1974), respectively. The term anteriormost infraorbital is used instead of lacrimal. Scale row number between the upper lateral line and body axis was counted at the center of the body, between (and exclusive of) the scale rows bearing the upper lateral line and on the body axis, which bore the lower lateral line when it was present. Standard length was measured with dividers or Mitutoyo Absolute Digimatic Solar Calipers to the nearest 0.1 mm.

A data matrix of 37 characters for all 72 taxa was analyzed with PAUP ver. 3.0s (Swofford, 1991), using the heuristic algorithm of the maximum-parsimonious (MP) analysis with 100 random addition replicates (starting seed = 1). The maximum tree number to be saved was set at 1000. Characters were not weighted. To avoid imposing unjustified models of evolution, multistate characters were treated as unordered. A question mark in the matrix indicates missing data. Trees were rooted by comparisons with the outgroups. Consistency (CI) and retention indices (RI) for the cladogram as a whole and for each character were generated using PAUP.

Results

Characters used in the analysis. Characters and state numbers correspond to the numbers in the data matrix (Table 2). CI and RI for each character follow the character description; when equivalent, only one number is shown. Among all of the observed internal and external morphological features, 37 informative characters for the analysis were found.

Character 1: infraorbitals.—(0) type A (sensu Takahashi, 2003a), basically composed of six elements, lateral line on anteriormost infraorbital (IO1) branched into five tubules, opening at these external ends, each of the other infraorbitals (IO2–IO6) bearing a tube like structure, opening at both ends; (1) type B, composed of four elements, elongated IO2 not overlapping IO1; (2) type C, lateral line opening through extremely well-developed foramina, adjacent foramina being almost in contact, no dermosphenotic; (3) type D, atrophied between IO1 and dermosphenotic (or usual dermosphenotic position); (4) type F, lateral walls of tubules on IO1 deeply notched; (5) type G, composed of three elements, elongated IO2 not overlapping IO1; (6) type H, no tube like structure on IO2. See Takahashi (2003a) for detailed descriptions of the infraorbital types. (0.857, 0.966)

Character 2: ethmovomerine region.—(0) tylochromine type (sensu Takahashi, 2001), mesethmoid arm reaching vomer, dorsal bony bridge similar width or broader than mesethmoid arm, dorsolateral fenestra large; (1) bathybatine type, mesethmoid arm reaching vomer, dorsal bony bridge narrower than mesethmoid arm or absent,

Table 2. Character matrix of Tanganyikan cichlid fishes for cladistic analysis

	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–
Ingroups								
Bathybatini								
Bathybates fasciatus	41001	00000	00001	00200	11100	00121	00020	00
Bathybates graueri	41001	00000	00001	00200	11100	00121	00020	00
Bathybates minor	41001	00000	00001	00200	11100	00121	00a20	00
Hemibates stenosoma	01011	00000	00001	00200	11000	00011	00a20	00
Trematocara macrostoma	21011	00000	00001	00200	21010	01111	11110	00
Trematocara marginatum	21011	00000	00101	00200	21010	01111	11110	00
Trematocara nigrifrons	21011	00000	00101	00200	21010	01111	11110	00
Benthochromini								
Benthochromis tricoti	00010	00000	00001	00200	01000	00031	00022	00
Boulengerochromini								
Boulengerochromis microlepis	00010	00000	00000	02000	01000	00031	00020	00
Cyphotilapiini								
Cyphotilapia frontosa	02000	00000	00000	00200	00000	01031	00002	01
Cyphotilapia sp.	02010	00000	00000	00200	00000	01031	00022	01
Cyprichromini								
Cyprichromis microlepidotus	04110	00000	00001	00200	11000	00031	10022	10
Cyprichromis sp.	04110	00000	00001	00200	11000	00031	10022	10
Paracyprichromis brieni	64110	00000	00001	00100	11000	00031	10002	00
Ectodini								
Aulonocranus dewindti	12010	00000	01001	00100	11000	00031	10002	00
Callochromis macrops	12010	00000	01001	00100	01000	00031	10002	00
Cardiopharynx schoutedeni	12010	00000	01001	00100	11000	00031	10002	00
Cunningtonia longiventralis	12010	30010	01001	00100	11000	00031	10022	00
Cyathopharynx furcifer	12010	00000	01001	00100	11000	00031	10022	00
Ectodus descampsi	12010	00000	01001	00100	11000	00031	10002	00
Grammatotria lemairii	12010	00000	01001	00200	01000	00031	10022	00
Lestradea perspicax	12010	00000	01001	00100	11000	00031	10002	00
Ophthalmotilapia nasuta	12010	00000	01001	00100	11000	00031	100b2	00
Xenotilapia boulengeri	15010	00000	01001	00200	01000	00031	10002	00
Xenotilapia leptura	15010	30010	01001	00100	01000	00031	10002	00
Xenotilapia melanogenys	15010	00000	01000	00200	01000	00031	10002	00
Xenotilapia tenuidentata	15010	000b0	01001	00200	01000	00031	10002	00
Eretmodini								
Eretmodus cyanostictus	04000	00121	00001	00201	00000	01031	10102	00
Spathodus marlieri	04000	00121	00000	01201	00000	01031	10102	00
Tanganicodus irsacae	04010	00120	00000	00201	00000	01031	10102	00
Greenwoodochromini								
Greenwoodochromis christyi	00011	00000	00000	00200	00000	01031	00022	00
Haplochromini								
Astatoreochromis straeleni	02000	20010	00000	000a0	?0000	01031	10002	00
Astatotilapia burtoni	02010	20010	00000	00000	00000	01031	10002	00
Lamprologini								
Altolamprologus compressiceps	34100	01001	10000	01121	10001	01031	10102	00
Chalinochromis brichardi	34000	01001	00010	00111	10001	01031	10102	00
Julidochromis ornatus	34000	01001	00010	00111	10001	01031	10102	00
Lamprologus lemairii	34110	01000	10000	02211	00001	01031	10102	00
Lepidiolamprologus attenuatus	33100	01000	10000	01211	10001	01031	10122	00
Lepidiolamprologus elongatus	33100	01000	10000	01111	10001	01031	10122	00
Neolamprologus fasciatus	34100	01000	10000	01121	10001	01031	10102	00
Neolamprologus tetracanthus	34000	01000	00000	02211	10001	01031	10102	00
Telmatochromis temporalis	34000	3a010	00000	00111	00001	01031	10102	00
Variabilichromis moorii	04000	01000	00000	01111	10001	01031	10102	00
Limnochromini								
Baileychromis centropomoides	50010	00000	00001	00100	12000	01130	00022	00
Gnathochromis permaxillaris	54010	00002	00000	00100	00000	01031	00002	00
Limnochromis auritus	50010	00000	00000	00200	00000	01031	00002	00

Table 2. *Continued*

	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–
Reganochromis calliurus	50010	00000	00000	00200	02000	01030	00002	00
Tangachromis dhanisi	54010	00000	00000	00200	00000	01031	00002	00
Triglachromis otostigma	54010	00000	00000	00100	00000	01031	00002	00
Perissodini								
Haplotaxodon microlepis	02010	00020	00000	00200	01000	01031	00022	00
Perissodus microlepis	02010	10020	00000	00200	01000	10031	00020	00
Plecodus paradoxus	02010	10020	00000	00200	01000	11031	00020	00
Xenochromis hecqui	05010	10020	00000	00200	01000	01031	10022	00
Tilapiini								
Oreochromis karomo	04010	20010	00000	10000	?0000	01031	00000	00
Oreochromis niloticus eduardianus	04010	20010	00000	10000	00000	01031	00000	00
Oreochromis tanganicae	04010	30010	00000	10000	00000	01031	00000	00
Tilapia rendalli	04011	20010	00000	10000	?0000	00031	00000	00
Tropheini								
“Ctenochromis” horei	02010	00010	00000	00000	00000	01031	00101	00
“Gnathochromis” pfefferi	02010	00010	00000	00100	00000	01031	00001	00
Interochromis loocki	02000	20010	00000	00000	00000	01031	00001	00
Limnotilapia dardennii	02000	20010	00000	00000	00000	01031	00001	00
Lobochilotes labiatus	02000	00000	00000	00000	00000	01031	00001	00
Petrochromis fasciolatus	02000	30010	00000	00000	00000	01031	00001	00
Pseudosimochromis curvifrons	02001	20010	00000	00000	00000	01031	00001	00
Simochromis diagramma	02000	20010	00000	00000	00000	01031	00001	00
Tropheus moorii	02000	20010	00000	00010	00000	01031	00001	00
New tribe								
“Ctenochromis” benthicola	02010	00000	00000	00200	10000	01031	10002	00
Outgroups								
Tylochromini								
Tylochromis jentinki	00000	00000	00000	01000	?1000	01000	00000	00
Tylochromis labrodon	00010	00000	00000	00000	?0000	00000	00000	00
Tylochromis lateralis	00000	00000	00000	00000	?0000	00000	00000	00
Tylochromis polylepis	00000	00000	00000	00000	01000	00000	00020	00
Tylochromis variabilis	00010	00000	00000	01000	?0000	00000	00000	00

Character numbers as in text
Tribes follow the classification proposed by the present study
a, “0&1”; b, “0&2”

dorsolateral fenestra present; (2) haplochromine type, mesethmoid arm reaching vomer, dorsal bony bridge similar width or broader than mesethmoid arm, dorsolateral fenestra narrow or absent; (3) lepidiolamprologine type, mesethmoid arm reaching vomer, dorsal bony bridge narrower than mesethmoid arm, dorsolateral fenestra absent; (4) oreochromine type, mesethmoid arm absent; (5) asprotilapiine type, mesethmoid arm not reaching vomer. See Takahashi (2001) for detailed descriptions of the ethmovomerine types. (0.455, 0.854)

Character 3: neurocranial lateral line foramen 0 (NLF0).—(0) combined with opposite member into a single pore; (1) separated from opposite member. Stiassny (1991, 1992) treated the combined NLF0 as a synapomorphy of all cichlid fishes except ptychochromines, the most primitive group within the family. Stiassny (1992) also showed that some species of the lamprologine subgroup (=Lamprologini) had the plesiomorphic configuration (NLF0 pores distinctly separated), which she treated as a reversal. In the present study, separated NLF0 were also observed in Cyprichromini. (0.333, 0.714)

Character 4: epioccipital.—(0) projecting ventrally, sutured to pterotic (Fig. 1A); (1) not projecting ventrally, separated from pterotic (Fig. 1B). (0.100, 0.640 in 15 MP trees, 0.111, 0.680 in 129 MP trees, 0.125, 0.720 in 72 MP trees)

Character 5: intercalar.—(0) not extending anteriorly, exoccipital connected with pterotic (Fig. 2A); (1) extending anteriorly, inserted between exoccipital and pterotic which are separated, often reaching prootic (Fig. 2B). (0.250, 0.667)

Character 6: shape of outer teeth on both jaws.—(0) unicuspid, slightly recurved; (1) unicuspid, strongly recurved; (2) bicuspid, unicuspid teeth often present posteriorly on jaws; (3) tricuspid, unicuspid teeth often present posteriorly on jaws. Detailed character description of state 1 given in Liem and Stewart (1976). Pellegrin (1904), Poll (1956, 1986),

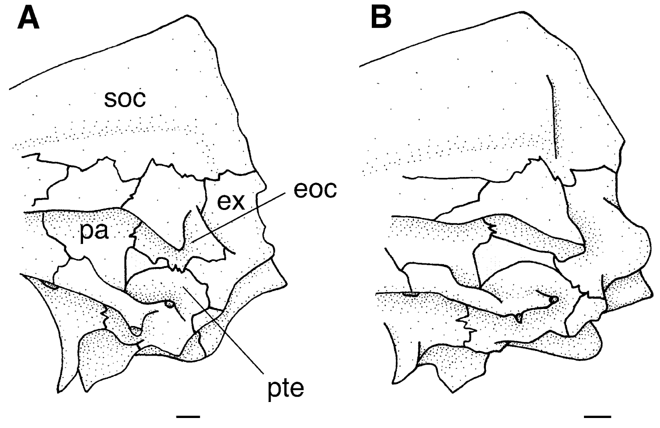

Fig. 1. Dorsolateral view of posterior part of neurocranium. **A** *Tropheus moorii*; **B** *"Ctenochromis" horei*. *eoc*, epioccipital; *ex*, exoccipital; *pa*, parietal, *pte*, pterotic; *soc*, supraoccipital. *Bars* 1 mm

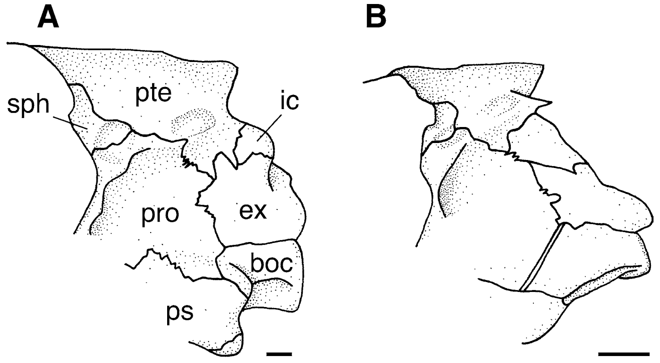

Fig. 2. Ventrolateral view of posterior part of neurocranium. **A** *"Ctenochromis" horei*; **B** *Trematocara marginatum*. *boc*, basioccipital; *ex*, exoccipital; *ic*, intercalar; *pro*, prootic; *ps* parasphenoid; *pte*, pterotic; *sph*, sphenotic. *Bars* 1 mm

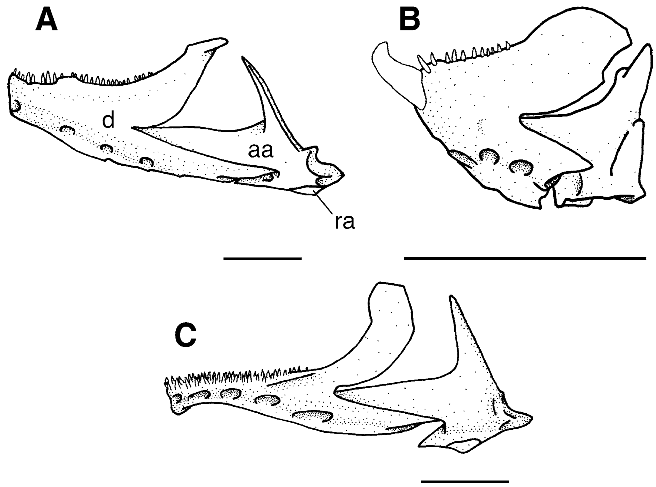

Fig. 3. Lateral view of lower jaw. **A** *Hemibates stenosoma*; **B** *Chalinochromis brichardi*; **C** *Gnathochromis permaxillaris*. *aa*, anguloarticular; *d*, dentary; *ra*, retroarticular. *Bars* 5 mm

Trewavas (1983), Yamaoka (1987), and Takahashi and Nakaya (1997) described ontogenetic variations of the outer tooth shape in several Tanganyikan cichlids. In the present study, however, only the adult condition was considered, because of the scarcity of young specimens. (0.375, 0.667 in 81 MP trees, 0.429, 0.733 in 135 MP trees)

Character 7: anteriormost four to ten outer teeth on upper jaw.—(0) equal size to or a little larger than other outer teeth (Poll, 1986: fig. 1); (1) larger than other outer teeth, among these large teeth, tooth on each side largest, others smaller medially (Poll, 1986: fig. 11). In *Telmatochromis*, both states are found, the character being coded as polymorphic (0&1). (1.000)

Character 8: arrangement of outer teeth on both jaws.—(0) a regular single row; (1) divided into three to five groups, each group consisting of three to four teeth arranged in a tier. Detailed description of latter state given in Yamaoka et al. (1986). (1.000)

Character 9: shape of inner teeth on both jaws.—(0) unicuspid; (1) tricuspid; (2) inner teeth absent. In *Xenotilapia tenuidentata*, the inner teeth are unicuspid or absent, the character being coded as polymorphic (0&2). Poll (1956, 1986), Yamaoka (1987), and Takahashi and Nakaya (1997) described ontogenetic variations of the inner tooth shape in several Tanganyikan cichlids. In the present study, however, only the adult condition was considered, because of the scarcity of young specimens. (0.375, 0.773 in 81 MP trees, 0.429, 0.818 in 135 MP trees)

Character 10: number of lateral line foramina on dentary.—(0) five (Fig. 3A); (1) four (Fig. 3B); (2) six (Fig. 3C). (0.500)

Character 11: labial cartilage.—(0) unossified; (1) ossified. Detailed description of latter state given in Stiassny (1997). (0.500, 0.750)

Character 12: palatopterygoid gap.—(0) absent; (1) present, broadly separating endopterygoid and palatine. Liem (1981) and Greenwood (1983) treated the palatopterygoid gap as a synapomorphy supporting the monophyly of five and ten genera, respectively, of Ectodini. During the present study, however, such a gap was observed in all Ectodini taxa. (1.000)

Character 13: number of lateral line foramina on preopercle.—(0) seven (Takahashi, 2002: fig. 2A); (1) eight (Takahashi, 2002: fig. 2B). (1.000)

Character 14: hyoid arch.—(0) anterior ceratohyal becoming abruptly slender anterior to midline, interhyal rod-shaped with cartilaginous caps on both ends (Fig. 4A); (1) anterior ceratohyal not becoming slender anteriorly, interhyal rectangular without cartilaginous caps (Fig. 4B). (1.000)

Character 15: projection on anterodorsal surface of urohyal.—(0) present, shape variable (Fig. 5A–C); (1) absent or very small, dorsal surface of urohyal smooth (Fig. 5D). (0.250, 0.875)

Character 16: foramen on posterior wall of fifth ceratobranchial.—(0) absent; (1) present. Detailed foramen description given in Stiassny (1991). (1.000)

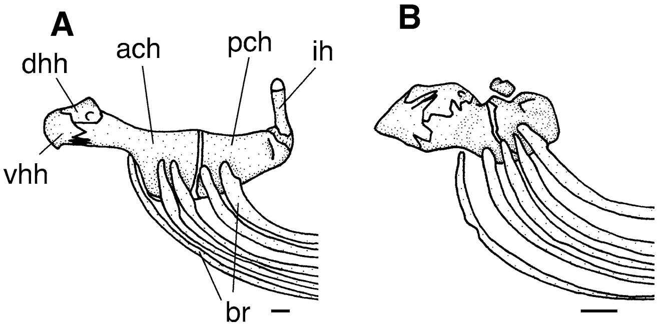

Fig. 4. Lateral view of hyoid arch. **A** *Cyathopharynx furcifer*; **B** *Chalinochromis brichardi*. *ach*, anterior ceratohyal; *br*, branchiostegals; *dhh*, dorsal hypohyal; *ih*, interhyal; *pch*, posterior ceratohyal; *vhh*, ventral hypohyal. *Bars* 1 mm

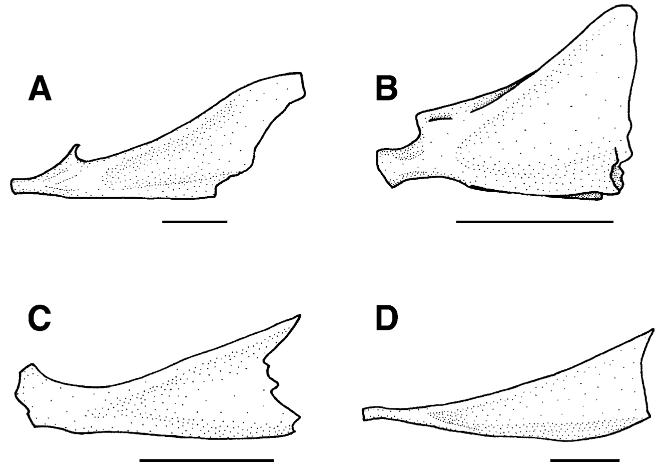

Fig. 5. Lateral view of urohyal. **A** *Haplotaxodon microlepis*; **B** *Tropheus moorii*; **C** *Lepidiolamprologus elongatus*; **D** *Hemibates stenosoma*. *Bars* 5 mm

Character 17: surface of gill rakers on first ceratobranchial.—(0) smooth (Fig. 6A); (1) serrated (Fig. 6B); (2) denticulated on dorsomedial aspect (Fig. 6C,D). Stiassny (1992) described the absence of gill raker denticulations was a synapomorphy of African cichlids. Among Tanganyikan cichlids, she also recognized denticulations in certain Lamprologini, treating such as a reversal because of an apparent ontogenetic sequence. In the present study, this character was observed in *Boulengerochromis*, as well as in two Lamprologini taxa. (0.286, 0.444 in 192 MP trees, 0.333, 0.556 in 24 MP trees)

Character 18: projection on anterior abdominal vertebrae.—(0) large, comprising two parts placed on either side of third or third and fourth vertebrae, and meeting ventrally (Takahashi, 2003b: fig. 5C); (1) small, comprising two parts placed on either side of third, fourth, or fifth vertebrae, and separated ventrally (Takahashi, 2003b: fig. 5B); (2) absent, ventral surfaces of anterior vertebrae smooth (Takahashi, 2003b: fig. 5A). (0.182, 0.769 in 96 MP trees, 0.200, 0.795 in 120 MP trees)

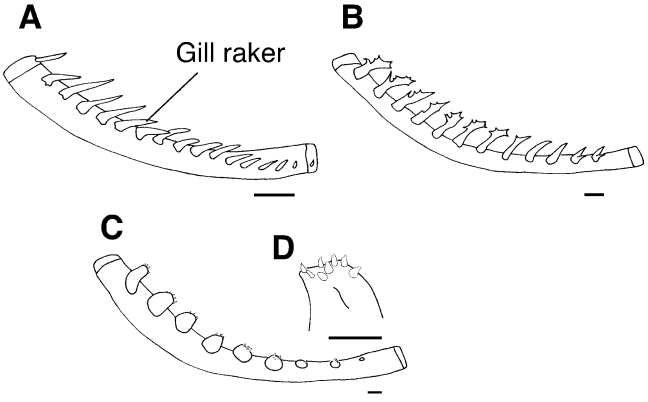

Fig. 6. Lateral view of first ceratobranchial and gill rakers in outer row (**A–C**) and anteromedial view of gill raker (**D**). **A** *Perissodus microlepis*; **B** *Lepidiolamprologus elongatus*; **C,D** *Lamprologus lemairii*. *Bars* 1 mm

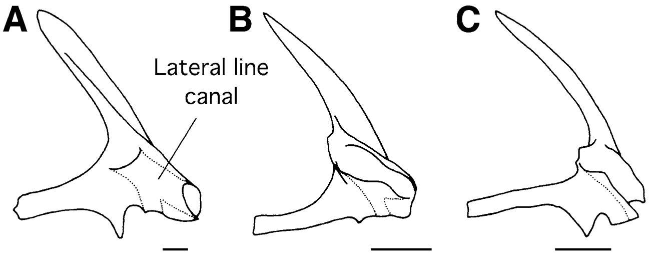

Fig. 7. Lateral view of posttemporal. **A** *Oreochromis niloticus eduardianus*; **B** *Ectodus descampsi*; **C** *Trematocara nigrifrons*. *Bars* 1 mm

Character 19: number of anal spines.—(0) three; (1) four to nine; (2) ten or more. The character is coded such that states do not overlap in any taxa, with the exception of *Astatoreochromis*, in which the anal spine number ranges from three to four (Poll, 1974), the character being coded as polymorphic (0&1). (0.750, 0.889)

Character 20: posterior outline of pectoral fin.—(0) acutely pointed (Poll, 1986: fig. 1); (1) rounded (Poll, 1986: fig. 17). (1.000)

Character 21: lateral line canal on posttemporal.—(0) opening through three foramina (Fig. 7A); (1) two foramina at anterior and posterior ends of canal continuous, forming a single large foramen (Fig. 7B); (2) all three foramina continuous, forming a single, extremely large foramen (Fig. 7C). *Astatoreochromis*, *Oreochromis karomo*, *Tilapia*, and Tylochromini (except *Tylochromis polylepis*) not examined. (0.250, 0.760 in 120 MP trees, 0.286, 0.800 in 96 MP trees)

Character 22: outline of caudal fin.—(0) rounded, truncated, or emarginated (Poll, 1986: fig. 1), but these conditions not separable because of intraspecific variations; (1) forked (Poll, 1986: fig. 2); (2) upper lobe a little elongated posteriorly, lower lobe rounded (Poll, 1986: fig. 47). (0.667, 0.968)

Character 23: tendon "a" of adductor mandibulae section 1.—(0) elongated; (1) reduced. Detailed description of latter state given in Stiassny (1981). (1.000)

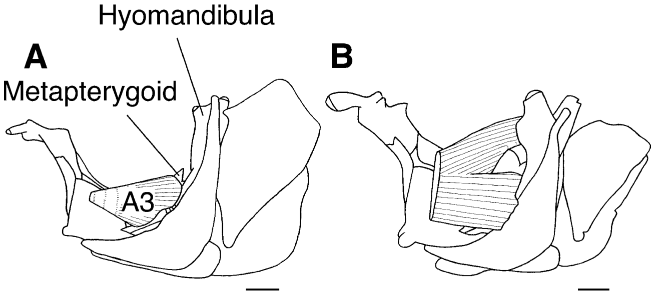

Fig. 8. Lateral view of adductor mandibulae section 3 (*A3*). **A** *Hemibates stenosoma*; **B** *Lamprologus lemairii*. *Bars* 5 mm

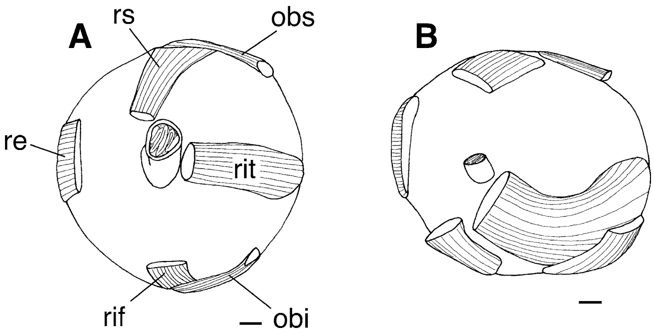

Fig. 9. Medial view of eye. **A** *Oreochromis niloticus eduardianus*; **B** *Bathybates fasciatus*. *obi*, obliquus inferior; *obs*, obliquus superior; *re*, rectus externus; *rif*, rectus inferior; *rit*, rectus internus; *rs*, rectus superior. *Bars* 5 mm

Character 24: tendon "c" of adductor mandibulae section 1.—(0) absent; (1) present. Detailed description of this tendon given in Stiassny (1981). (1.000)

Character 25: adductor mandibulae section 3.—(0) originating posteriorly from metapterygoid (Fig. 8A); (1) posterior part dorsally extended, originating from both metapterygoid and hyomandibula (Fig. 8B). (1.000)

Character 26: intermandibularis.—(0) present; (1) absent (Liem and Stewart, 1976: fig. 10B). (1.000)

Character 27: extrascapular epaxial muscle slip.—(0) present, inserted onto proximal extrascapula; (1) absent. Stiassny (1989, 1990) described the extrascapular epaxial muscle slip as a synapomorphy supporting the genus *Tylochromis*. In the present study, however, this slip was also found in many other Tanganyikan genera. (0.200, 0852)

Character 28: obliquus inferior.—(0) overlying rectus inferior (Fig. 9A); (1) separated from rectus inferior (Fig. 9B). The obliquus superior generally overlies the rectus superior, but these muscles are separated in *Baileychromis*, *Bathybates*, and *Trematocara* (Fig. 9). Because this condition is completely linked with character 28, the overall condition was treated as a single character. (0.500, 0.833)

Character 29: anterior ethmopalatine ligament.—(0) inserted dorsally onto both vomer and lateral ethmoid; (1) extending beyond vomer to mesethmoid (Stiassny, 1981: fig. 5); (2) absent (Stiassny, 1981: fig. 4); (3) inserted onto ventral aspect of lateral ethmoid (Stiassny, 1981: fig. 2). Stiassny (1981) treated variations of the anterior ethmopalatine ligament as two separate characters in her cladistic analysis, i.e., presence or absence of "palatine-lateral ethmoid ligament" and presence or absence of "palatine-mesethmoid ligament." In the present study, these two ligaments were considered homologous, owing to the ligaments, which never occur together, having identical origins on the palatine. (1.000)

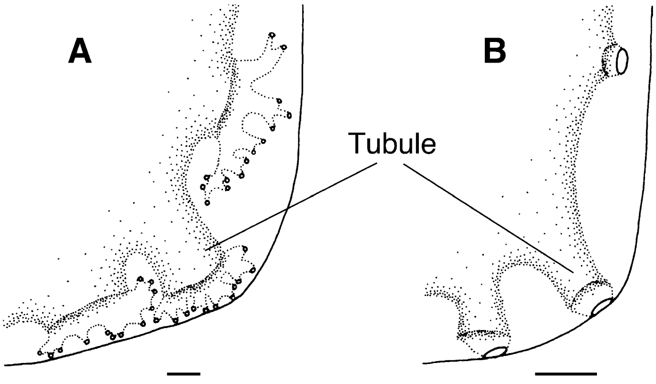

Fig. 10. Tubules on preopercle. **A** *Bathybates graueri*; **B** *Astatotilapia burtoni*. *Bars* 1 mm

Character 30: ligament connecting palatine to anteriormost infraorbital.—(0) absent; (1) present. Detailed description of the former state given in Stiassny (1989). (0.500, 0.833)

Character 31: tubules extending from lateral line canals on preopercle and anteriormost infraorbital.—(0) each branching into a few or several secondary tubules (Fig. 10A); (1) each not branching (Fig. 10B). (0.200, 0.886)

Character 32: scales with a canal on lower lateral line.—(0) present (Poll, 1986: fig. 1); (1) absent (Poll, 1986: fig. 46). (1.000)

Character 33: cheek scales.—(0) arranged in several rows (Poll, 1986: fig. 1); (1) absent (Poll, 1986: fig. 6). In *Bathybates minor* and *Hemibates*, the cheek is naked or covered by scales only on the upper half, the character being coded as ambiguous (0&1). (0.600, 0.875)

Character 34: number of scale rows between upper lateral line and body axis.—(0) two, with no intraspecific variations; (1) one, with no intraspecific variations; (2) three or more, sometimes with intraspecific variations. The character is coded such that states do not overlap in any taxa, with the exception of *Ophthalmotilapia*. One of three specimens of *Ophthalmotilapia*, collected from the northwestern region of the lake, possessed three scale rows between upper lateral line and body axis. Although Hanssens and Snoeks (1999) described the scale row number of *Ophthalmotilapia nasuta* was two, sampling locality and other morphological characters of the present specimen were included in the ranges of this species. Therefore, this specimen was identified with *O. nasuta*, the number of scale rows between upper lateral line and body axis of this species being extended to two or three. Therefore, the character was coded as polymorphic (0&2) in *Ophthalmotilapia*. (0.333, 0.727)

Character 35: midbody scales between upper and lower lateral lines.—(0) cycloid, granulation absent (Fig. 11A) or present restricted to sector region in middle of caudal field,

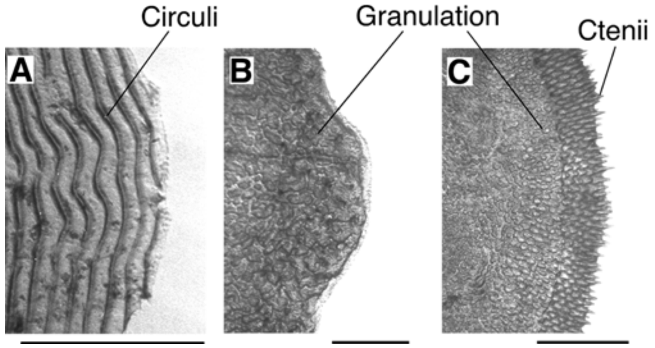

Fig. 11. Caudal region of scale at midbody between upper and lower lateral lines. **A** *Tylochromis polylepis*; **B** *Tropheus moorii*; **C** *Lamprologus lemairii*. *Bars* 1 mm

consisting of regularly arranged, oblong or near-circular protrusions; present and absent conditions of such granulation not separable because of intraspecific variations; (1) cycloid, granulation extending over almost entire exposed part of scale, consisting of irregularly arranged, variously shaped protrusions (Fig. 11B); (2) ctenoid, granulation restricted to posterior marginal region of scale or extending over almost entire exposed part, consisting of caudal or radially directed ctenii; extent of such granulation not separable due to various intermediate conditions (Fig. 11C). (0.333, 0.846 in 135 MP trees, 0.400, 0.885 in 81 MP trees)

Character 36: abdominal cavity.—(0) not extending posteriorly; (1) extending posteriorly beyond anal fin origin. Detailed description of latter state given in Poll (1981, 1986) and Büscher (1994). (1.000)

Character 37: hump on forehead.—(0) absent or small, never projecting anteriorly; (1) present, more developed with growth, projecting anteriorly in large adult (Takahashi and Nakaya, 2003: fig. 3). (1.000)

Cladistic analysis. As a result of the analysis, 216 maximum-parsimonious trees were obtained (TL = 142, CI = 0.458, RI = 0.845). Strict consensus tree and character optimizations on each branch are shown in Fig. 12 and Table 3. The multiple furcations within clades I, Q, V, AF, AG, and BM are the result of insufficient rather than conflicting data; no characters were found to resolve the relationships. The multiple furcations within clades AO and AU are the result of conflict between characters 4, 6, 9, and 35 and 4, 17, 18, and 21, respectively.

Discussion

Poll (1986) classified the Tanganyikan cichlid fishes into 12 tribes. However, the present morphological analysis treating 11 tribes as ingroups, and Tylochromini as an outgroup, showed that each of 6 tribes was a monophyletic group, viz. Cyprichromini, Ectodini, Eretmodini, Lamprologini, Perissodini, and Trematocarini, and the remaining 5 tribes were each nonmonophyletic (Fig. 12). These results agree with other morphological and molecular phylogenetic studies except for Bathybatini, which was treated as a monophyletic group by Lippitsch (1998) (Table 1).

Poll (1986) recognized two genera, *Bathybates* and *Hemibates*, in Bathybatini. The present morphological cladogram and Stiassny's (1981) analysis indicated that Bathybatini was paraphyletic unless Trematocarini was included (clade F), despite the conflicting phylogenetic position of *Hemibates* in these analyses, the genus being a sister group of Trematocarini according to Stiassny (1981). Lippitsch (1998) proposed Bathybatini and Trematocarini shared three lepidological synapomorphies, although she treated the former as a monophyly. Trematocarini is therefore treated as a junior synonym of Bathybatini, being in agreement with the classification of Stiassny (1997).

Poll's (1986) Tilapiini was separated into two clades; the first including *Boulengerochromis* (clade A) and the second including *Oreochromis* and *Tilapia* (clade BM). The separation of *Boulengerochromis* from the other Tilapiini taxa is supported by some previous molecular phylogenies, although the bootstrap probabilities were always low (less than 75%) (Kocher et al., 1995; Nishida, 1997; Salzburger et al., 2002). A new tribe, therefore, should be established for *Boulengerochromis*.

In clade AO of the present cladogram, the relationships among clade BL [Poll's (1986) Haplochromini, except *Ctenochromis*], clade BM (Poll's Tilapiini, except *Boulengerochromis*), Poll's Tropheini taxa (except *Cyphotilapia*), *Ctenochromis horei*, and *Gnathochromis pfefferi* were unresolved. The conflicting branching patterns within the clade were classified into two patterns: in the first, *Ctenochromis horei*, *G. pfefferi*, and Tropheini (except *Cyphotilapia*) were closely affiliated (clade BO, Fig. 13A), and in the second, *Lobochilotes* was placed at the basal position of the clade, *Ctenochromis horei* and *G. pfefferi* branching next, and other taxa forming clade BP (Fig. 13B). In the other studies, the lepidological analysis of Lippitsch (1998) indicated that *G. pfefferi* resembled the members of Tropheini. According to some molecular phylogenies, *G. pfefferi* and *Lobochilotes* belonged to the Tropheini clade, but Haplochromini (*Astatoreochromis* and *Astatotilapia*) and Tilapiini (*Oreochromis*) were excluded from the clade (such a Tropheini clade was supported by 97% bootstrap probability in Salzburger et al., 2002, 78% in Kocher et al., 1995). Additionally, Nishida (1997) included *Ctenochromis horei* in the Tropheini clade, although this clade was not supported by the bootstrap consensus tree. Therefore, clade BO (Fig. 13A) is more likely to be monophyletic than clade BP (Fig. 13B). In the present morphological tree, *Cyphotilapia* (clade AM) was excluded from the Tropheini clade BO, although Poll (1986) treated the former as a member of Tropheini. Lepidological study (Lippitsch, 1998) and molecular trees (Kocher et al., 1995; Nishida, 1997; Salzburger et al., 2002) lend support to the present result rather than to Poll's (1986) classification of *Cyphotilapia*. Tropheini, therefore, should include *Ctenochromis horei* and *Gnathochromis pfefferi* but exclude *Cyphotilapia*. A new tribe should be established for *Cyphotilapia*.

Poll's (1986) Limnochromini was separated into four clades, the first including *Benthochromis* (sister group of

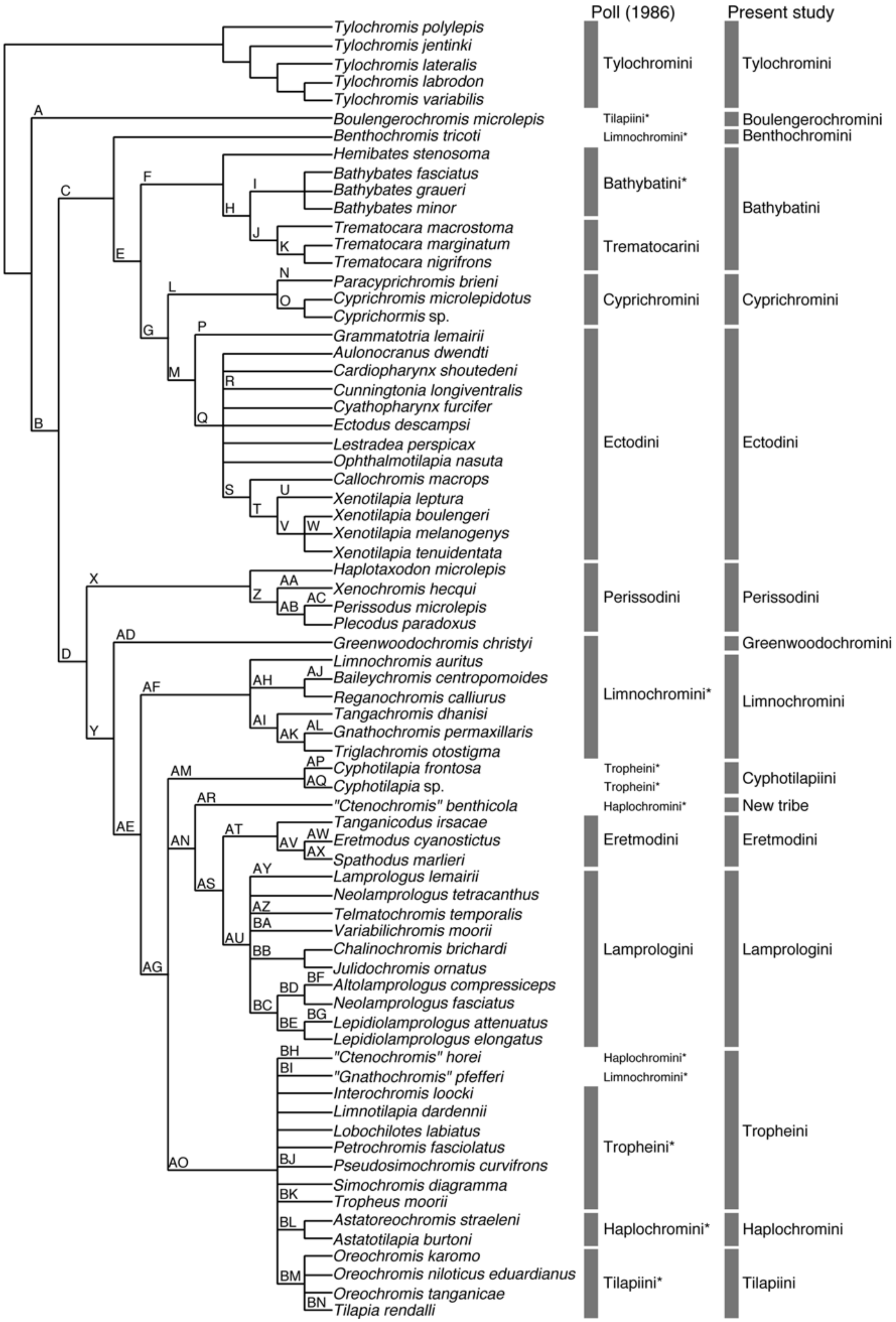

Fig. 12. Strict consensus tree of 216 cladograms generated by parsimony analysis of 37 morphological characters for 67 species representing 52 genera of Tanganyikan cichlids (ingroup) and five Tylochromini species (outgroup) (tree length 142, consistency index 0.458, retention index 0.845). Classifications of Poll (1986) and the present study are shown. *Asterisk* indicates tribe not forming a clade. Character state changes listed in Table 3

Table 3. Character optimizations on branches of strict consensus tree of maximum parsimonious trees (see Fig. 12)

Branch	Character (plesiomorphy-apomorphy)
A	17 (0–2)
B	18 (0–2), 35(0–2)
C	15 (0–1)
D	27 (0–1)
E	21 (0–1)
F	2 (0–1)D, 5 (0–1), 29 (3–1), 35 (2–0)
G	31 (0–1)
H	28 (0–1)
I	1 (0–4)D, 4 (1–0), 23 (0–1), 29 (1–2)
J	1 (0–2)D, 21 (1–2), 24 (0–1), 27 (0–1), 31 (0–1), 32 (0–1), 33 (0–1), 34 (2–1)
K	13 (0–1)
L	2 (0–4)D, 3 (0–1)
M	1 (0–1), 2 (0–2)D, 12 (0–1)
N	1 (0–6), 18 (2–1), 34 (2–0)
O	36 (0–1)
P	21 (1–0)
Q	18 (2–1)
R	6 (0–3), 9 (0–1)
S	21 (1–0)
T	2 (2–5)
U	6 (0–3), 9 (0–1)
V	18 (1–2)
W	15 (1–0)
X	2 (0–2), 9 (0–2)
Y	22 (1–0)
Z	6 (0–1)
AA	2 (2–5), 31 (0–1)
AB	26 (0–1), 35 (2–0)
AC	27 (1–0)
AD	5 (0–1)
AE	34 (2–0)
AF	1 (0–5)
AG	2 (0–2)
AH	22 (0–2), 30 (1–0)
AI	2 (0–4)
AJ	15 (0–1), 18 (2–1), 21 (0–1), 28 (0–1), 34 (0–2)
AK	18 (2–1)
AL	10 (0–2)
AM	37 (0–1)
AN	31 (0–1)
AO	18 (2–0)
AP	4 (1–0)
AQ	34 (0–2)
AR	21 (0–1)
AS	2 (2–4), 20 (0–1), 33 (0–1)
AT	8 (0–1), 9 (0–2)
AU	1 (0–3), 7 (0–1), 19 (0–1), 25 (0–1)
AV	4 (1–0) or (1–0)D, 10 (0–1)
AW	15 (0–1)
AX	17 (0–1)
AY	3 (0–1), 11 (0–1)
AZ	6 (0–3), 9 (0–1)
BA	1 (3–0)
BB	10 (0–1), 14 (0–1)
BC	3 (0–1), 11 (0–1)
BD	19 (1–2)
BE	2 (4–3), 34 (0–2)
BF	10 (0–1)
BG	18 (1–2)
BH	33 (0–1)
BI	18 (0–1)
BJ	5 (0–1)
BK	19 (0–1)
BL	31 (0–1)
BM	2 (2–4), 16 (0–1), 35 (1–0) or (1–0)D or (2–0)
BN	5 (0–1), 27 (1–0)

Characters 4, 6, 9, 17, 18, 21, 34, and 35 only partially indicated owing to uncertain optimization

"D" following parentheses indicates transformations found with DELTRAN only; others found with both ACCTRAN and DELTRAN

clade E), the second including *Greenwoodochromis* (clade AD), the third including *Gnathochromis pfefferi* (clade BI), and the fourth including the remaining Limnochromini taxa (clade AF). As discussed above, *G. pfefferi* is included in the revised Tropheini. Because clade AF includes *Limnochromis*, this clade was treated as a revised Limnochromini, necessitating the establishment of two new tribes for *Benthochromis* and *Greenwoodochromis*.

Poll's (1986) Haplochromini was separated into three clades; the first including *Ctenochromis benthicola* (clade AR), the second including *C. horei* (clade BH), and the third including *Astatoreochromis* and *Astatotilapia* (clade BL). As already discussed, *C. horei* is a member of the revised Tropheini. As for the first and third clades, it could not be concluded which was the more appropriate for Haplochromini, because the phylogenetic position of the type genus, *Haplochromis*, was not resolved in the present study. Mayer et al. (1998) and Verheyen et al. (2003) suggested a single ancestor for *Astatoreochromis*, *Astatotilapia*, and Victorian *Haplochromis* species, based on DNA sequences. Therefore, Haplochromini is tentatively recognized for the third clade (*Astatoreochromis* and *Astatotilapia*), with a new tribe being required for *C. benthicola*.

In the present cladogram, the revised Tilapiini (clade BM, including *Oreochromis* and *Tilapia*) was closely affiliated with Haplochromini (clade BL, including *Astatoreochromis* and *Astatotilapia*), but relatively basal among African lineage in the molecular studies (Meyer, 1993; Nishida, 1997; Salzburger et al., 2002). Tilapiini and Haplochromini are distributed in rivers and lakes of Africa, not being endemic to Lake Tanganyika (Trewavas, 1983; Barel et al., 1991). If an ancestor of the African cichlids had been initially distributed in the rivers as the present distribution of Tylochromini (Stiassny, 1989), which was suggested as the oldest lineage of

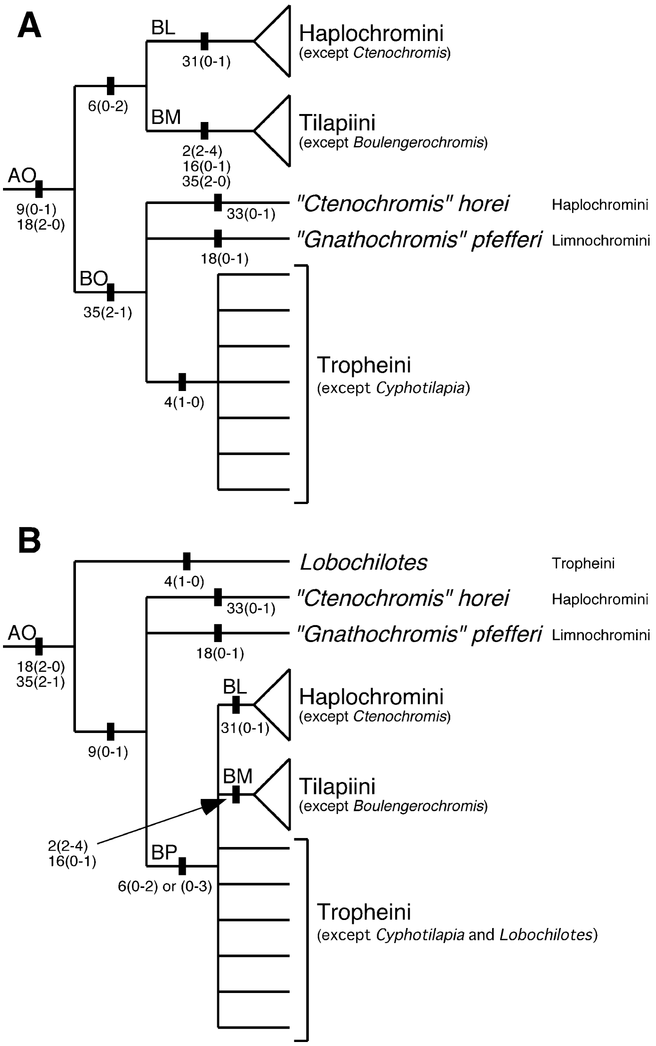

Fig. 13. Two equally parsimonious branching patterns within clade AO. **A** Strict consensus tree of 81 cladograms supporting the monophyly of clade BO. **B** Strict consensus tree of 135 cladograms supporting the monophyly of clade BP. Tribes followed classification of Poll (1986). Character numbers, with plesiomorphic (left) and apomorphic (right) state numbers in parentheses, correspond to those listed in Table 2

African cichlids (Stiassny, 1990, 1991; Lippitsch, 1995; Salzburger et al., 2002), Tilapiini and Haplochromini might have retained plesiomorphies of the African cichlids. The plesiomorphies might join these tribes.

Classification

A revised classification of Tanganyikan cichlid fishes, reflecting their morphological cladogram, recognized 16 tribes, 5 of them new (see Fig. 12). Morphological descriptions are shown in the Results section and Table 2. Distribution of each tribe follows Daget et al. (1991). Brooding method follows Trewavas (1983), Brichard (1989), and Herrmann (1996).

Bathybatini Poll, 1986

Genera. *Bathybates* Boulenger, 1898, *Hemibates* Regan, 1920, and *Trematocara* Boulenger, 1899.

Distribution. Endemic to Lake Tanganyika.

Brooding method. Mouth brooders.

Diagnosis. This tribe is characterized exclusively by a bathybatine type ethmovomerine region (sensu Takahashi, 2001). Anterior ethmopalatine ligament extending to mesethmoid or absent also characterize this tribe [absent also in an African fluvial genus *Hemichromis* (Greenwood, 1985)].

Benthochromini new tribe

Genus. *Benthochromis* Poll, 1986.

Distribution. Endemic to Lake Tanganyika.

Brooding method. Mouth brooder.

Diagnosis. This tribe is characterized by a combination of type A infraorbitals (sensu Takahashi, 2003a), unicuspid outer and inner teeth on both jaws, forked caudal fin, ctenoid scales at midbody, and neurocranial lateral line foramen 0 combined with opposite member into a single pore.

Boulengerochromini new tribe

Genus. *Boulengerochromis* Pellegrin, 1904.

Distribution. Endemic to Lake Tanganyika.

Brooding method. Substrate brooder.

Diagnosis. This tribe is characterized by a combination of type A infraorbitals (sensu Takahashi, 2003a), unicuspid outer and inner teeth on both jaws in adults, bicuspid outer and tricuspid inner teeth in young (Poll, 1986), forked caudal fin, anterior ethmopalatine ligament inserted onto lateral ethmoid, six scale rows between upper lateral line and body axis, and cycloid scales at midbody.

Cyphotilapiini new tribe

Genus. *Cyphotilapia* Regan, 1920.

Distribution. Endemic to Lake Tanganyika.

Brooding method. Mouth brooder.

Diagnosis. This tribe is characterized by hump on forehead, more developed with age.

Cyprichromini Poll, 1986

Genera. *Cyprichromis* Scheuermann, 1977 and *Paracyprichromis* Poll, 1986.

Distribution. Endemic to Lake Tanganyika.

Brooding method. Mouth brooders.

Diagnosis. This tribe is characterized by a combination of neurocranial lateral line foramen 0 separated from opposite member, forked caudal fin, and ctenoid scales at midbody. This tribe is also characterized by a unique spawning system, which does not utilize the substratum (Konings, 1988, 1998; Takahashi et al., 2002).

Ectodini Poll, 1986

Genera. *Aulonocranus* Regan, 1920, *Callochromis* Regan, 1920, *Cardiopharynx* Poll, 1942, *Cunningtonia* Boulenger, 1906, *Cyathopharynx* Regan, 1920, *Ectodus* Boulenger, 1898, *Grammatotria* Boulenger, 1899, *Lestradea* Poll, 1943, *Ophthalmotilapia* Pellegrin, 1904, and *Xenotilapia* Boulenger, 1899.

Distribution. Endemic to Lake Tanganyika (*Aulonocranus* also found in Rusisi and Lukuga Rivers).

Brooding method. Mouth brooders.

Diagnosis. This tribe is characterized exclusively by type B infraorbitals (sensu Takahashi, 2003a) and a palatopterygoid gap.

Eretmodini Poll, 1986

Genera. *Eretmodus* Boulenger, 1898, *Spathodus* Boulenger, 1900, and *Tanganicodus* Poll, 1950.

Distribution. Endemic to Lake Tanganyika.

Brooding method. Mouth brooders.

Diagnosis. This tribe is characterized exclusively by unique dentition on both jaws, in which outer teeth are divided into three to five groups, each group comprising three to four teeth arranged in a tier, and inner teeth are absent.

Greenwoodochromini new tribe

Genus. *Greenwoodochromis* Poll, 1983.

Distribution. Endemic to Lake Tanganyika.

Brooding method. Mouth brooder.

Diagnosis. This tribe is characterized by a combination of type A infraorbitals (sensu Takahashi, 2003a), intercalar extending anteriorly to prootic, unicuspid inner and outer teeth on both jaws, truncate caudal fin, and three scale rows between upper lateral line and body axis.

Haplochromini Trewavas, 1983

Genera. *Astatoreochromis* Pellegrin, 1904 and *Astatotilapia* Pellegrin, 1904.

Distribution. East African rivers and lakes.

Brooding method. Mouth brooders (brooding method of *Astatoreochromis* apparently not reported, but probably a mouth brooder owing to egg spots occurring on anal fin).

Diagnosis. This tribe is characterized by a combination of type A infraorbitals (sensu Takahashi, 2003a), bicuspid outer and tricuspid inner teeth on both jaws, and ctenoid scales at midbody.

Note. The remaining haplochromine genera distributed in the East African Rift Valley (e.g., *Haplochromis* Hilgendorf, 1888, *Cyrtocara* Boulenger, 1902, *Petrotilapia* Trewavas, 1935, etc.) are probably included in this tribe, because they, together with *Astatoreochromis* and *Astatotilapia*, form a single clade in molecular trees (Mayer et al., 1998; Verheyen et al., 2003).

Lamprologini Poll, 1986

Genera. *Altolamprologus* Poll, 1986, *Chalinochromis* Poll, 1974, *Julidochromis* Boulenger, 1898, *Lamprologus* Schilthuis, 1891, *Lepidiolamprologus* Pellegrin, 1904, *Neolamprologus* Colombe and Allgayer, 1985, *Telmatochromis* Boulenger, 1898, and *Variabilichromis* Colombe and Allgayer, 1985.

Distribution. Endemic to Lake Tanganyika excepting seven *Lamprologus* species distributed in Zaire river system.

Brooding method. Substrate brooders.

Diagnosis. This tribe is characterized by a combination of ctenoid scales at midbody, four or more anal fin spines, and dorsally expanded adductor mandibulae section 3. The expanded adductor mandibulae section 3 is unique to the Lamprologini among Tanganyikan cichlids, but is also found in African fluvial genera, *Teleogramma* and *Hemichromis* (Takahashi and Nakaya, 2002).

Limnochromini Poll, 1986

Genera. *Baileychromis* Poll, 1986, *Gnathochromis* Poll, 1981 (excluding *"G." pfefferi*), *Limnochromis* Regan, 1920, *Reganochromis* Whitley, 1929, *Tangachromis* Poll, 1981, and *Triglachromis* Poll and Thys van den Audenaerde, 1974.

Distribution. Endemic to Lake Tanganyika.

Brooding method. Mouth brooders (brooding method unknown for *Baileychromis* and *Tangachromis*).

Diagnosis. This tribe is characterized exclusively by type G infraorbitals (sensu Takahashi, 2003a).

Perissodini Poll, 1986

Genera. *Haplotaxodon* Boulenger, 1906, *Perissodus* Boulenger, 1898, *Plecodus* Boulenger, 1898, and *Xenochromis* Boulenger, 1899.

Distribution. Endemic to Lake Tanganyika.

Brooding method. Mouth brooders (brooding method unknown for *Xenochromis*).

Diagnosis. This tribe is characterized by a combination of the outer teeth on jaws arranged in a single regular row, no inner teeth, and four or five scale rows between upper lateral line and body axis. In *Perissodus*, *Plecodus*, and *Xenochromis*, the outer teeth are large and strongly recurved for stripping off and eating the scales from living fishes (Liem and Stewart, 1976; Poll, 1986).

Tilapiini Trewavas, 1983

Genera. *Oreochromis* Günther, 1889 and *Tilapia* Smith, 1840.

Distribution. Widespread in African rivers and lakes.

Brooding method. Mouth brooder (*Oreochromis*) or substrate brooder (*Tilapia*).

Diagnosis. This tribe is characterized exclusively by a foramen on posterior wall of fifth ceratobranchial.

Note. *Danakilia* Thys van den Audenaerde, 1969, *Iranocichla* Coad, 1982, *Konia* Trewavas, Green and Corbet, 1972, *Myaka* Trewavas, 1972, *Pungu* Trewavas, 1972, *Sarotherodon* Rüppell, 1852, *Stomatepia* Trewavas, 1962, and *Tristramella* Trewavas, 1942, all possessing a foramen on the posterior wall of the fifth ceratobranchial (Stiassny, 1991), are probably included in this tribe.

Tropheini Poll, 1986

Genera. *"Ctenochromis" horei* (Günther, 1893), *"Gnathochromis" pfefferi* (Boulenger, 1898), *Interochromis* Yamaoka, Hori and Kuwamura, 1998, *Limnotilapia* Regan, 1920, *Lobochilotes* Boulenger, 1915, *Petrochromis* Boulenger, 1898, *Pseudosimochromis* Nelissen, 1977, *Simochromis* Boulenger, 1898, and *Tropheus* Boulenger, 1898.

Distribution. Endemic to Lake Tanganyika.

Brooding method. Mouth brooders.

Diagnosis. This tribe is characterized exclusively by extensively granulated cycloid scales at midbody (granulations comprising irregularly arranged, variously shaped protrusions over almost entire exposed surface).

Note. The correct generic allocation of *Ctenochromis horei* could not be decided, because a congener, *C. benthicola* (Matthes, 1962), belongs to a "new tribe," and the phylogenetic relationships among these species and the type species of *Ctenochromis* Pfeffer, 1893, *Ctenochromis pectoralis* Pfeffer, 1893, are unknown. The former is therefore tentatively referred to as *"Ctenochromis" horei*.

The generic allocation of *Gnathochromis pfefferi* should be changed, because the type species of *Gnathochromis*, *Gnathochromis permaxillaris* (David, 1936), belongs to Limnochromini. Because the phylogenetic position of *G. pfefferi* in the revised Tropheini is not clear, the former is tentatively referred to as *"Gnathochromis" pfefferi*.

Tylochromini Poll, 1986

Genus. *Tylochromis* Regan, 1920.

Distribution. Zaire basin, Niger and Benue systems, and coastal rivers between Gambia and Ivory Coast.

Brooding method. Mouth brooder.

Diagnosis. This tribe is characterized exclusively by the *Tylochromis* type pharyngeal apophysis (sensu Greenwood, 1978).

Note. Greenwood (1978) classified the pharyngeal apophyses into *Tilapia*, *Haplochromis*, *Tilapia*, and *Tylochromis* types. In the present observations, the former three types were not clearly separable, due to the presence of intermediate conditions. Only *Tylochromis* type was clearly distinct from other types.

New Tribe

Genus. *"Ctenochromis" benthicola* (Matthes, 1962).

Distribution. Endemic to Lake Tanganyika.

Brooding method. Unknown.

Diagnosis. This tribe is characterized by a combination of type A infraorbitals (sensu Takahashi, 2003a), unicuspid outer and inner teeth on both jaws, no projection on ventral surface of anterior abdominal vertebrae, tubules extending from lateral line canals on preopercle and anteriormost infraorbital each not branching into secondary tubules, and two scale rows between upper lateral line and body axis.

Note. The correct generic allocation of *Ctenochromis benthicola* could not be decided for similar reasons pertaining to *"Ctenochromis" horei* (see Tropheini). The former is therefore tentatively referred to as *"Ctenochromis" benthicola*. It is inappropriate to denominate the tribe at this time.

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Appendix

Specimens examined are listed following the present tribal classification. Most ingroup specimens were collected from Lake Tanganyika, *Astatoreochromis straeleni*, *Oreochromis karomo*, and *Tilapia rendalli* being from its drainage. Outgroup specimens were taken from Lake Tanganyika or other African lakes or rivers. Letters in parentheses following the individual registration number indicate sampling locality: A, African water except for Lake Tanganyika; B, northeastern region of the Lake Tanganyika, Burundi; C, northwestern region of the lake, Democratic Republic of the Congo; Z, southern end of the lake, Zambia. Asterisks after individual registration numbers indicate dissected specimens. Institutional abbreviations follow Leviton et al. (1985), except for Lake Biwa Museum, Japan (LBM).

Ingroup.—Bathybatini. *Bathybates fasciatus* Boulenger, 1901: HUMZ 116685 (C), 123127 (Z), 123202 (Z), 138010* (C), 144.9–188.2 mm SL. *Bathybates graueri* Steindachner, 1911: HUMZ 116686 (C), 116693* (C), 122977 (Z), 123134 (Z), 119.2–155.0 mm SL. *Bathybates minor* Boulenger, 1906: HUMZ 116683 (C), 123199 (Z), 123249 (Z), 125382* (Z), 133.6–151.5 mm SL. *Hemibates stenosoma* (Boulenger, 1901): HUMZ 123094 (Z), 123189 (Z), 125365* (Z), 125750 (Z), 102.2–175.5 mm SL. *Trematocara macrostoma* Poll, 1952: UMMZ 196106* (Z), 88.0 mm SL. *Trematocara marginatum* Boulenger, 1899: HUMZ 128704 (B), 128717 (B), 128729* (B), 43.8–46.4 mm SL. *Trematocara nigrifrons* Boulenger, 1906: HUMZ 125658 (Z), 125659 (Z), 125663* (Z), 66.0–74.1 mm SL.

Benthochromini. *Benthochromis tricoti* (Poll, 1948): HUMZ 128636 (B), 128906 (B), 128982* (B), 111.2–114.4 mm SL.

Boulengerochromini. *Boulengerochromis microlepis* (Boulenger, 1899): HUMZ 123097* (Z), LBM 25209 (Z), 25210 (Z), 84.4–159.5 mm SL.

Cyphotilapiini. *Cyphotilapia frontosa* (Boulenger, 1906): HUMZ 137775* (C), 138292 (C), 120.9–169.4 mm SL. *Cyphotilapia* sp. (this species will be described by Takahashi and Nakaya, in press): HUMZ 122999* (Z), LBM 25538 (Z), 25539 (Z), 93.9–117.3 mm SL.

Cyprichromini. *Cyprichromis microlepidotus* (Poll, 1956): HUMZ 127578 (B), 127976 (C), 137463 (C), 137465 (C), 137742* (C), 89.3–96.3 mm SL. *Cyprichromis* sp. (sensu Takahashi et al., 2002): HUMZ 125341* (Z), LBM 26232 (Z), 26233 (Z), 80.0–95.8 mm SL. *Paracyprichromis brieni* (Poll, 1981): HUMZ 118389 (C), 118433 (C), 122560* (Z), 65.0–70.6 mm SL.

Ectodini. *Aulonocranus dewindti* (Boulenger, 1899): HUMZ 127954* (C), LBM 25049 (Z), 25054 (Z), 76.0–95.8 mm SL. *Callochromis macrops* (Boulenger, 1898): HUMZ 125813* (Z), LBM 25463–25566 (Z), 89.3–101.5 mm SL. *Cardiopharynx schoutedeni* Poll, 1942: HUMZ 116861 (C), 125738 (Z), 125936* (Z), 73.5–88.1 mm SL. *Cunningtonia longiventralis* Boulenger, 1906: HUMZ 125773* (Z), LBM 25100 (Z), 104.2–118.6 mm SL. *Cyathopharynx furcifer* (Boulenger, 1898): HUMZ 118284* (C), LBM 25567 (Z), 108.1–127.6 mm SL. *Ectodus descampsi* Boulenger, 1898: HUMZ 116702 (C), 116672* (C), 117910 (C), 70.4–79.3 mm SL. *Grammatotria lemairii* Boulenger, 1899: HUMZ 127521* (B), LBM 25245 (Z), 25246 (Z), 79.5–117.9 mm SL. *Lestradea perspicax* Poll, 1943: HUMZ 116627 (C), 116872 (C), 118218* (C), 76.6–86.0 mm SL. *Ophthalmotilapia nasuta* (Poll and Matthes, 1962): HUMZ 138281* (C), LBM 25873 (Z), 25874 (Z), 93.1–120.3 mm SL. *Xenotilapia boulengeri* (Poll, 1942): HUMZ 125887* (Z), LBM 25306 (Z), 25432 (Z), 68.2–111.9 mm SL. *Xenotilapia leptura* (Boulenger, 1901): HUMZ 116625* (C), LBM 25447 (Z), 25448 (Z), 77.1–84.1 mm SL. *Xenotilapia melanogenys* (Boulenger, 1898): HUMZ 125911* (Z), LBM 25276 (Z), 25595 (Z), 66.3–112.9 mm SL. *Xenotilapia tenuidentata* Poll, 1951: HUMZ 141873* (C), LBM 25198 (Z), 25199 (Z), 45.0–73.5 mm SL.

Eretmodini. *Eretmodus cyanostictus* Boulenger, 1898: HUMZ 125254* (Z), LBM 25095 (Z), 25735 (Z), 64.5–73.6 mm SL. *Spathodus marlieri* Poll, 1950: HUMZ 128426* (B), 57.8 mm SL. *Tanganicodus irsacae* Poll, 1950: HUMZ 137961* (C), 47.0 mm SL.

Greenwoodochromini. *Greenwoodochromis christyi* (Trewavas, 1953): HUMZ 128463 (B), 128464 (B), 128465* (B), 128468 (B), 75.1–77.9 mm SL.

Haplochromini. *Astatoreochromis straeleni* (Poll, 1944): MRAC 91–89-P-85* (A), 99.1 mm SL, plaine de Gatumba, marais, Burundi. *Astatotilapia burtoni* (Günther, 1893): HUMZ 125825* (Z), LBM 25618 (Z), 25758 (Z), 61.4–74.1 mm SL.

Lamprologini. *Altolamprologus compressiceps* (Boulenger, 1898): HUMZ 118292* (C), LBM 25008 (Z), 25014 (Z), 70.4–109.4 mm SL. *Chalinochromis brichardi* Poll, 1974: HUMZ 125327* (Z), LBM 25917 (Z), 26313 (Z), 63.9–86.8 mm SL. *Julidochromis ornatus* Boulenger, 1898: HUMZ 116930* (C), LBM 25526 (Z), 25625 (Z), 56.9–76.5 mm SL. *Lamprologus lemairii* Boulenger, 1899: HUMZ 128372* (C), LBM 25435 (Z), 25462 (Z), 98.5–165.8 mm SL. *Lepidiolamprologus attenuatus* (Steindachner, 1909): HUMZ 138293* (C), LBM 25430 (Z), 25431 (Z), 99.1–120.0 mm SL. *Lepidiolamprologus elongatus* (Boulenger, 1898): HUMZ 125634* (Z), LBM 25396 (Z), 25823 (Z), 115.8–122.8 mm SL. *Neolamprologus fasciatus* (Boulenger, 1898): HUMZ 127809* (C), LBM 25012 (Z), 25573 (Z), 100.3–108.2 mm SL. *Neolamprologus tetracanthus* (Boulenger, 1899): HUMZ 125828* (Z), LBM 25087 (Z), 25226 (Z), 85.0–96.9 mm SL. *Telmatochromis temporalis* Boulenger, 1898: HUMZ 125133* (Z), LBM 25451 (Z), 25452 (Z), 25953 (Z), 25.0–89.8 mm SL. *Variabilichromis moorii* (Boulenger, 1898): HUMZ 125713* (Z), 70.6 mm SL.

Limnochromini. *Baileychromis centropomoides* (Bailey and Stewart, 1977): HUMZ 125555 (Z), LBM 38487* (Z), 122.9–123.5 mm SL. *Gnathochromis permaxillaris* (David, 1936): HUMZ 123122 (Z), 123221 (Z), 123245* (Z), 123.8–128.4 mm SL. *Limnochromis auritus* (Boulenger, 1901): MRAC 95-098-P-209* (B), 148.0 mm SL. *Reganochromis calliurus* (Boulenger, 1901): MRAC 115081* (C), two specimens of LBM 38488 (Z), 73.9–85.2 mm SL. *Tangachromis dhanisi* (Poll, 1949): MRAC 107302* (B), LBM 38490 (Z), 51.5–58.1 mm SL. *Triglachromis otostigma* (Regan, 1920): MRAC 95-098-P-0268* (B), LBM 38489 (Z), 56.7–72.0 mm SL.

Perissodini. *Haplotaxodon microlepis* Boulenger, 1906: HUMZ 128381* (C), LBM 25882 (Z), 119.7–192.4 mm SL. *Perissodus microlepis* Boulenger, 1898: HUMZ 125121* (Z), LBM 25647 (Z), 25717 (Z), 91.0–102.2 mm SL. *Plecodus paradoxus* Boulenger, 1898: HUMZ 127963* (C), LBM 26337 (Z), 93.2–98.5 mm SL. *Xenochromis hecqui* Boulenger, 1899: HUMZ 116697* (C), 110.7 mm SL.

Tilapiini. *Oreochromis karomo* (Poll, 1948): MRAC 93-152-P-103* (A), 89.1 mm SL, Uvinza, small swamp near ferry of salt mine, Tanzania. *O. niloticus eduardianus* (Boulenger, 1912): HUMZ 116860* (C), 131.1 mm SL. *O. tanganicae* (Günther, 1893): HUMZ 116794* (C), LBM 25041–25043 (Z), 105.3–135.3 mm SL. *Tilapia rendalli* (Boulenger, 1896): MRAC P-105567* (A), 117.8 mm SL, village Amisi, région d'Albertville, riv. Lukuga, DR Congo.

Tropheini. *"Ctenochromis" horei* (Günther, 1893): HUMZ 125557* (Z), LBM 25019 (Z), 25097 (Z), 77.1–113.6 mm SL. *"Gnathochromis" pfefferi* (Boulenger, 1898): HUMZ 116914 (C), 118261* (C), 137268 (C), 96.9–99.5 mm SL. *Interochromis loocki* (Poll, 1949): HUMZ 163238* (Z), LBM 25662 (Z), 25663 (Z), 25739 (Z), 94.2–107.8 mm SL. *Limnotilapia dardennii* (Boulenger, 1899): HUMZ 122867* (Z), LBM 25427 (Z), 25588 (Z), 104.9–136.8 mm SL. *Lobochilotes labiatus* (Boulenger, 1898): HUMZ 127730* (C), LBM 25123 (Z), 25205 (Z), 109.5–293.5 mm SL. *Petrochromis fasciolatus* Boulenger, 1914: HUMZ 118088 (C), LBM 25043 (Z), 25373 (Z), 116.1–128.8 mm SL. *Pseudosimochromis curvifrons* (Poll, 1942): HUMZ 123048* (Z), LBM 25839 (Z), 26139 (Z), 90.6–108.3 mm SL. *Simochromis diagramma* (Günther, 1893): HUMZ 127930* (C), LBM 25223 (Z), 25411 (Z), 97.0–130.0 mm SL. *Tropheus moorii* Boulenger, 1898: HUMZ 122563* (Z), LBM 25088 (Z), 25324 (Z), 82.3–98.7 mm SL.

New tribe. *Ctenochromis benthicola* (Matthes, 1962): HUMZ 127370* (B), 137924 (C), 137925 (C), 138290 (C), 74.2–99.5 mm SL.

Outgroup.—Tylochromini. *Tylochromis jentinki* (Steindachner, 1894): MRAC 74-014-P-7102* (A), 101.2 mm SL, Lagune Ebrie, Republic of Cote d'Ivoire. *Tylochromis labrodon* Regan, 1920: MRAC 90-002-P-24* (A), 118.7 mm SL, Kisangani, River Tshopo, Democratic Republic of the Congo. *Tylochromis lateralis* (Boulenger, 1898): MRAC 1063* (A), 202.1 mm SL, Lake Mai-Ndombe, Democratic Republic of the Congo. *Tylochromis polylepis* (Boulenger, 1900): HUMZ 117943 (C), 117944 (C), 125794* (Z), 137558 (C), 92.0–137.3 mm SL. *Tylochromis variabilis* Stiassny, 1989: MRAC 34763* (A), 163.2 mm SL, Kiambi, River Luvua, Democratic Republic of the Congo.