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A Revision of the *Pseudotropheus elongatus* species group (Teleostei: Cichlidae) With Description of a New Genus and Seven New Species

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Abstract

Lake Malaŵi is known for its endemic haplochromine species flock, most notably the rock-dwelling cichlids known as mbuna. The group of mbuna referred to as the *Pseudotropheus elongatus* species group is currently comprised of *Metriaclima* spp., *Tropheops* spp., *Cynotilapia* spp., and *Pseudotropheus* spp. In this study, *Chindongo*, a new genus with the type species *C. bellicosus*, is described for additional species in this group. *Chindongo* is distinguished from other mbuna genera by 1) the presence of bicuspid teeth in the anterior portion of the outer row of both upper and lower jaw; 2) a moderately to steeply sloped vomer with a narrow rostral tip which makes an angle of between 53° and 68° with the parasphenoid; 3) a small mouth with the lower jaw slightly shorter than the upper; 4) a broad anterior dentigerous area on both premaxilla and dentary with three or more rows of teeth (usually 5–6 rows); 5) a flank melanin pattern consisting of vertical bars without horizontal elements at any stage of development. *Chindongo bellicosus* is distinguished by its color pattern and shallower body from the other species which we have transferred to *Chindongo*. We also describe six new elongate mbuna species and place them into three available genera, they include: *Metriaclima flavicauda*, *M. usisyae*, *Tropheops kumwera*, *T. biriwera*, *T. kamtambo*, and *Cynotilapia chilundu*.

Key words: mbuna, Lake Malaŵi, *Metriaclima*, *Tropheops*, *Cynotilapia*

Introduction

The endemic, small and colorful rock-dwelling haplochromine cichlid fishes of Lake Malaŵi are well known as mbuna; they include the following 13 genera: *Abactochromis*, *Cyathochromis*, *Cynotilapia*, *Genyochromis*, *Gephyrochromis*, *Iodotropheus*, *Labeotropheus*, *Labidochromis*, *Petrotilapia*, *Melanochromis*, *Metriaclima*, *Tropheops*, and *Pseudotropheus* (Trewavas 1935; Oliver & Loisele 1972; Stauffer *et al.* 1997; Oliver & Arnegard 2010). Although there has been no formal taxonomic diagnosis of the mbuna on the basis of synapomorphies, they share the following characteristics: 1) large number of small scales on the nape and chest region; 2) abrupt transition from large flank scales to small chest scales; 3) reduction of the left ovary; and 4) possession of true ocelli (Fryer 1959; Oliver 1984). Most mbuna occur over rocky substrates in water less than 40 m deep. A few groups, however, are found over soft substrate (Fryer 1959; Fryer & Iles 1972; Ribbink *et al.* 1983; Stauffer 1991). It has been suggested that the sandy bottoms and deep waters that separate rocky shores and islands may be a barrier to the migration of mbuna, and thus may facilitate intralacustrine allopatric speciation due to restricted gene flow (Fryer 1959; Ribbink *et al.* 1983; Stauffer 1991). Most mbuna exhibit sexual dimorphism consisting of males having brighter color patterns and larger sizes than females, and females retaining their juvenile coloration. Males intensify their coloration when defending a territory or maintaining a position in the hierarchy. Some females may express a muted version of the male breeding coloration especially when they are mouth brooding (Konings 2007). Many mbuna species express geographical variation in the male breeding coloration with a unique set of colors and markings exhibited at each location (Ribbink *et al.* 1983). Female mate choice is believed to have accelerated the

divergence of mate recognition systems among mbuna populations, such as coloration, and thus may have accounted for their rapid speciation (Danley *et al.* 2012). Mate choice studies by Knight & Turner (2004) have shown that females are able to select their correct mates based on coloration. Study by Van Oppen *et al.* (1998) has shown that assortative mating among taxa that differ in male color supports the species richness. These studies provided further evidence that female mate choice is a driving force in speciation of cichlids. Therefore, live coloration is an important characteristic that has been used describing cichlid species, especially in mbuna where male coloration has been used as the primary trait delimiting species (Ribbink *et al.* 1983; Stauffer *et al.* 1997; Stauffer *et al.* 2013). Besides the males' color patterns, rock-dwelling cichlids in Lake Malaŵi are well known also for their diversity of feeding behavior and associated morphology. Mbuna employ different feeding strategies including algal feeding, piscivory, planktivory, fin biting, scale eating, cleaning, and sand sifting (Stauffer 1991; Konings 2007). In addition, no matter what feeding specialization they have, mbuna may feed on different items when these become available. It has been suggested (Seehausen & Van Alphen 1999; Kocher 2004) that while adaptations in trophic morphology influenced early evolution of cichlid species, these probably played a lesser role in recent speciation events.

Pseudotropheus is the most speciose among mbuna genera and is certainly polyphyletic and for a long period of time it served as a catch-all genus for mbuna. The type species is *P. williamsi* Günther 1894. The five species groups within the genus originally recognized by Ribbink *et al.* (1983) include: the *Pseudotropheus zebra* complex, *Pseudotropheus tropheops* complex, *Pseudotropheus williamsi* complex, the *Pseudotropheus elongatus* species-group, and the *Pseudotropheus* 'aggressive' species-group. The *P. zebra* complex and the *P. tropheops* complex were later split from *Pseudotropheus* as separate genera, i.e. *Metriaclima* and *Tropheops*, respectively (Trewavas 1984; Stauffer *et al.* 1997; Konings 2001).

The *Pseudotropheus elongatus* species-group of Ribbink *et al.* (1983) contained 24 different mbuna with a slender body, similar to *Pseudotropheus elongatus* Fryer 1956, which was described from specimens collected in Mbamba Bay (Ribbink *et al.* 1983), Tanzania. Most members of the group were small species with a standard length of less than 10 cm. Ribbink *et al.* (1983) mentioned, however, that this group was undoubtedly polyphyletic as it included species which show differences in head shape and dentition. Konings (2007) argued that the diagnoses of the three genera *Metriaclima*, *Tropheops*, and *Cynotilapia* do not exclude taxa with elongate body morphologies and that they can thus contain species from the *P. elongatus* species-group. He recognized four different sub-groups that could be separated on the basis of characters other than a shallow body and assigned three of the four sub-groups to the genera *Metriaclima*, *Tropheops*, and *Cynotilapia*. The fourth sub-group of the elongate mbuna cannot be readily accommodated within the diagnosis of any of the above three genera, and the species bear little resemblance to *P. williamsi* and should therefore be placed into a new genus as suggested by Konings (2007).

The purposes of this study are to 1) investigate and diagnose some of the species previously placed in the *P. elongatus* group and to assign them to *Metriaclima*, *Tropheops*, or *Cynotilapia*; 2) diagnose a new genus for those elongate species that cannot be assigned to any existing genus but that can be differentiated from *P. williamsi*, the type species of *Pseudotropheus*.

Taxonomic summary

Metriaclima (type species *Metriaclima zebra*, Boulenger)

Metriaclima is diagnosed by the following morphological characteristics (Stauffer *et al.* 1997; Konings & Stauffer 2006): 1) the presence of bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws; 2) a moderately-sloped (31–48° to the parasphenoid) ethmo-vomerine block with a swollen rostral tip; 3) the cleft of the upper and lower jaws forms a 23–40° angle with the body axis; 4) the lower jaw is often slightly longer and thicker than the upper jaw; 5) a large part of the upper dental arcade is normally exposed when the mouth is closed; 6) the tips of the teeth in the premaxilla and dentary are in a V-shaped line with the anterior-most in upper and lower jaw furthest apart; and 7) the placement of the bicuspid teeth in the outer row along the side of the jaws does not follow the contour of the jaw, while the lateral teeth are rotated so that the plane of their two-pronged tips runs parallel with those in the anterior part of the jaw.

We propose that two of the undescribed elongate species, *Pseudotropheus elongatus* 'yellow tail' and

Pseudotropheus elongatus ‘Mara’ that Ribbink *et al.* (1983) had placed in their *P. elongatus* species-group should be placed in *Metriaclima*. Although they possess elongate bodies, their feeding mechanism, terminal mouth, and ranges of vomer angles all place these two species in *Metriaclima*.

Tropheops (type species *Tropheops tropheops*, Regan)

Tropheops is diagnosed by the following morphological characteristics: 1) the presence of bicuspid teeth in outer rows and enlarged conical teeth on the posterior ends of the dentigerous arms of the premaxilla; 2) a steeply sloped (71–96° to the parasphenoid) ethmo-vomerine block; 3) narrow ventral mouth with lower jaw shorter than the upper; 4) the cleft of the upper and lower jaws forms a 15–35° angle with the body axis.

We propose that two of the undescribed elongate species, *Pseudotropheus elongatus* ‘boadzulu’ and *Pseudotropheus elongatus* ‘reef’, that Ribbink *et al.* (1983) had placed in their *P. elongatus* species-group, and one form later given the cheironym *Pseudotropheus elongatus* ‘greenback’ by Reinthal (1990), should all three be placed in *Tropheops*. These elongate *Tropheops* appear to be less aggressive than members retained in the *P. elongatus* group, and they are often found around small to medium sized rocks with behaviors more like that observed in other *Tropheops* spp.

Cynotilapia (type species *Cynotilapia afra*, Günther)

Cynotilapia is diagnosed by the following morphological characteristics: 1) the teeth of the oral jaws are unicuspid and widely spaced; 2) the ethmo-vomerine block is moderately-sloped (26–41° to the parasphenoid); 3) the lower jaw is strong and usually a little longer than the upper jaw; 4) the cleft of upper and lower jaws forms a 30–42° angle with the body axis. *Cynotilapia* have a few (4–8) large conical teeth in the outer row of the upper and lower jaws. Their function is not known, as it appears they are not used in feeding, because individuals belonging to this genus all appear to suction-feed on plankton in the water column (Konings 2007). Species of *Cynotilapia* and *Metriaclima* share certain morphological and behavioral features and it has been suggested that that may be closely related (Kassam *et al.* 2005). *Microchromis* Johnson 1975 is generally considered a junior synonym of *Cynotilapia*, although Tawil (2011) proposed that it might be used to separate species with a lesser degree of divergence in the size of the central jaw teeth compared to the other teeth. We found this particular characteristic to be variable between individuals of the same population and we therefore do not consider this to be useful distinction and continue to regard *Microchromis* a junior synonym of *Cynotilapia*.

The unicuspid teeth and plankton-feeding behavior of *Pseudotropheus* sp. ‘elongatus taiwan’ (Konings 1995) suggest it is best placed in *Cynotilapia*.

Methods and materials

Fish specimens were collected in Lake Malaŵi by SCUBA divers who chased them into a monofilament net (7m×1m; 1.5cm mesh). Fish were anesthetized with clove oil (IACUC 110784), preserved in 10% formalin, and then placed in 70% ethanol for permanent storage in the Pennsylvania State University Fish Museum (PSUFM). Permits for all collections were issued by the government of Malaŵi. Color and pigmentation patterns of males and females in breeding color were recorded in the field at the time of capture. Habitat and behavior were recorded with digital photo and video cameras. Color and melanin patterns varied within the species, so variation was designated by placing a slash between different colors, such as blue/white was used to indicate that the color ranged from blue to white. Both photographs and color/pigmentation notes of the type material of the newly described species are stored at PSUFM; catalogue numbers are provided under the species descriptions.

Figure 1 shows the collection sites in Lake Malaŵi of the seven new species. Twenty-four measurements and 14 counts were taken on the left side of the fish except for gill-raker counts, which were taken on the right side (Barel *et al.* 1977; Konings & Stauffer 2006).

This study includes the morphological and meristic analysis of 255 specimens from 14 collections in Lake Malaŵi. Morphometric measurements were taken with electronic calipers and measured to the nearest 0.1 mm. Morphological data were analyzed with sheared principal component analysis (SPCA), in which the covariance matrix was factored and meristic data were analyzed using PCA with the correlation matrix factored (Humphries *et al.* 1981; Stauffer *et al.* 1997). Differences among species were illustrated by plotting the sheared second and/or third principal components of the morphometric data against the first principal components of the meristic data.

Minimum polygon clusters were drawn to encompass the points of a population on the principal component plots. The minimum polygon clusters that showed the most separation were used.

We performed whole body CT scans with surface rendering of ten specimens of each new species. The angles of the ethmo-vomerine and its shape are measured and observed on the image reconstructed with Avizo 8 (FEI, Hillsboro, Oregon).

The new genus and species are distinguished based on color patterns, morphometric, meristic, and ecological differences. They are also compared with and distinguished from nearby populations having similar pigmentation patterns or occupying similar habitats.



FIGURE 1. Map of Lake Malaŵi indicating the collection localities mentioned in this study.

Results

Metriaclima flavicauda, new species

Fig. 2 A–C

Pseudotropheus elongatus 'yellow tail', Ribbink *et al.* 1983 (part)

Metriaclima sp. 'elongatus yellow tail', Konings 2007



FIGURE 2. *Metriaclima flavicauda*. A. Holotype, PSU 12756, adult male, 97.2 mm SL, Zimbabwe Rock, Lake Malaŵi; B. Male in breeding coloration (approx. 90 mm SL) at type locality; C. Female (approx. 65 mm SL) at type locality.

Holotype. PSU 12756, adult male, 97.2 mm SL, S 13°57.919', E 34°48.167', Zimbabwe Rock, Lake Malaŵi, Malaŵi, Africa, 7 Feb. 2006, A. F. Konings & J. R. Stauffer Jr.

Paratypes. PSU12757, 30, (58.7 mm–100.7 mm SL), same data as holotype.

Diagnosis. The presence of bicuspid teeth in the outer rows on both the upper and lower jaws and a moderately sloped vomer (46° in holotype) with a swollen rostral tip place this species in *Metriaclima*. Male and female *M. flavicauda* are distinguished by an elongate body (BD 23.6–28.5% SL) from all other species in *Metriaclima* (BD 28.8–40.8% SL) except *M. tarakiki* (BD 25.8–32.9% SL) and *M. usisyae* (BD 25.9–30.6% SL). *Metriaclima flavicauda* is distinguished from *M. usisyae* by a deeper preorbital bone (PRE 18.0–26.9% HL) and a longer snout (SNL 34.3–47.3% HL), which are 17.6–21.2% and 32.0–37.6% HL in *M. usisyae*, respectively. Based on the color pattern, males of *M. flavicauda* possess 5–6 black lateral bars, black pelvic fins, a black anal fin, a yellow caudal fin, and a black dorsal fin with yellow/orange spots distally. Males of *M. usisyae* have a yellow dorsal fin with a black submarginal band, a yellow pelvic fin and a yellow anal fin with a black leading edge. Males of *M. tarakiki* have 7–9 lateral bars, and gray-blue/dark gray caudal fin. Females of *M. flavicauda* can be distinguished from those of *M. tarakiki* by a bluish/brown ground coloration without lateral bars. In female *M. tarakiki*, the ground color is light brown with blue center-flank scales and dark brown lateral bars. Based on coloration alone, females of *M. flavicauda* cannot reliably be distinguished from those of *M. usisyae*. *Metriaclima flavicauda* also possess a relatively smaller eye than *M. tarakiki* (HED 20.5–30.6% HL vs. HED 27.2–36.3% HL).

Description. Morphometric and meristic data in Table 1. Elongate species (BD 23.6–28.5% SL) with greatest body depth at base of fourth dorsal-fin spine. Dorsal body profile with gradual curve to caudal peduncle with highest point at fourth dorsal-fin spine; ventral body profile between pelvic fin and anal fin flat with upward curve

TABLE 1. Morphological and meristic data for *Metriaclima flavicauda* from Zimbabwe Rock, Lake Malaŵi, PSU 12756, holotype; PSU 12757, n=30. Ranges include holotype.

Variable	Holotype PSU12756	Mean PSU12757	Std Dev	Min	Max
Standard length (mm)	97.2	79.4	13.0	58.7	100.7
Head length (mm)	29.8	24.3	3.9	17.6	30.5
Percent head length (%)					
Snout length	38.5	38.2	2.7	34.3	47.3
Postorbital head length	42.9	41.5	1.5	38.8	44.8
Horizontal eye diameter	24.4	26.4	2.7	20.5	30.6
Vertical eye diameter	24.0	24.7	2.7	19.2	30.1
Preorbital depth	24.9	22.4	2.3	18.0	26.9
Cheek depth	26.9	25.3	2.2	21.0	29.8
Lower jaw length	45.1	40.2	3.3	34.3	47.5
Head depth	79.3	75.8	4.3	66.0	84.3
Percent standard length (%)					
Body depth	28.5	25.9	1.4	23.6	28.5
Snout to dorsal fin origin	31.3	31.7	1.2	29.8	34.0
Snout to pelvic fin origin	35.6	35.4	1.4	33.4	38.6
Dorsal fin base length	61.5	61.7	1.9	57.7	65.4
Anterior dorsal to anterior anal	48.9	46.5	1.8	43.4	49.8
Anterior dorsal to posterior anal	63.6	63.0	1.8	59.3	65.8
Posterior dorsal to anterior anal	28.2	27.7	1.1	25.7	29.4
Posterior dorsal to posterior anal	14.7	13.7	0.7	12.5	15.6
Posterior anal to dorsal caudal	16.5	16.1	0.7	14.4	17.4
Posterior dorsal to ventral caudal	19.7	18.9	1.0	17.2	21.5
Anterior dorsal to pelvic-fin origin	31.2	28.5	1.6	25.9	31.3
Posterior dorsal to pelvic-fin origin	57.6	57.0	1.3	54.2	59.9
Caudal peduncle length	11.7	11.4	0.9	9.3	13.5
Least caudal peduncle depth	12.1	11.5	0.5	10.5	12.6
Meristics		Mode	Frequency(%)	Min	Max
Dorsal-fin spines	17	18	67.7	17	19
Dorsal-fin rays	10	9	58.1	8	10
Anal-fin spines	3	3	96.8	2	3
Anal-fin rays	8	8	83.9	8	9
Pelvic-fin rays	5	5	100.0	5	5
Pectoral-fin rays	13	13	93.5	12	14
Lateral line scales	35	33	54.8	32	35
Pored scales caudal	2	2	71.0	1	2
Cheek scale rows	4	5	58.1	3	5
Gill rakers 1st ceratobranchial	12	11	64.5	10	12
Gill rakers 1st epibranchial	3	4	71.0	2	5
Teeth outer left lower jaw	10	10	45.2	8	12
Tooth rows upper jaw	3	3	83.9	2	4
Tooth rows lower jaw	3	3	90.3	3	4

to caudal fin. Anterior head profile straight to slightly convex between snout tip and interorbital; cleft of the upper and lower jaws with 23–39° angle with body axis; then round to dorsal-fin origin. Snout short with isognathic jaws. Teeth on lower jaw in 3–4 rows; upper jaw in 2–4 rows; outer rows bicuspid; inner rows tricuspid or unicuspid. First 3–4 Dorsal-fin spines longer posteriorly with first spine less than half length of fourth spine; last dorsal-fin spine slightly (10%) longer than fourth spine. Dorsal fin with subacuminate tip, fourth ray longest, about to base of caudal fin in both males and females. Pectoral fin rounded, paddle-shaped. Anal fin with 3 spines progressively longer posteriorly; third or fourth ray longest, length to base of caudal fin in both males and females, tip slightly longer than dorsal fin. Caudal fin subtruncate to emarginated.

Lateral scales large, ctenoid; small, cycloid scales on breast and belly; cheek with 3–5 rows of small scales. Rayed section of dorsal and anal fins with narrow proximal band of tiny scales; tiny scales from base to 50% length of caudal fin.

Color notes and photos of live breeding adults (PSU 12758). Males in territorial color with light blue ground coloration and 5–6 distinct black bars. Head black with 2 light blue interorbital bars; throat dark brown. Anal fin black with 4–6 yellow ocelli; light yellow marginal band. Pectoral-fin rays black with clear membranes (Fig. 2B).

Females with beige/brown/light blue ground coloration. Belly and breast white/beige. Head with beige/brown ground coloration and blue/green highlights; yellow/green opercular spot; interorbital green/light gray; throat white. Dorsal fin light brown/light blue without black submarginal band. Pectoral, pelvic, and caudal fins beige/brown/light blue proximally, and dark brown distally (Fig. 2C).

Distribution. *Metriaclima flavicauda* is known from Zimbabwe Rock (S 13°57.925', E 34°48.189') and Mumbo Island (S 13°59.5', E 34°45.4'), Lake Malaŵi.

Etymology. The name *flavicauda* is a noun in apposition and derives from the Latin *flavus* meaning “yellow” and “*cauda*” meaning “tail”, and refers to the yellow tail of territorial males.

***Metriaclima usisyae*, new species**

Fig. 3 A–C

Pseudotropheus elongatus ‘mara’, Ribbink *et al.* 1983 (part)

Metriaclima sp. ‘elongatus usisyae’, Konings 2007

Holotype. PSU 12759, adult male, 74.8 mm SL, S 11°14.834', E 34°13.862', Usisyae, Lake Malaŵi, Malaŵi, Africa, 1 Jan. 1991, J. R. Stauffer Jr.

Paratypes. PSU 12760, 14, (52.4 mm–74.8 mm SL), same data as holotype.

Diagnosis. The presence of bicuspid teeth in the outer rows on both the upper and lower jaws and a moderately sloped vomer block (48° in holotype) with a swollen rostral tip place this species in *Metriaclima*. Male and female *M. usisyae* are distinguished by an elongate body (BD 25.9–30.6% SL) from all the other species in *Metriaclima* (BD 28.8–40.8% SL) except *M. tarakiki* (BD 25.8–32.9% SL) and *M. flavicauda* (BD 23.6–28.5% SL). *Metriaclima usisyae* differs from *M. tarakiki* by a smaller eye, VED 23.1–28.1% HL vs. VED 30.2–36.5% HL in *M. tarakiki*; and a shorter lower jaw length, LJL 29.9–33.4% HL vs. LJL 34.8–38.9% HL in *M. tarakiki*. Based on the color pattern, male *M. usisyae* possess a yellow dorsal fin with a black submarginal band, yellow pelvic fins and yellow anal fin with a black leading edge. Male *M. flavicauda* possess black pelvic and anal fins, and a black dorsal fin with yellow/orange spots distally. The ground coloration of male *M. flavicauda* is blue with 2 light blue/purple interorbital bars vs. yellow with 2 white/light blue interorbital bars in male *M. usisyae*. Females of *M. usisyae* cannot reliably be distinguished by color from those of *M. flavicauda*. *Metriaclima flavicauda* also possess a deeper preorbital bone (PRE 18.0–26.9% HL) and a longer snout (SNL 34.3–47.3% HL), which are 17.6–21.2% and 32.0–37.6% in *M. usisyae*, respectively.

Description. Morphometric and meristic data in Table 2. Elongate species (BD 25.9–30.6% SL) with greatest body depth at base of seventh or eighth dorsal-fin spine. Dorsal body profile with gradual curve to caudal peduncle with highest point at seventh or eighth dorsal-fin spine (greater body depth in males (mean BD 28.9% SL) than in females (mean BD 28.2% SL)); ventral body profile between pelvic and anal fins flat with upward curve to caudal fin. Dorsal head profile straight to slightly concave between snout tip and interorbital area, making 40–50° (45.5° in holotype) angle with body axis (greater angle in males than females), then round to dorsal-fin origin. Snout short with isognathic jaws. Teeth on lower jaw in 3–4 rows; upper jaw in 3–4 rows; outer rows bicuspid; inner rows

tricuspid. First 3–4 dorsal-fin spines gradually longer posteriorly with first spine less than half length of fourth spine. Last dorsal-fin spine slightly longer than fourth spine. Soft dorsal fin with subacuminate tip, third or fourth ray longest, to about base of caudal fin in both males and females. Pectoral fin rounded, paddle-shaped. First ray of pelvic fin longer than other rays. Anal fin with 3 spines progressively longer posteriorly; third or fourth ray longest, length beyond base of caudal fin in males and to base of caudal fin in females. Caudal fin subtruncate to emarginate.



FIGURE 3. *Metriaclima usisyae*. A. Holotype, PSU 12759, adult male, 74.8 mm SL, Usisya, Lake Malaŵi; B. Male in breeding coloration (approx. 70 mm SL) at type locality; C. Female (approx. 58 mm SL) at type locality.

Lateral scales large, ctenoid; small cycloid scales on breast and belly; cheek with 5 rows of small scales. Dorsal fin and anal fin with narrow proximal band of tiny scales; tiny scales from base to 50% length of caudal fin.

Color notes and photos of live breeding adults (PSU 12761). Males in territorial color with brown/yellow ground coloration and faint light brown bars. Head brown with 2 light blue/white interorbital bars and purple highlights; throat light blue. Dorsal fin black/yellow proximally, black distally with light blue lappets. Anal fin dark blue with 5–6 yellow ocelli and black/blue margin. Pectoral-fin rays brown with clear membranes (Fig. 3B).

Females with brown ground coloration and 2–3 faint dark brown bars with purple/blue highlights on edge of scales. Belly and breast beige/brown. Head dark brown; black/gray opercular spot; interorbital bars purple/brown. Dorsal fin yellow/light brown proximally and black distally. Pectoral fin and pelvic fin brown/purple. Caudal fin light brown with dark brown ventral and dorsal margins (Fig. 3C).

Distribution. *Metriaclima usisyae* is found on a submerged reef near Usisya (S 11°14.834', E 34°13.862') and at Mara Rocks (S 11°14.86', E 34°15.38'), Malaŵi.

Etymology. The specific epithet *usisyae* is the genitive of Usisya, the village near which the type specimens were collected.

TABLE 2. Morphological and meristic data for *Metriaclima usisyae* from Usisya, Lake Malawi, PSU 12759, holotype; PSU 12760, n=14. Ranges include holotype.

Variable	Holotype PSU12759	Mean PSU12760	Std Dev	Min	Max
Standard length (mm)	74.8	62.4	7.6	52.4	74.8
Head length (mm)	22.7	20.0	1.9	16.9	23.9
Percent head length (%)					
Snout length	33.6	34.1	1.6	32.0	37.6
Postorbital head length	42.4	42.4	1.9	38.5	45.6
Horizontal eye diameter	27.2	28.1	2.2	23.8	33.3
Vertical eye diameter	24.1	26.1	1.8	23.1	28.1
Preorbital depth	21.2	19.6	1.0	17.6	21.2
Cheek depth	29.5	26.2	1.9	23.7	30.0
Lower jaw length	33.0	31.3	1.2	29.9	33.4
Head depth	82.9	80.7	3.1	76.4	87.0
Percent standard length (%)					
Body depth	28.6	28.5	1.3	25.9	30.6
Snout to dorsal fin origin	31.8	32.7	1.6	29.2	35.3
Snout to pelvic fin origin	37.2	37.5	1.4	35.2	40.3
Dorsal fin base length	60.7	60.8	2.0	58.3	65.4
Anterior dorsal to anterior anal	51.3	49.2	1.7	46.9	52.5
Anterior dorsal to posterior anal	63.4	62.5	2.0	59.4	66.3
Posterior dorsal to anterior anal	26.8	26.9	1.3	24.5	29.8
Posterior dorsal to posterior anal	14.1	14.2	0.7	13.3	15.9
Posterior anal to dorsal caudal	15.9	16.5	1.0	15.2	18.0
Posterior dorsal to ventral caudal	18.7	19.3	0.9	17.8	21.0
Anterior dorsal to pelvic-fin origin	30.0	30.0	1.7	26.8	33.4
Posterior dorsal to pelvic-fin origin	55.8	54.3	1.8	51.0	56.8
Caudal peduncle length	10.8	11.8	1.4	10.2	15.1
Least caudal peduncle depth	11.9	11.9	0.5	11.3	13.1
Meristics		Mode	Frequency(%)	Min	Max
Dorsal-fin spines	18	18	93.3	17	18
Dorsal-fin rays	9	8	53.3	8	9
Anal-fin spines	3	3	100.0	3	3
Anal-fin rays	8	8	66.7	7	8
Pelvic-fin rays	5	5	100.0	5	5
Pectoral-fin rays	13	13	100.0	13	13
Lateral line scales	31	32	53.3	31	33
Pored scales caudal	2	2	93.3	1	2
Cheek scale rows	5	5	100.0	5	5
Gill rakers 1st ceratobranchial	12	12	60.0	10	14
Gill rakers 1st epibranchial	4	4	73.3	4	5
Teeth outer left lower jaw	9	9	33.3	7	9
Tooth rows upper jaw	3	3	66.7	3	4
Tooth rows lower jaw	3	3	80.0	3	4

***Tropheops kumwera*, new species**

Fig. 4 A–E

Pseudotropheus elongatus 'boadzulu', Ribbink *et al.* 1983

Tropheops sp. 'elongatus boadzulu', Konings 2007

Holotype. PSU 12762, adult male, 66.8 mm SL, S 14°15.004', E 35°8.597', Boadzulu Island, Lake Malaŵi, Malaŵi, Africa, 16 Jan. 1991, J. R. Stauffer Jr.

Paratypes. PSU 12763, 23, (52.0 mm–70.5 mm SL), same data as holotype; PSU 12764, 7, (53.3 mm–69.9 mm SL), S 14°15.569', E 35°7.550', Makokola Reef, Lake Malaŵi, Malaŵi, Africa, 19 Feb. 2008, J. R. Stauffer Jr.; PSU 12765, 15, (55.9 mm–67.0 mm SL), S 14°2.472', E 34°54.714', Tsano Rock, Lake Malaŵi, Malaŵi, Africa, 12 Oct. 2004, A. F. Konings & J. R. Stauffer Jr.

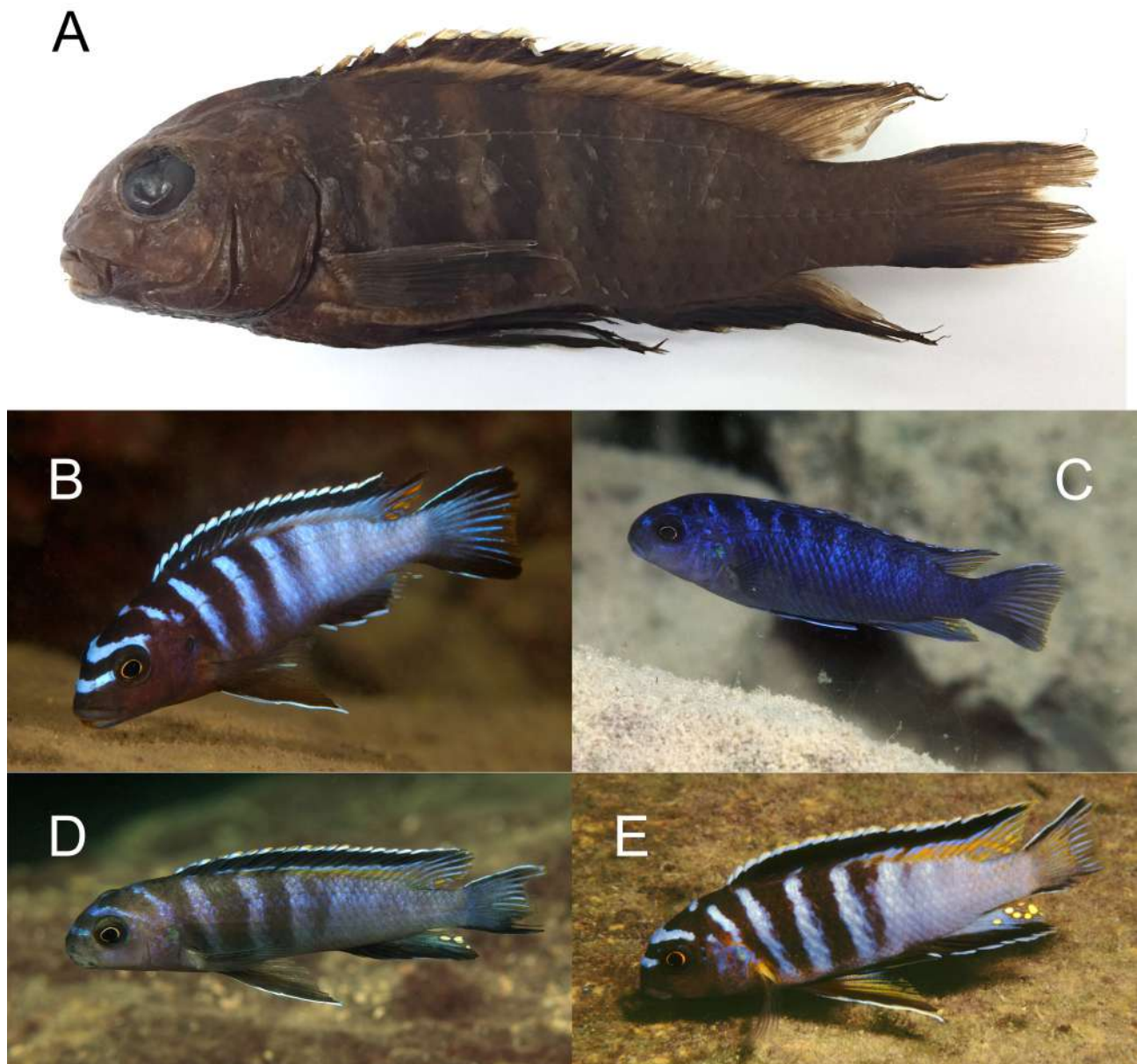


FIGURE 4. *Tropheops kumwera*. A. Holotype, PSU 12762, adult male, 66.8 mm SL, Boadzulu Island, Lake Malaŵi, Malaŵi, Africa; B. Male in breeding coloration (approx. 65 mm SL) at type locality; C. Female (approx. 55 mm SL) at type locality; D. Male in breeding coloration (approx. 63 mm SL) at Makokola Reef, Malaŵi; E. Male in breeding coloration (approx. 65 mm SL) at Tsano Rock, Malaŵi.

TABLE 3. Morphological and meristic data for *Tropheops kumwera* from Boadzulu Island, Lake Malaŵi (PSU 12762, holotype; PSU 12763, n=23); Makokola Reef, Lake Malaŵi (PSU 12764, n=7); Tsano Rock, Lake Malaŵi, Malaŵi (PSU 12765, n=15). Ranges include holotype.

Variable	Holotype	Mean	Std Dev	Min–Max		
				Makokola Reef PSU12764	Tsano Rocks PSU12765	Boadzulu Island PSU12763
Standard length (mm)	66.8	62.5	4.5	52.0–70.5	53.3–69.9	55.9–67.0
Head length (mm)	22.1	19.9	1.5	16.6–23.1	16.9–21.4	17.8–21.2
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Percent head length (%)						
Snout length	41.7	37.7	2.5	36.5–42.8	34.1–39.8	28.0–39.8
Postorbital head length	41.4	42.0	1.3	39.2–43.4	41.3–45.5	40.9–44.0
Horizontal eye diameter	29.1	29.2	1.7	25.8–32.6	26.7–31.3	26.1–31.4
Vertical eye diameter	27.6	27.3	1.4	24.2–29.9	26.5–31.4	26.0–29.3
Preorbital depth	22.9	22.8	1.7	20.4–26.0	19.4–25.4	19.4–25.3
Cheek depth	25.2	24.8	1.9	23.7–30.2	21.5–28.3	20.9–27.1
Lower jaw length	35.2	34.1	1.7	32.3–38.0	31.1–34.1	31.4–36.3
Head depth	82.2	78.5	4.6	72.3–84.5	70.2–79.0	70.4–82.2
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Percent standard length (%)						
Body depth	29.2	27.9	1.7	27.1–31.0	23.6–27.9	25.6–29.1
Snout to dorsal fin origin	35.5	34.5	1.2	32.5–37.8	32.6–36.8	32.9–36.4
Snout to pelvic fin origin	39.0	36.9	1.6	36.0–40.9	34.8–37.1	33.0–37.2
Dorsal fin base length	62.5	61.4	1.7	55.7–64.9	58.7–64.3	60.6–64.1
Anterior dorsal to anterior anal	47.0	49.3	1.7	45.4–52.3	46.8–50.3	46.0–50.3
Anterior dorsal to posterior anal	64.2	63.3	1.7	57.7–66.2	61.7–64.6	61.8–64.3
Posterior dorsal to anterior anal	28.3	27.9	1.0	25.8–29.1	25.8–27.8	27.5–29.9
Posterior dorsal to posterior anal	14.1	13.8	0.7	12.8–15.2	12.4–14.4	12.8–15.1
Posterior anal to dorsal caudal	15.6	15.8	0.6	14.7–16.7	14.7–17.1	15.1–17.1
Posterior dorsal to ventral caudal	18.0	18.1	0.9	16.2–19.8	16.2–19.0	16.9–19.7
Anterior dorsal to pelvic-fin origin	32.2	30.9	1.6	29.2–34.0	26.7–31.9	27.8–32.2
Posterior dorsal to pelvic-fin origin	52.8	56.2	1.8	50.6–57.5	53.5–58.3	55.8–59.4
Caudal peduncle length	10.3	10.1	0.7	8.8–11.9	8.6–11.2	9.5–11.1
Least caudal peduncle depth	12.6	11.8	0.6	11.1–12.9	10.8–11.9	10.8–12.2
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Meristics		Mode	Freq(%)			
Dorsal-fin spines	18	18	67.4	18–19	18–19	17–19
Dorsal-fin rays	8	8	52.2	8–10	8–10	8–10
Anal-fin spines	3	3	100.0	3	3	3
Anal-fin rays	7	8	89.1	8	7–8	7–8
Pelvic-fin rays	5	5	100.0	5	5	5
Pectoral-fin rays	13	13	97.8	13	13	12–13
Lateral-line scales	32	32	71.7	31–33	32–33	31–33
Pored scales caudal	2	2	97.8	2	2	1–2
Cheek scale rows	5	5	91.3	5	4–5	4–7
Gill rakers 1st ceratobranchial	10	10	58.7	9–10	9–10	9–11
Gill rakers 1st epibranchial	4	4	80.4	3–4	3–4	3–5
Teeth outer left lower jaw	11	10	32.6	9–12	9–12	6–12
Tooth rows upper jaw	4	4	52.2	4–5	4–5	4–6
Tooth rows lower jaw	4	4	69.6	4–5	4–5	4–6

Diagnosis. The steeply-sloped vomer (74.0° in holotype) without a swollen rostral tip, a small mouth, retrognathic jaws, and the presence of bicuspid teeth in the outer rows of the oral jaws and enlarged conical teeth at the back of the jaws place this species in *Tropheops*. *Tropheops kumwera* (BD 23.6–31.0% SL) cannot reliably be distinguished from other *Tropheops* in body depth (26.6–34.5%). *Tropheops kumwera* (HED 25.8–32.6% HL, VED 24.2–31.4% HL) does have relatively smaller eye than other described *Tropheops* spp. (HED 31.2–43.8% HL, VED 29.9–43.3% HL) except *T. kamtambo* (HED 26.3–30.2% HL, VED 24.0–29.7% HL). *Tropheops kumwera* can often be distinguished from *T. kamtambo* by a shallower head depth than in *T. kamtambo* (HD 70.2–84.5% HL vs. HD 79.4–97.1% HL). Males of *T. kumwera* in territorial color are distinguished from those of *T. biriwira* by their blue ground coloration and a blue dorsal fin, which are olive green/light blue and yellow-green in *T. biriwira*, respectively. Breeding male *T. kumwera* usually exhibit only the first 3–4 flank bars while male *T. kamtambo* exhibit all 9–10 bars. Female *T. kumwera* lack a black submarginal band in the dorsal fin which is present in female *T. kamtambo*.

Description. Morphometric and meristic data in Table 3. Elongate species (BD 23.6–31.0% SL) with greatest body depth at base of fifth or sixth dorsal-fin spine. Dorsal body profile with gradual downward curve to soft-rayed portion of dorsal fin then more acute curve to posterior origin of dorsal fin, gradual taper to caudal fin; ventral body profile between pelvic and anal fins flat with upward curve from anterior point of anal fin to caudal fin. Dorsal head profile concave to almost straight between snout tip and interorbital area, with about 70° angle with body axis, then round to dorsal-fin origin. Teeth on outer rows mostly bicuspid, all inner rows tricuspid towards the center and unicuspid laterally with greatly enlarged conical teeth on sides of upper jaw. First dorsal-fin spine about one fourth length of last spine. Dorsal fin with subacuminate posterior tip, third or fourth ray longest, slightly beyond base of caudal fin. Pectoral fin rounded, paddle-shaped reaching to ninth dorsal-fin spine. Anal fin with third or fourth ray longest, length beyond base of caudal fin in both male and female, to about as far as dorsal-fin tip. Caudal fin subtruncate to emarginate. Length of longest ray of pelvic fin not to anal fin in females; to first anal-fin ray in males.

Flank scales large, ctenoid; abrupt difference to small cycloid scales on breast and belly; cheek with 4–7 (mode 5) rows of small scales. Dorsal-fin and anal-fin rays with narrow proximal band of tiny scales; tiny scales from base to $3/4$ length caudal fin.

Color notes and photos of live breeding adults (PSU 12766).

Population at Boadzulu Island (Fig. 4B–C). Males in territorial color with blue flank and 7–9 dark bars, first 4–6 distinct, posterior bars faint. Head black with 2 light blue interorbital bars; throat dark brown; cheek and preopercle dark brown to black. Dorsal fin proximally blue with black submarginal band, white/light blue lappets; posterior 5 rays light blue with light gray/clear membranes and yellow highlights. Pectoral fin with black rays and clear membranes; fin base yellow. Pelvic fin black to yellow ventrally with white leading edge. Anal fin black with 4–6 yellow ocelli; light blue marginal band (Fig. 4B).

Females with purple/dark blue flank and 6–8 black bars, less distinct on center flank. Belly and breast light gray/beige. Head blue/purple with 1–2 faint blue interorbital bars; green highlights on opercle; throat brown/gray. Anal-fin spines gray; rays light gray without ocelli. Pectoral fin with gray rays and clear membranes. Pelvic fin with white leading edge, dark gray rays, and clear membranes (Fig. 4C).

Population at Makokola Reef (Fig. 4D). Males in territorial color with similar color pattern as those of Boadzulu Island, except with blue/purple/gray flank and 4–5 black bars; belly gray. Cheek purple/blue with green highlight on opercle. Anal fin with 3–6 ocelli.

Females with same color pattern as those found around Boadzulu Island.

Population at Tsano Rock (Fig. 4E). Males in territorial color with similar color pattern as those of Boadzulu Island, except with orange highlights on opercle. Anal fin black with leading edge light blue fading to green/blue with 3–6 ocelli.

Females with similar color pattern as those of Boadzulu Island, except with blue/light gray flank; caudal peduncle light gray. Head light gray with 1 green interorbital bar; throat light gray/beige. Dorsal fin light gray proximally, dark gray distally with blue lappets and blue/green highlights. Caudal fin gray with clear membranes and blue dorsal and ventral margin. Anal fin with green highlights proximally.

Distribution. *Tropheops kumwera* is known from Boadzulu Island, Makokola Reef (S $14^\circ 15.569'$, E $35^\circ 7.550'$), and Tsano Rock (S $14^\circ 2.472'$, E $34^\circ 54.714'$), Lake Malaŵi, Malaŵi.

Etymology. The name *kumwera* means “south” in Chichewa, alluding to the species’ distribution in the southern part of Lake Malaŵi, and it is used as a noun in apposition.

***Tropheops biriwira*, new species**

Fig. 5 A–C

Pseudotropheus elongatus ‘yellow tail’, Ribbink *et al.* 1983 (part)

Pseudotropheus sp. ‘elongatus greenback’, Reinthal 1990

Tropheops sp. ‘elongatus greenback’, Konings 2007

Holotype. PSU 12767, adult male, 67.7 mm SL, S 14°02.459', E 34°49.296', Otter Island, Lake Malaŵi, Malaŵi, Africa, 7 Feb. 2004, A. F. Konings & J. R. Stauffer Jr.

Paratypes. PSU 12768, 24, (44.6 mm–68.3 mm SL), same data as holotype; PSU 12769, 7, (58.7 mm–68.8 mm SL), at type locality, 16 Feb. 2004, J. R. Stauffer Jr.

Diagnosis. The steeply sloped vomer (75.3° in holotype), the small retrognathic jaw, and the presence of bicuspid teeth in the outer rows of both lower and upper jaws and enlarged conical teeth at the back of the jaws place this species in *Tropheops*. *Tropheops biriwira* (BD 26.8–32.1 % SL) cannot reliably be distinguished from other *Tropheops* spp. on body depth (23.6–34.5%). The breeding male of *T. biriwira* has green/light blue ground coloration with a green dorsal fin, while those of *T. kumwera* and *T. kamtambo* both have blue ground coloration and a blue dorsal fin. Females of *T. biriwira* cannot reliably be distinguished from those of *T. kumwera*, but lack a black submarginal band in the dorsal fin that characterizes female *T. kamtambo*. There are fewer tooth rows (range 2–5) on both upper and lower jaws in *T. biriwira* than in other species of *Tropheops* (range 6–8) except in *T. kumwera* and *T. kamtambo*. *Tropheops biriwira* can be distinguished from *T. kumwera* and *T. kamtambo* by an on average larger eye (HED 30.8–40.4% HL; VED 29.6–35.4% HL vs. HED 25.8–32.6% HL; VED 24.0–31.4% HL in *T. kumwera* and *T. kamtambo*). *Tropheops biriwira* also has on average a shorter snout (SNL 26.5–37.8% HL) than *T. kumwera* (SNL 28.0–42.8% HL).



FIGURE 5. *Tropheops biriwira*. A. Holotype, PSU 12767, adult male, 67.7 mm SL, Otter Island, Lake Malaŵi, Malaŵi, Africa; B. Male in breeding coloration (approx. 62 mm SL) at type locality; C. Female (approx. 50 mm SL) at type locality.

TABLE 4. Morphological and meristic data for *Tropheops biriwira* from Otter Island, Lake Malaŵi, Malaŵi, PSU 12767, holotype; PSU 12768/12769, n=31. Ranges include holotype.

Variable	Holotype PSU12767	Mean PSU12768–12769	Std Dev	Min	Max
Standard length (mm)	67.7	57.6	7.1	44.6	68.8
Head length (mm)	21.1	18.8	2.3	14.9	22.6
Percent head length (%)					
Snout length	33.3	33.8	2.3	26.5	37.8
Postorbital head length	39.2	40.4	1.3	37.9	42.8
Horizontal eye diameter	33.2	34.2	2.2	30.8	40.4
Vertical eye diameter	30.3	32.1	1.5	29.6	35.4
Preorbital depth	24.5	20.8	1.9	17.4	24.6
Cheek depth	24.3	22.7	1.6	20.2	27.7
Lower jaw length	30.9	32.6	2.5	26.9	37.5
Head depth	81.5	80.5	4.2	72.3	90.5
Percent standard length (%)					
Body depth	29.3	29.5	1.4	26.8	32.1
Snout to dorsal fin origin	34.5	35.8	1.4	33.1	38.2
Snout to pelvic fin origin	37.5	37.9	1.0	36.3	39.7
Dorsal fin base length	62.3	61.1	1.4	58.0	63.4
Anterior dorsal to anterior anal	48.9	49.0	1.1	46.8	50.8
Anterior dorsal to posterior anal	63.5	63.1	1.1	60.6	65.0
Posterior dorsal to anterior anal	28.1	27.7	0.8	26.4	30.0
Posterior dorsal to posterior anal	13.5	13.5	0.6	12.5	14.8
Posterior anal to dorsal caudal	14.1	15.4	0.7	14.1	16.6
Posterior dorsal to ventral caudal	16.8	18.3	0.7	16.8	19.5
Anterior dorsal to pelvic-fin origin	32.6	32.3	1.2	29.4	34.8
Posterior dorsal to pelvic-fin origin	56.9	54.7	1.6	51.8	57.5
Caudal peduncle length	9.7	10.5	0.7	9.2	11.9
Least caudal peduncle depth	11.5	11.9	0.5	11.1	12.7
Meristics		Mode	Frequency(%)	Min	Max
Dorsal-fin spines	18	18	84.4	18	19
Dorsal-fin rays	9	9	75.0	8	10
Anal-fin spines	3	3	100.0	3	3
Anal-fin rays	7	8	87.5	7	8
Pelvic-fin rays	5	5	100.0	5	5
Pectoral-fin rays	13	13	90.6	12	14
Lateral line scales	32	32	56.3	31	33
Pored scales caudal	2	2	87.5	1	2
Cheek scale rows	4	4	65.6	4	5
Gill rakers 1st ceratobranchial	10	11	65.6	7	11
Gill rakers 1st epibranchial	3	3	84.4	2	4
Teeth outer left lower jaw	13	10	31.3	9	13
Tooth rows upper jaw	3	4	56.3	2	5
Tooth rows lower jaw	4	4	62.5	2	5

Description. Morphometric and meristic data in Table 4. Elongate species (BD 26.8–32.1% SL) with greatest body depth at base of fourth or fifth dorsal-fin spine. Dorsal body profile with gradual downward curve to soft-rayed portion of dorsal fin then more acute curve to posterior origin of dorsal fin, gradual taper to caudal fin; ventral body profile between pelvic and anal fin flat with upward curve from anterior point of anal fin to caudal fin. Head profile straight to slightly convex between snout tip and interorbital area; snout with 80–90° (84° in holotype) angle with body axis; dorsal head profile round to dorsal-fin origin. Teeth in outer rows bicuspid anteriorly and unicuspid posteriorly; all inner rows have tricuspid teeth medially and unicuspid laterally, with greatly enlarged conical teeth on lateral part of upper jaw.

First dorsal-fin spine about one fourth length of last spine. Soft dorsal fin with subacuminate tip, fourth ray longest, reaching to 1/3 of caudal fin in both males and females. Pectoral fin rounded, paddle-shaped. Fourth ray longest, length reaching to 1/3 of caudal fin in both males and females. Caudal fin subtruncate to emarginate. Pelvic fin not to anal fin in female; length in male to first anal-fin rays.

Flank scales large, ctenoid; abrupt difference to small cycloid scales on breast and belly; cheek with 4–5 (mode 4) rows of small scales. Tiny scales from base to 3/4 length of caudal fin.

Color notes and photos of live breeding adults (PSU 12770).

Population at Otter Island (Fig. 5 B–C). Males in territorial color with greenish-blue ground coloration and 5–6 distinct brown bars. Caudal peduncle greenish-brown. Head brown with 1 light blue interorbital bar and green highlights. Anal fin greenish-brown with 4–6 yellow ocelli; green marginal band. Pectoral-fin rays brown with clear membranes (Fig. 5B).

Females with light brown ground coloration and 4–5 faint lateral dark brown bars. Belly and breast beige/brown. Head with light brown coloration and 1–2 faint greenish/beige/brown interorbital bars; dark brown opercle spot with green highlights. Pectoral fin and pelvic fin brown with light blue margins bands (Fig. 5C).

Distribution. *Tropheops biriwira* is found at Mumbo and Otter islands.

Etymology. The name *biriwira* is from Chichewa meaning “green”, referring to the greenish color of males in territorial coloration. The specific epithet is used as a noun in apposition.

***Tropheops kamtambo*, new species**

Fig. 6 A–C

Pseudotropheus elongatus ‘reef’, Ribbink *et al.* 1983

Tropheops sp. ‘elongatus reef’, Konings 2007

Holotype. PSU 12771, adult male, 90.2 mm SL, S 13°46.240', E 34°57.770', Chimwalani Reef, Lake Malaŵi, Malaŵi, Africa, 12 Oct. 2006, A. F. Konings.

Paratypes. PSU 12772, 22, (58.7 mm–92.6 mm SL), same data as holotype.

Diagnosis. The steeply sloped vomer (76.8° in holotype), a small mouth with retrognathic jaw and the presence of bicuspid teeth in the outer rows of the oral jaws and enlarged conical teeth at the back of the jaws place this species in *Tropheops*. *Tropheops kamtambo* (BD 26.6–30.8% SL) cannot reliably be distinguished from other *Tropheops* spp. on body depth (23.6–34.5%). Breeding male *T. kamtambo* have a blue ground coloration, while those of *T. biriwira* are green/light blue. Female *T. kamtambo* have a distinct black submarginal band on the dorsal fin, which is absent in females of *T. kumwera* and *T. biriwira*. *Tropheops kamtambo* can be distinguished from other *Tropheops* spp., except *T. kumwera* and *T. biriwira*, by the presence of fewer tooth rows (range 3–5 vs. 6–8) on both upper and lower jaws. The smaller eye (HED 26.3–30.2% HL; VED 24.0–29.7% HL) distinguishes *T. kamtambo* from *T. biriwira* (HED 30.8–40.4% HL; VED 29.6–35.4% HL). *Tropheops kamtambo* generally has a deeper head than *T. kumwera* (HD 79.4–97.1% HL vs. HD 70.2–84.5% HL in *T. kumwera*).

Description. Morphometric and meristic data in Table 5. Elongate species (BD 26.6–30.8% SL) with greatest body depth at fifth or sixth dorsal-fin spine. Dorsal body profile with gradual downward curve to soft-rayed portion of dorsal fin then more acute curve to posterior origin of dorsal fin, gradual taper to caudal fin; ventral body profile between pelvic and anal fins flat with upward curve from anterior point of anal fin to caudal fin. Head profile convex between snout tip and interorbital area, with premaxillary pedicel about 80–90° (82.7° in holotype) angle with body axis; dorsal head profile rounded to dorsal-fin origin. Teeth in outer rows bicuspid with large unicuspid teeth on posterior dentigerous arms of premaxilla, all inner rows tricuspid. Dorsal-fin spines progressively longer

posteriorly from first to fourth spine, last spine slightly longer than fourth, and first spine about one fourth length of last spine. Soft dorsal fin with subacuminate tip, fourth ray longest, reaching to base of caudal fin in both male and female. Pectoral fin rounded, paddle-shaped. Anal fin with 3 spines progressively longer posteriorly; fourth ray longest, reaching to 1/3 of caudal fin in both males and females. Caudal fin subtruncate to emarginate. Pelvic fin not to anal fin in females; length in adult males to anal-fin base.



FIGURE 6. *Tropheops kamtambo*. A. Holotype, PSU 12771, adult male, 90.2 mm SL, Chimwalani Reef, Lake Malaŵi, Malaŵi, Africa; B. Male in breeding coloration (approx. 85 mm SL) at type locality; C. Female (approx. 72 mm SL) at type locality.

Flank scales large, ctenoid; abrupt shift to small cycloid scales on breast and belly; cheek with 4–6 (mode 5) rows of small scales. Dorsal fin and anal fin with narrow proximal band of tiny scales; tiny scales on 2/3 of caudal fin.

Color notes and photos of live breeding adults (PSU 12773).

Males in territorial color with blue ground coloration and 9–10 distinct black bars, posterior 1–3 bars often vague. Head black with 2 dark blue interorbital bars; throat light blue; cheek and preopercle dark blue. Anal fin dark gray/black with 4–6 orange ocelli. Pectoral-fin with gray rays and clear membranes (Fig. 6B).

Females blue/green ground coloration with 7–8 brown bars; belly and breast light brown. Head with brown coloration and 2 faint blue/green interorbital bars; dark brown opercle spot with green highlights. Anal-fin spines black; rays gray; with 1–3 yellow ocelli. Pectoral fin with gray rays and clear membranes (Fig. 6C).

Distribution. *Tropheops kamtambo* occurs at Chimwalani (S 13°46.240', E 34°57.770') and Luwala (S 13°45.975', E 34°56.255') reefs, and a very similar form has been reported (Konings 2007) from the area between the Mozambique-Malaŵi border and the Nsinje River, but no specimens were available to confirm their possible conspecificity.

Etymology. The name *kamtambo* is a noun in apposition and means “blue” in Chichewa (Nyanja). It refers to the blue coloration of breeding males.

TABLE 5. Morphological and meristic data for *Tropheops kamtambo* from Chimwalani Reef, Lake Malaŵi, PSU 12771, Holotype; PSU 12772, n=22. Ranges include holotype.

Variable	Holotype PSU12771	Mean PSU12772	Std Dev	Min	Max
Standard length (mm)	90.2	76.0	8.3	58.7	92.6
Head length (mm)	25.5	22.7	1.6	18.5	25.8
Percent head length (%)					
Snout length	39.8	38.9	2.0	34.7	42.4
Postorbital head length	42.7	42.5	1.2	40.0	45.2
Horizontal eye diameter	27.4	28.1	1.1	26.3	30.2
Vertical eye diameter	26.6	26.7	1.4	24.0	29.7
Preorbital depth	24.9	22.8	1.9	19.6	26.4
Cheek depth	30.2	27.4	2.5	24.9	36.9
Lower jaw length	34.5	34.2	2.0	30.0	36.9
Head depth	93.6	87.9	5.8	79.4	97.1
Percent standard length (%)					
Body depth	30.2	28.8	1.1	26.6	30.8
Snout to dorsal fin origin	31.5	32.3	1.3	30.0	35.1
Snout to pelvic fin origin	34.7	35.6	1.3	33.6	38.6
Dorsal fin base length	66.1	65.4	1.7	60.8	68.0
Anterior dorsal to anterior anal	51.4	51.1	1.4	47.6	53.2
Anterior dorsal to posterior anal	67.6	66.9	1.6	64.6	70.0
Posterior dorsal to anterior anal	29.5	28.6	1.0	27.3	31.0
Posterior dorsal to posterior anal	14.2	13.9	0.5	12.8	15.0
Posterior anal to dorsal caudal	17.3	15.8	0.6	14.6	17.3
Posterior dorsal to ventral caudal	18.4	17.9	0.7	16.8	19.4
Anterior dorsal to pelvic-fin origin	34.2	32.4	1.5	29.7	34.6
Posterior dorsal to pelvic-fin origin	57.3	57.6	1.9	52.8	61.7
Caudal peduncle length	12.0	10.2	0.8	8.7	12.0
Least caudal peduncle depth	12.3	11.8	0.4	10.9	12.4
Meristics		Mode	Frequency(%)	Min	Max
Dorsal-fin spines	19	19	56.5	18	21
Dorsal-fin rays	9	9	65.2	8	10
Anal-fin spines	3	3	100.0	3	3
Anal-fin rays	8	8	95.7	7	8
Pelvic-fin rays	5	5	100.0	5	5
Pectoral-fin rays	13	13	100.0	13	13
Lateral line scales	33	33	60.9	31	34
Pored scales caudal	2	2	87.0	1	3
Cheek scale rows	5	5	65.2	4	6
Gill rakers 1st ceratobranchial	10	10	56.5	9	11
Gill rakers 1st epibranchial	2	3	47.8	2	4
Teeth outer left lower jaw	12	12	39.1	10	13
Tooth rows upper jaw	5	5	43.5	3	6
Tooth rows lower jaw	4	4	73.9	3	5

***Cynotilapia chilundu*, new species**

Fig. 7 A–C

Pseudotropheus sp. ‘elongatus taiwan’, Konings 2001

Cynotilapia sp. ‘elongatus taiwan’, Konings 2007

Holotype. PSU 12774, adult male, 82.9 mm SL, S 11°57.448', E 34°35.298', Taiwanee Reef, Lake Malaŵi, Malaŵi, Africa, 13Jan. 2008, A. F. Konings & J. R. Stauffer Jr.

Paratypes. PSU 12775, 24, (52.6 mm–82.9 mm SL), same data as holotype.

Diagnosis. The presence of widely spaced unicuspid teeth on both the upper and lower oral jaws and a moderately inclined vomer place this species in *Cynotilapia*. *Cynotilapia chilundu* is distinguished from *C. afra*, *C. zebroides* and *C. aurifrons* by its slender body with BD 24.9%–31.1% SL (mean 28.3%) vs. BD 31.8–37.2% SL (mean 34.9%) in the other three species. Male *C. chilundu* differ from those of *C. axelrodi* by the presence of a black submarginal band in the dorsal fin which is absent in *C. axelrodi*. Females of the latter species lack distinct bars on the flank and interorbital bars on the head, while both these characters are evident in female *C. chilundu*.

Description. Morphometric and meristic data in Table 6. Vomer moderately inclined (38.4° in holotype). Elongate species (BD 22.6–28.5% SL) with greatest body depth at base of seventh or eighth dorsal-fin spine; ventral body profile between pelvic and anal fins flat with upward curve to caudal fin. Head profile slightly concave between snout tip and interorbital area, with 40–50° (42.6° in holotype) angle with body axis, then round to dorsal-fin origin. Snout short with thick, slightly prognathic lower jaw. First 5 dorsal-fin spines gradually longer posteriorly with first spine less than one third length of fifth spine. Soft dorsal fin with subacuminate tip, fourth ray longest, reaching to one third of caudal fin in males and slightly beyond caudal-fin base in females. Pectoral fin rounded, paddle-shaped. Anal fin with 3 spines progressively longer posteriorly; fourth ray longest, length to base of caudal fin in both male and female. Caudal fin subtruncate to emarginate.



FIGURE 7. *Cynotilapia chilundu*. A. Holotype, PSU 12774, adult male, 82.9 mm SL, Taiwanee Reef, Lake Malaŵi, Malaŵi, Africa; B. Male in breeding coloration (approx. 75 mm SL) at type locality; C. Female (approx. 60 mm SL) at type locality.

TABLE 6. Morphometric and meristic data for *Cynotilapia chilundu* from Taiwane Reef, Lake Malaŵi, PSU 12774, holotype; PSU 12775, n=24. Ranges include holotype.

Variable	Holotype PSU12774	Mean PSU12775	Std Dev	Min	Max
Standard length (mm)	82.9	67.1	8.5	52.6	82.9
Head length (mm)	24.5	20.4	2.4	16.4	25.3
<hr/>					
Percent head length (%)					
Snout length	35.3	34.7	1.7	31.1	39.0
Postorbital head length	39.2	39.9	1.4	38.2	42.9
Horizontal eye diameter	27.4	28.2	1.2	25.6	30.5
Vertical eye diameter	22.8	25.2	1.6	22.1	27.7
Preorbital depth	20.5	20.2	1.3	17.4	22.0
Cheek depth	28.3	26.8	1.6	24.4	30.3
Lower jaw length	38.4	38.1	2.0	34.1	41.2
Head depth	78.8	78.5	4.3	70.6	88.8
<hr/>					
Percent standard length (%)					
Body depth	25.1	26.2	1.2	22.6	28.5
Snout to dorsal fin origin	30.2	31.1	1.1	29.4	33.3
Snout to pelvic fin origin	37.4	36.5	1.0	34.3	38.5
Dorsal fin base length	62.3	61.7	1.6	59.2	64.8
Anterior dorsal to anterior anal	47.0	46.3	1.5	43.7	49.5
Anterior dorsal to posterior anal	63.6	62.1	1.8	58.6	65.1
Posterior dorsal to anterior anal	27.7	27.2	1.0	24.7	28.5
Posterior dorsal to posterior anal	13.1	13.2	0.6	11.9	14.0
Posterior anal to dorsal caudal	17.2	15.6	0.7	14.5	17.2
Posterior dorsal to ventral caudal	18.8	18.4	0.7	16.3	19.7
Anterior dorsal to pelvic-fin origin	29.4	28.9	1.4	25.7	32.1
Posterior dorsal to pelvic-fin origin	56.1	56.0	1.4	53.1	58.8
Caudal peduncle length	10.9	10.4	0.8	8.6	11.8
Least caudal peduncle depth	10.8	11.3	0.4	10.5	11.9
<hr/>					
Meristics		Mode	Frequency(%)	Min	Max
Dorsal-fin spines	18	18	80	17	19
Dorsal-fin rays	9	9	72	7	10
Anal-fin spines	3	3	100	3	3
Anal-fin rays	8	8	88	7	8
Pelvic-fin rays	5	5	96	4	5
Pectoral-fin rays	13	13	96	13	14
Lateral-line scales	33	33	52	31	34
Pored scales caudal	3	2	84	1	3
Cheek-scale rows	5	5	64	4	7
Gill rakers 1st ceratobranchial	12	12	48	11	14
Gill rakers 1st epibranchial	4	4	68	4	5
Teeth outer left lower jaw	6	6	36	3	8
Tooth rows upper jaw	3	3	80	2	4
Tooth rows lower jaw	3	3	88	2	4

Flank scales ctenoid; small cycloid scales on breast and belly; cheek with 4–7 (mode 5) rows of small scales. Dorsal fin and anal fin with narrow proximal band of tiny scales; tiny scales on proximal 3/4 caudal fin.

Color notes and photos of live breeding adults (PSU 12776).

Males in territorial color with blue ground coloration and 5–6 distinct dark blue/black bars. Caudal peduncle dark blue; breast dark brown; belly light brown/white. Head black with 2 blue interorbital bars; throat black. Anal fin black/blue with 4–6 yellow ocelli; light blue leading margin. Pectoral fin rays gray with clear membranes. Pelvic fin black with blue leading edge; membranes dark gray (Fig. 7B).

Females' ventral flank light brown; rest of body light blue with 4 light brown bars on flank, less pronounced posteriorly. Belly and breast white/beige. Head light brown with 2 faint light blue interorbital bars; throat light brown. Anal fin proximally 2/3 dark gray, remaining 1/3 light gray with 2–4 yellow/orange ocelli. Pectoral fin light gray with clear membranes (Fig. 7C).

Distribution. *Cynotilapia chilundu* is only known from Taiwanese Reef (S 11°57.448', E 34°35.298').

Etymology. The name *chilundu* is derived from Chichewa meaning “reef”, and refers to the fact that the species is only found on a reef.

***Chindongo* gen. nov.**

Pseudotropheus elongatus was described from specimens collected in Mbamba Bay, Tanzania (Fryer 1956). Most members of the *P. elongatus* species group are small species with a standard length less than 10 cm (Ribbink *et al.* 1983). Members of this complex which are morphologically distinct from *Metriaclima*, *Tropheops*, *Cynotilapia*, or from the type species of *Pseudotropheus*, *P. williamsi*, will be placed into the newly defined genus.

Type species. *Chindongo bellicosus* sp. nov.

Diagnosis. This genus is comprised of small, rock-dwelling haplochromine cichlids endemic to Lake Malaŵi. The possession of the following characteristics aligns *Chindongo* with the other 13 mbuna genera in Lake Malaŵi: 1) large number of small scales on the nape and chest region; 2) abrupt transition from large flank scales to small chest scales; 3) reduction of the left ovary; and 4) possession of true ocelli (Fryer, 1959). The following morphological characteristics distinguish *Chindongo*: 1) the presence of bicuspid teeth in the anterior portion of the outer row of both upper and lower jaws; 2) a moderately to steeply sloped vomer with a narrow rostral tip making an angle of between 53° and 68° with the parasphenoid; 3) small mouth with lower jaw slightly shorter than upper; 4) broad anterior dentigerous area on both premaxilla and dentary with 3 or more rows of teeth (usually 5–6 rows); 5) a flank melanin pattern consisting of vertical bars without horizontal elements at any stage of development.

Chindongo is distinguished from *Abactochromis*, *Cynotilapia*, *Gephyrochromis*, and some *Labidochromis* by the presence of bicuspid teeth in the anterior portion of the outer row of both the upper and lower jaws, which are unicuspid in the other genera, and from *Petrotilapia* and *Labeotropheus* as representatives of these two genera have tricuspid teeth. *Chindongo* is further distinguished from *Labidochromis* by the absence of an inclination of the anterior dentigerous area of the dentary which makes an angle of 30–45° with the dentigerous arms in *Labidochromis* (in *Chindongo* the anterior and posterior dentigerous areas of the dentary are in about the same plane as the arms), and by a wide U-shaped dentary which is narrowly V-shaped in *Labidochromis*. The presence of teeth consisting of narrow shafts with recurved, spoonlike, compressed crowns distinguishes *Cyathochromis* from *Chindongo*. The isognathic to slightly retrognathic jaws of *Chindongo* distinguish it from *Genyochromis* which possess a prognathic mouth with a strong chin. *Chindongo* is distinguished from *Melanochromis* by a lack of longitudinal stripes in its flank melanin pattern and by the absence of a sex-related reversal in the color pattern which characterizes the latter. *Iodotropheus* can be distinguished by a narrow U-shaped dentary with a width about 3/4 of its length while that in *Chindongo* is as wide as long.

Chindongo is distinguished from *Pseudotropheus* (here characterized by its type species *P. williamsi* and by *P. brevis*) by a smaller mouth with relatively large outer teeth. The outer row teeth in *Pseudotropheus* are about twice the size of those in the second row, while in *Chindongo* the outer row teeth are 4–10 times as large (Fig. 8). *Chindongo* is characterized by a melanin pattern consisting of vertical bars on the flank while the pattern in *Pseudotropheus* consists of two longitudinal bands of spots. *Chindongo* differs from *Tropheops* by the placement of the teeth in the dentary; in *Chindongo* all teeth are implanted at about the same plane and the dentigerous area extends posteriorly to about halfway the coronoid process, while in *Tropheops* almost all teeth are anterior of the

coronoid process and the anterior most teeth are implanted at a considerably lower level (the crown tips of the larger anterior teeth are at about the same level as those of the minute posterior teeth) (Fig. 9). *Chindongo* differs from *Tropheops* and *Metriaclima* by a consistently different range in the angle of the vomer (53–68° in *Chindongo* vs. 71–96° in *Tropheops* vs. 32–49° in *Metriaclima*).

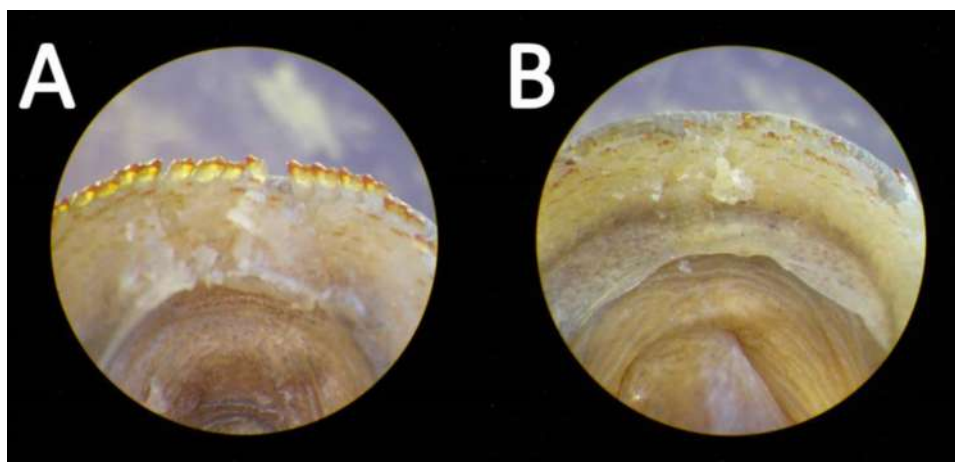


FIGURE 8. Occlusal view of the dentary *Chindongo bellicosus* (A) and *Pseudotropheus williamsi* (B). Note that the outer-row teeth of *Chindongo* (A) are much larger than those of the second row while those of *P. williamsi* are only slightly larger (B).



FIGURE 9. Occlusal view of the dentary *Chindongo bellicosus* (A) and *Tropheops kamtambo* (B). In *Chindongo* all teeth are implanted at about the same plane and the dentigerous area extends posteriorly to about halfway the coronoid process, while in *Tropheops* almost all teeth are anterior of the coronoid process and the anterior most teeth are implanted at a considerable lower level.

Representatives of *Chindongo* are further diagnosed by their feeding technique. Members of *Chindongo* feed mostly on aufwuchs extracting loose material (diatoms and cyanobacteria) from the algal matrix on rocks by biting (Konings 2007), and they feed at a 30–60° angle to the substrate (Stauffer & Posner 2006). They favor patches with a lush growth so that the bites yield sufficient food. In order to prevent other algae-eaters access to such lush aufwuchs, members of *Chindongo* protect their feeding grounds aggressively with most species defending so-called algal gardens. Members of *Metriaclima* rake the algal matrix with their teeth collecting only the loose material while *Tropheops* species feed by shearing and twisting algal strands from the substrate. *Pseudotropheus* (*P. williamsi* and *P. brevis*) do not feed on algae but instead on insects that fall on the water surface or even by jumping partly out of the water snapping lake flies hovering above the surface (Konings 2007).

In addition to the newly described *C. bellicosus*, we assign the following species, which were previously in *Pseudotropheus*, to *Chindongo*: *C. ater*, *C. cyaneus*, *C. demasoni*, *C. elongatus*, *C. flavus*, *C. heteropictus*, *C. longior*, *C. minutus*, *C. saulosi*, and *C. socolofi*.

Etymology. The name *Chindongo* is a commonly-used name for “small, rock-dwelling fish” in the local vernacular of Malaŵi. The gender is masculine.

Chindongo bellicosus, new species

Fig. 10 A–G

Pseudotropheus elongatus 'aggressive', Ribbink *et al.* 1983

Pseudotropheus elongatus 'slab', Ribbink *et al.* 1983

Pseudotropheus sp. 'elongatus aggressive', Konings 2007

Pseudotropheus sp. 'elongatus slab', Konings 2007

Holotype. PSU 12576, adult male, 92.6 mm SL, S 13°57.919', E 34°48.167', Zimbabwe Rock, Lake Malaŵi, Malaŵi, Africa, 7 Feb. 2003, J. R. Stauffer Jr.

Paratypes. PSU 12577, 10, (72.4 mm–92.2 mm SL), same data as holotype; PSU 12578, 24, (62.2 mm–90.5 mm SL), Zimbabwe Rock, Lake Malaŵi, Malaŵi, Africa, 12 Feb. 2004, J. R. Stauffer Jr.; PSU 12579, 10, (63.5 mm–93.4 mm SL), Zimbabwe Rock, Lake Malaŵi, Malaŵi, Africa, 17 Feb. 2005, J. R. Stauffer Jr.; PSU 12580, 18, (56.9 mm–80.2 mm SL), S 13°59.513', E 34°45.437', Mumbo Island, Lake Malaŵi, Malaŵi, Africa, 8 Feb. 2003, J. R. Stauffer Jr.; PSU 12581, 20, (56.9 mm–78.2 mm SL), Thumbi West Island, Lake Malaŵi, Malaŵi, Africa, 13 Apr. 1984, J. R. Stauffer Jr.

Diagnosis. The possession of the following characteristics place this species in *Chindongo*: 1) the presence of bicuspid teeth in the outer row of both upper and lower jaws; 2) a vomer without a bulbous rostral tip and angled 53°–68° with the parasphenoid; 3) small mouth with isognathic to slightly retrognathic jaws. Morphologically *C. bellicosus* is difficult to distinguish from most congeners, but male and female color patterns provide usable distinctions between most of them. *Chindongo bellicosus* is characterized by 6–8 (usually 7) dark, vertical bars below the dorsal fin and is thus distinguished from *C. demasoni* (4 bars) and from *C. saulosi* (5 bars). It is further distinguished from the latter species by a shallower body (22.8–30.9% SL vs. 31.3–37.0% SL in *C. saulosi*). Female and juvenile male *C. bellicosus* have light beige to bluish ground color and are distinguished from those of *C. saulosi* and *C. heteropictus* which are entirely yellow, and from those of *C. demasoni* which are blue with black bars and from female *C. socolofi* which are light blue without bars. *Chindongo bellicosus* is distinguished from *C. minutus* by a larger number of gill rakers on the first ceratobranchial (10–13 vs. 7 in *C. minutus*) and by a shallower body (22.8–30.9% SL vs. 31.1–35.5% SL in *C. minutus*). *Chindongo bellicosus* can be distinguished from *C. elongatus* by its incomplete barring pattern that lacks bars on the posterior half of the flank and on the caudal peduncle while both male and female *C. elongatus* exhibit a bar pattern over the full length of the flank and caudal peduncle. *Chindongo bellicosus* can be distinguished from *C. ater* by its barring pattern which is still visible in very dark individuals while absent in male *C. ater*. Females of the latter species may sometimes show a few faint bars but their body coloration is blue, lacking any yellow pigment, while that of female *C. bellicosus* always contains yellow pigment. *C. cyaneus* is distinguished from *C. bellicosus* by the yellow cheek and breast which is black in male and gray to brown in female *C. bellicosus*. Male *C. flavus* differ from those of *C. bellicosus* by their bright yellow/mustard ground color, but females can have a similar coloration. Female *C. bellicosus* have on average a deeper cheek than those of *C. flavus* (25.6% vs. 20.7% HL), but the ranges are overlapping (21.6–30.9% vs. 17.4–23.4% HL). Male *C. bellicosus* are distinguished from those of *C. longior* by a black cheek and breast while this is fawn to gray-brown in *C. longior*. Female *C. longior* are fawn with distinct black margins in the dorsal and anal fins while similar-colored females of *C. bellicosus* lack such distinct black margins.

Description. Morphometric and meristic data in Table 7. Elongate species (mean BD 27.6% SL; range 22.8–30.9% SL) with greatest body depth at base of fifth or sixth dorsal-fin spine. Dorsal body profile with gradual downward curve to soft-rayed portion of dorsal fin then more steeply to posterior origin of dorsal fin, gradual taper to caudal fin; ventral body profile between pelvic and anal fins very flat with upward curve from anterior point of anal fin to caudal fin. Head profile straight between snout tip and interorbital area, the snout makes about 70° angle with body axis; dorsal head profile round to dorsal-fin origin. Small subterminal mouth with lower jaw slightly shorter than upper. Snout short with isognathic to retrognathic jaws; teeth in outer rows bicuspid anteriorly with small unicuspid teeth posteriorly in lower jaw and large unicuspid teeth in upper jaw; teeth tricuspid in anterior inner rows, unicuspid in posterior rows. First dorsal-fin spine about one fourth length of last spine. Soft dorsal fin with subacuminate tip, third or fourth ray longest, reaching to base of caudal fin in male and female. Pectoral fin rounded, paddle-shaped. Pelvic fin with 1 spine and 5 rays. Anal fin with 3 spines progressively longer posteriorly; 7–9 rays with third or fourth longest, length reaching to base of caudal fin in both males and females. Caudal fin subtruncate to emarginate. Length of pelvic fin not to anal fin in females, to anterior base of anal fin in males.

TABLE 7. Morphometric and meristic data for *Chindongo bellicosus* from Zimbabwe Rock, Mumbo Island, and West Thumbi Island, Lake Malawi (PSU 12576, holotype; PSU 12577, n=10; PSU 12578, n=24; PSU 12579, n=10; PSU 12580, n=18; PSU 12581, n=20).

Variable	Holotype	Mean	Std Dev	Min-Max					
				Zimbabwe Rock Coll.1	Zimbabwe Rock Coll.2	Zimbabwe Rock Coll.3	Mumbo Island	West Thumbi Island	
Standard length (mm)	PSU12576	73.1	9.1	72.4–92.6	62.2–90.5	63.5–93.4	56.9–80.2	56.9–78.2	
Head length (mm)		22.5	3.0	23.0–29.0	20.0–27.2	20.2–28.9	17.7–24.4	16.6–23.0	
Percent head length (%)									
Snout length		38.2	2.1	37.0–41.8	35.7–43.7	29.0–41.3	34.5–40.3	34.5–40.7	
Postorbital head length		41.5	1.7	39.1–42.6	36.9–42.6	36.9–42.2	39.4–45.2	40.9–45.8	
Horizontal eye diameter		27.8	1.7	24.8–27.6	25.1–30.1	27.2–30.6	25.3–32.0	24.2–32.6	
Vertical eye diameter		26.4	1.7	22.9–26.4	23.8–28.8	24.6–29.5	24.4–31.2	23.4–30.0	
Preorbital depth		24.5	2.6	21.0–24.4	20.5–24.8	20.5–24.6	24.4–31.2	23.4–30.0	
Cheek depth		25.6	1.9	23.3–29.0	22.2–26.7	21.6–30.6	24.3–28.4	21.7–30.9	
Lower jaw length		33.9	3.7	31.5–36.6	32.1–44.6	27.8–33.9	23.5–36.1	25.5–36.1	
Head depth		78.4	4.5	77.2–88.8	67.5–86.3	77.0–87.3	66.3–81.3	74.1–83.0	
Percent standard length (%)									
Body depth		26.4	2.0	27.9–30.9	23.3–28.8	25.6–30.2	22.8–26.6	22.9–26.9	
Snout to dorsal fin origin		32.2	1.6	31.4–35.2	30.0–35.7	33.1–35.6	28.2–33.6	29.5–32.2	
Snout to pelvic fin origin		36.8	1.5	35.1–38.4	34.2–42.2	35.5–39.4	34.5–40.5	34.7–37.7	
Dorsal fin base length		60.4	1.8	59.0–62.7	56.9–64.8	56.4–61.6	57.7–64.5	57.6–62.4	
Anterior dorsal to anterior anal		46.4	1.6	46.3–49.6	43.4–48.8	46.3–49.7	43.4–47.7	42.2–48.8	
Anterior dorsal to posterior anal		61.8	1.5	60.6–64.6	59.1–65.8	61.0–63.5	58.0–65.3	58.2–62.6	
Posterior dorsal to anterior anal		27.0	1.4	25.9–29.1	26.7–29.2	25.9–29.1	23.7–29.4	23.9–27.0	
Posterior dorsal to posterior anal		13.4	0.8	13.7–14.7	12.3–14.3	13.0–15.0	12.1–14.2	11.3–13.7	
Posterior anal to dorsal caudal		16.3	0.8	15.6–18.1	13.9–18.0	15.9–18.4	15.4–17.1	15.3–17.4	
Posterior dorsal to ventral caudal		18.7	0.8	17.2–19.6	17.3–20.2	17.5–19.5	16.7–19.3	16.9–20.5	

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TABLE 7. (Continued)

Variable	Holotype	Mean	Std Dev	Min-Max					
				Zimbabwe Rock Coll.1	Zimbabwe Rock Coll.2	Zimbabwe Rock Coll.3	Mumbo Island	West Thumbi Island	PSU12581
Anterior dorsal to pelvic-fin origin	32.9	28.7	1.9	PSU12577 29.2-32.9	PSU12578 26.6-32.3	PSU12579 28.0-31.9	PSU12580 24.6-29.1	PSU12581 24.8-29.2	
Posterior dorsal to pelvic-fin origin	56.4	54.9	1.8	54.3-58.4	51.5-58.9	52.8-58.3	50.6-56.7	51.7-57.3	
Caudal peduncle length	12.1	11.5	1.0	10.3-12.8	9.1-12.3	11.5-12.7	9.9-11.9	11.4-13.6	
Least caudal peduncle depth	11.7	11.5	0.5	11.6-12.4	10.7-12.5	11.0-12.6	11.0-12.2	10.2-11.8	
Meristic counts		Mode	Freq(%)						
Dorsal-fin spines	17	18	67.5	17-19	17-19	17-18	17-19	17-19	
Dorsal-fin rays	9	9	71.1	7-10	8-10	8-10	8-10	9-10	
Anal-fin spines	3	3	100.0	3	3	3	3	3	
Anal-fin rays	8	8	88.0	8	7-9	7-8	8	7-9	
Pelvic-fin rays	5	5	100.0	5	5	5	5	5	
Pectorial-fin rays	13	13	74.7	12-14	13-14	11-14	12-14	12-13	
Lateral-line scales	32	33	45.8	24-33	31-34	32-34	31-34	31-34	
Pored scales caudal	1	2	60.2	1-2	1-2	1-2	1-2	1-2	
Cheek-scale rows	4	4	49.4	4-5	4-6	4-6	4	3-5	
Gill rakers 1st ceratobranchial	11	11	73.5	10-13	10-11	10-12	10-12	10-11	
Gill rakers 1st epibranchial	3	4	75.9	3-4	4-5	3-4	4-5	3-4	
Teeth outer left lower jaw	11	10	32.5	8-12	9-11	9-13	8-11	7-12	
Tooth rows upper jaw	5	4	33.7	3-5	3-5	4-5	2-4	3-6	
Tooth rows lower jaw	5	4	41.0	2-5	3-5	3-5	2-3	4-5	

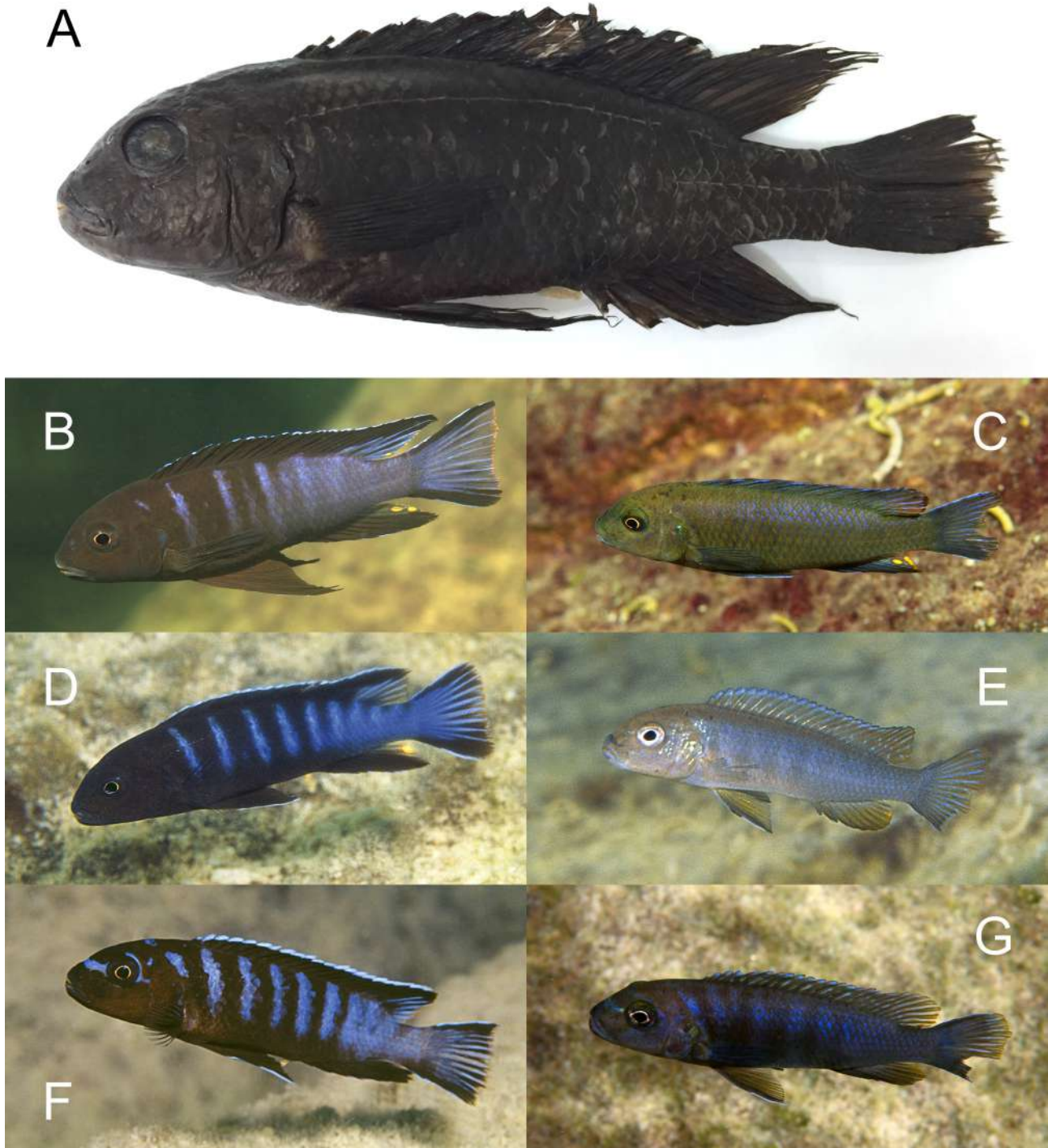


FIGURE 10. *Chindongo bellicosus*. A. Holotype, PSU 12576, adult male, 92.6 mm SL, Zimbabwe Rock, Lake Malaŵi, Malaŵi, Africa; B. Male in breeding coloration at type locality; C. Female at type locality; D. Male in breeding coloration at Thumbi West Island, Lake Malaŵi, Malaŵi; E. Female, at Thumbi West Island, Lake Malaŵi, Malaŵi; F. Male in breeding coloration at Mumbo Island, Lake Malaŵi, Malaŵi; G. Female, at Mumbo Island, Lake Malaŵi, Malaŵi.

Flank scales large, ctenoid; abrupt difference to small cycloid scales on breast and belly; cheek with 3–6 (mode 4) rows of small scales. Dorsal fin and anal fin with narrow proximal margin of tiny scales; tiny scales from base to 3/4 length of caudal fin.

Color notes and photos of live breeding adults (PSU 12582).

Population at Zimbabwe Rock (Fig. 10 B–C). Males in territorial color with blue/purple ground coloration and 4

distinct black bars on anterior half of flank. Caudal peduncle blue/purple; breast dark blue/dark gray; belly brown/black. Head black; dark brown opercle with lighter edge. Anal fin black with 2–3 brown/yellow ocelli in posterior margin. Pectoral fin with black rays and clear membranes (Fig. 10B).

Female with light blue-gray or light brown ground coloration without distinct vertical bars; lateral scales brown with light blue center. Caudal peduncle brown; belly and breast white/gray. Head brown/gray; opercle with blue/green highlights; throat gray. Anal fin gray without ocelli or with very small yellow/orange spots. Pectoral fins with gray rays and clear membranes. Pelvic fin with first two membranes black/gray and white leading edge (Fig. 10C).

Population at Thumbi West Island (Fig. 10 D–E). Males in territorial color with similar color pattern as those around Zimbabwe Rock, except with 4–6 distinct black bars on anterior half of flank (Fig. 10D).

Females with similar color pattern as those at Zimbabwe Rock except with beige/blue or light brown ground coloration and 4–6 brown bars; lateral scales blue. Caudal peduncle beige/blue. Head beige with blue highlights; throat light brown. Anal fin proximally blue. (Fig. 10E).

Population at Mumbo Island (Fig. 10F–G). Males in territorial color with similar color pattern as those at Zimbabwe Rock, except with 6 distinct black bars on anterior part of flank (Fig. 10F).

Females with similar color pattern as those at Zimbabwe Rock except 4–6 gray bars on the flank. Head brown with blue marks; opercle with light brown/yellow highlights; brown opercular spot (Fig. 10G).

Distribution. *Chindongo bellicosus* was collected from Zimbabwe Rock, Thumbi West Island, and Mumbo Island, but the species likely has a wider distribution as Ribbink *et al.* (1983) found it all along the Nankumba Peninsula, as far south as Nkudzi, while Konings (2007) reports it from Nakantenga as well as Maleri Island.

Etymology. *Bellicosus* is Latin for “warlike” or “fond of war” and refers to the aggressive behavior of the species (Ribbink *et al.* 1983).

Discussion

After Ribbink *et al.* (1983) categorized the mbuna of Lake Malaŵi in several groups of similar-looking species, the first step was taken in classifying this huge assortment of recently evolved haplochromines. Two of their species-complexes were later described as genera, i.e. *Tropheops* (the *Pseudotropheus tropheops* complex) and *Metriaclima* (the *Pseudotropheus zebra* complex), while others were referred to as species groups because they are polyphyletic. One of these species groups was named the *Pseudotropheus elongatus* species-group, as all the species in it possess a slender body. Later, it was suggested that a shared feeding technique may be an indicator of relationship for those mbuna species that are morphologically very similar, and that body slenderness in itself is not necessarily a synapomorphic character. The elongate body shape is likely the result of convergent evolution among mbuna, and a small size and dark coloration suggest the adaptation for life in small crevices between rocks. A number of elongate mbuna, originally grouped in the *Pseudotropheus elongatus* species-group by Ribbink *et al.* (1983), have subsequently been placed into the existing genera *Metriaclima*, *Tropheops*, and *Cynotilapia* (Konings & Stauffer 2006; Konings 2007).

All known species of *Cynotilapia* are specialized for suction-feeding on particles in the water column, and their dentition appears no longer to be functional for benthic feeding. Representatives of the other genera discussed here opportunistically feed from the water column, but have dentition specialized for different forms of benthic feeding. Members of *Metriaclima* are able to align their teeth of both upper and lower jaws on the same plane, and feed perpendicularly to the substrate (Konings 1995; Stauffer & Posner 2006). They collect loose material, such as diatoms and cyanobacteria, by combing through the algal matrix while little is torn from the substrate (Fryer 1959; Konings & Stauffer 2006). *Tropheops* spp. appear to spend more energy in obtaining food, as they twist and tear off the short filaments of algae by vigorously shaking their bodies. Most species of *Tropheops* feed at an angle of about 60° to the substrate (Stauffer & Posner 2006). In rocky habitats, most *Chindongo* spp. aggressively defend feeding territories. They usually feed at an angle of 45–50° (Stauffer & Posner 2006) biting in the lush algae of their gardens while extracting loose material.

The differences by which each of these four groups of mbuna feed is reflected in their anatomy, in particular that of the jaws, arrangement and shape of teeth, and in the angle and shape of the vomer. In fact, the angle the vomer makes with the parasphenoid is a useful character to distinguish among three of the four genera. The fourth

genus, *Cynotilapia*, has an overlapping range with *Metriaclima* but can be distinguished by its possession of large unicuspid teeth while members of the other three genera have bicuspid teeth in the outer and tricuspid teeth in the inner rows. *Chindongo* has a vomer angle of 53–68° with the parasphenoid, which is 32–49° in *Metriaclima*, and 71–96° in *Tropheops*. Based on the known angle of the vomer combined with underwater observations of the feeding behavior of the species in question, we have included in *Chindongo* a number of species. Undoubtedly, more species that are currently in *Pseudotropheus* will be placed into *Chindongo* in the future, but we neither had observed the feeding behavior nor examined the angle of the vomer of these other species.

Chindongo bellicosus includes both *Pseudotropheus* sp. ‘elongatus aggressive’ and *Pseudotropheus* sp. ‘elongatus slab’, which were suggested to be two different species by Ribbink *et al.* (1983) and later authors (e.g. Konings 2007). We failed to discover significant morphological distinctions between these two forms except for an average larger size of *P.* sp. ‘elongatus aggressive’ (62.2–93.4 mm SL vs. 56.9–80.2 mm SL for *P.* sp. ‘elongatus slab’). There are neither morphological/meristic differences nor color-pattern differences between the two forms. Both forms prefer a habitat consisting of small- to medium-sized rocks in shallow water, and both aggressively defend territories against intruders, creating algal gardens.

Ribbink *et al.* (1983) found these two groups allegedly sympatric around Thumbi West Island and Mumbo Island, but we were unable to distinguish more than a single form at either location. Both groups prefer habitat between small- and medium-sized rocks at depths of no more than 25 meters; and they aggressively defend their territories against intruders. They mostly feed on loose aufwuchs but also on benthic invertebrates and plankton.

Other material examined

Metriaclima zebra, *M. flavifemina*, *M. phaeos*, *M. pambazuko*, *M. lundoense*, *M. midomo*, *M. tarakiki*, *M. nigrodorsalis*. Data from Stauffer Jr, J.R., Black, K. & Konings, A.F. (2013).

Metriaclima chrysomallos, *M. mbenjii*, *M. cyneusmarginatus*, *M. benetos*, *M. pyrsonotos*. Data from Stauffer Jr, J.R., Bowers, N.J., Kellogg, K.A. & Mckaye K.R. (1997).

Tropheops gracilior, *T. microstoma*, *T. novemfasciatus*, *T. tropheops*, *T. macrophthalmus*, *T. romandi*. Data from Goldstein, H.M. (2009).

Cynotilapia afra, *C. zebroides*, *C. aurifrons*. Data from Tawil P. (2011).

Pseudotropheus williamsi. Data from Stauffer Jr., J.R. & Kellogg K.A. (2002).

Chindongo minutus. Data from Fryer, G. (1956).

Chindongo heteropictus. Paratypes SMF 15179, female, 76.0 mm SL & SMF 15180, male, 88.0 mm SL; both Thumbi West Island (never found at Thumbi West Island; with high probability types were collected at Chizumulu Island), Lake Malaŵi, Malaŵi; collector P. Davies *et al.*, Jul 1975.

Chindongo ater, *Chindongo cyaneus*, *Chindongo flavus*. Data from Stauffer Jr., J.R. (1988).

Chindongo saulosi. Data from Konings, A.F. (1990).

Chindongo demasoni. Data from Konings, A.F. (1994).

Chindongo elongatus. Lectotype BMNH1956.9.4.1, male, 65.9 mm SL, Mbamba Bay, Lake Nyasa, Tanzania. coll. G. Fryer.

Chindongo longior. Data from Seegers, L. (1996).

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