The Pennsylvania State University

The Graduate School

DESCRIPTIONS OF TWO NEW *METRIACLIMA* SPECIES AND ONE NEW *PSEUDOTROPHEUS* SPECIES FROM LAKE MALAWÎ, AFRICA

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Abstract

Some 80% of the world's cichlids (Actinopterygii: Cichliformes: Cichlidae) are found in Africa, and the majority of those are found in the African Great Lakes. Lake Malaŵi, lying over 31,000 km^2 in the East African countries of Malaŵi, Tanzania, and Mozambique, hosts over an estimated 850 haplochromine species of cichlids alone, making it the most speciose lake in the world. Among the 850 or so species of cichlids found in Lake Malaŵi is a highly diverse group of small, rock-dwelling fishes known locally as mbuna. *Metriaclima and Pseudotropheus* are two of the most speciose mbuna genera found in Lake Malaŵi. *Metriaclima* is comprised of at least 75 species, *Pseudotropheus* originally served as a catch-all genus for newly discovered mbuna species. Still, some species remain rooted in *Pseudotropheus*, although most regard it as polyphyletic. In this study, a new species of *Pseudotropheus*, *P. likoma*, is described. *Metriaclima* is comprised of many geographically narrow populations with high-fidelity to specific habitat landmarks, such as single reefs or islands. Only minute differences in male breeding coloration distinguish the many of the species of *Metriaclima*. Three primary morphological characteristics are used to diagnose *Metriaclima*: 1) bicuspid teeth in the anterior portion of the outer rows of the upper and lower jaws; 2) a moderately-sloped ethmo-vomerine block with a swollen rostral tip; and 3) the lower jaw forming a 45° angle line from the tip of the snout to the hypural plate. Notably, the swollen rostral tip of the ethmo-vomerine block distinguishes the genus from *Pseudotropheus*. Descriptions of two new *Metriaclima* spp., *M. ngara* and *M. gallireya*, are provided.

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Introduction

Lake Malaŵi, one of the three great lakes of Africa (Lake Malaŵi, Lake Victoria, and Lake Tanganyika), lies over 31,000 km^2 in the East African countries of Malaŵi, Tanzania, and Mozambique (Li *et al*. 2016). Some 80% of the world's cichlids are found in Africa, and the majority of those are found in the African Great Lakes (Stauffer *et al.* 2007). Lake Malaŵi hosts over an estimated 850 haplochromine species of cichlids alone, making it the most speciose lake in the world (Konings 2016). Still, only about half (450) of Malaŵian cichlid species have been described, and prior descriptions need revised and new species described (Stauffer *et al.* 2013). Ultimately, this paper diagnoses three additional new species. Lake Malaŵi began forming about 8.6 million years ago, and the present cichlid radiation event is estimated to have begun between 570,000 and 1 million years ago (Black 2010).

Among the 850 or so species of cichlids found in Lake Malaŵi is a highly diverse group of small, rock-dwelling fishes (Konings 2016) locally known as mbuna, which is characterized by 1) many scales on the nape and chest region; 2) a sharp contrast from large flank scales to small chest scales; 3) reduction of the left ovary; and 4) possession of true ocelli on the anal fins of males (Konings and Stauffer 2006). Typically, mbuna are found along the rocky shores and outcroppings of the lake, though they do occur over sand substrate or mixed rock and sand (Stauffer 1991). Fidelity to rocky shores and outcroppings, as well as lack of pelagic dispersal, has resulted in restricted gene flow among localized populations within Lake Malaŵi (Black 2010). As a result, allopatric populations exist at many localities (Stauffer et al. 2013).

Visually, allopatric populations of Malaŵian cichlids differ slightly, and difficulty discerning among species is compounded by convergence of morphological characters and phenotypic flexibility (Stauffer *et al.* 2016). Still, coloration, morphology, and behavioral characteristics are necessary diagnostic markers for distinguishing species (Stauffer *et al.* 2016). In the field, coloration and behavior (e.g., breeding and feeding behaviors) are accepted tools for delimiting species. Specifically, cichlid males express bright, dramatic coloration. Coloration is thought to be an important mate-selection factor and a potential reproductive barrier among populations of different localities (Stauffer *et al.* 2013). Male coloration of populations of mbuna vary (sometimes slightly) by location, but very little variation is exhibited within a population (Black 2010). Geographically close populations are sometimes indistinguishable based on coloration or behavior alone. As a result, morphology must also be considered. Prior to the 1980s, morphology was the primary basis for diagnosing species (Li *et al.* 2016). Often, allopatric species in Lake Malaŵi are distinguished by feeding techniques, and species vary significantly in mouth structure, dentition, and/or number of gill rakers (Stauffer *et al.* 2007). Morphology alone, just like coloration and behavior, is often not enough to recognize species due to recent and rapid speciation that has led to incredible diversity and similarity in morphological and genetic traits. (Li *et al*. 2016). For instance, allopatric species adapted to particular habitats have shown morphological differences in as little as 20 years (Li *et al*. 2016).

Lake Malaŵi is home to a dozen genera of mbuna, with two of the larger genera being *Metriaclima* and *Pseudotropheus*. *Metriaclima* is likely the most speciose genera of mbuna, and is comprised of at least 75 species (Stauffer et al. 2013). Members of both genera have been re-evaluated numerous times. *Pseudotropheus* originally served as a catch-all genus for newly discovered mbuna species (Konings & Stauffer 2006). Species placed in *Pseudotropheus* are sometimes arranged into complexes, and some complexes have been elevated to distinct genera (Konings & Stauffer 2006). Still, some species remain rooted in *Pseudotropheus*. As a catch-all genus, few characteristics diagnose species outside of those that diagnose all mbuna.

Metriaclima was removed from *Pseudotropheus* and was comprised of the *Pseudotropheus zebra* complex (Stauffer et al. 1997; Konings & Stauffer 2006). Included in *Metriaclima* are many geographically narrow populations with high-fidelity to specific habitat landmarks, such as single reefs or islands (Stauffer *et al.* 2013). It is likely that narrow habitat selection has led to the high richness of species in *Metriaclima* (Stauffer *et al.* 2013). Some populations within the genus are so similar that they're categorized as groups (Black 2010). Groups are generally formed by one or a few species, and groups may actually be incipient species – that is: differentiating populations that may eventually become unique enough to constitute separate species (Black 2010).

Often, only minute differences in male breeding coloration distinguish the many *Metriaclima* species (Stauffer *et al.* 2013). Color as a species delimiter has been adopted by cichlid taxonomists, specifically for species within Lake Malaŵi (Stauffer *et al.* 2013). In many cases, particularly for *Metriaclima*, male coloration serves as the primary diagnostic feature for many species (Stauffer *et al.* 2013). Coloration has been shown to be an important factor in mate selection and can even serve as a reproductive barrier (Stauffer *et al.* 2013).

Originally, Stauffer et al. (1997) provided three morphological characteristics used to diagnose *Metriaclima* species: 1) bicuspid teeth in the anterior portion of the outer rows of the upper and lower jaws; 2) a moderately-sloped ethmo-vomerine block with a swollen rostral tip; and 3) the lower jaw forming a 45° angle line from the tip of the snout to the hypural plate (Stauffer *et al.* 1997). Stauffer and Konings (2006) expanded diagnostic characteristics for the genus to include: 4) a lower jaw that 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 form a V-shaped line with the anterior most teeth furthest apart in both the upper and lower jaws; and 7) the bicuspid teeth in the outermost row along the side of the jaws do not follow the natural contour of the jaw bone, but rather lateral teeth are rotated so that the plane of their two-pronged tips runs parallel with those in the anterior part of the jaw (Konings & Stauffer 2006).

The swollen rostral tip of the ethmo-vomerine block distinguishes *Metriaclima* from *Pseudotropheus* (Black 2010). The feeding behavior of *Metriaclima* distinguishes the genus from *Pseudotropheus* even further. *Metriaclima* feeds perpendicularly on algal substrate by abducting its jaws to a nearly 180° angle – a feat of which *Pseudotropheus* is incapable (Konings & Stauffer 2006).

The objective of this study was to analyze morphometric and meristic characteristics of *Metriaclima* and *Pseuodtropheus* species to provide new species descriptions. Ideally, descriptions of new species of Cichlidae from Lake Malaŵi, Africa, aid in the understanding of biodiversity and rapid speciation both within the lake and within other ecosystems across the globe. Additionally, the diagnosis of new species within Lake Malaŵi aids in fisheries management of the lake. About 70% of all animal protein consumed in Malaŵi is fish (Government of Malaŵi 2019). Fisheries managers can only manage what they know is present, and the diagnosis of new species should aid in the creation of effective fisheries management plans, including season limits based on breeding timing, take limits based on fecundity, and size limits, in an effort to prevent overharvest of the resource. This paper provides new species descriptions on the basis of morphological examination of the type material and on behavioral differences obtained from field observations of the species described herein.

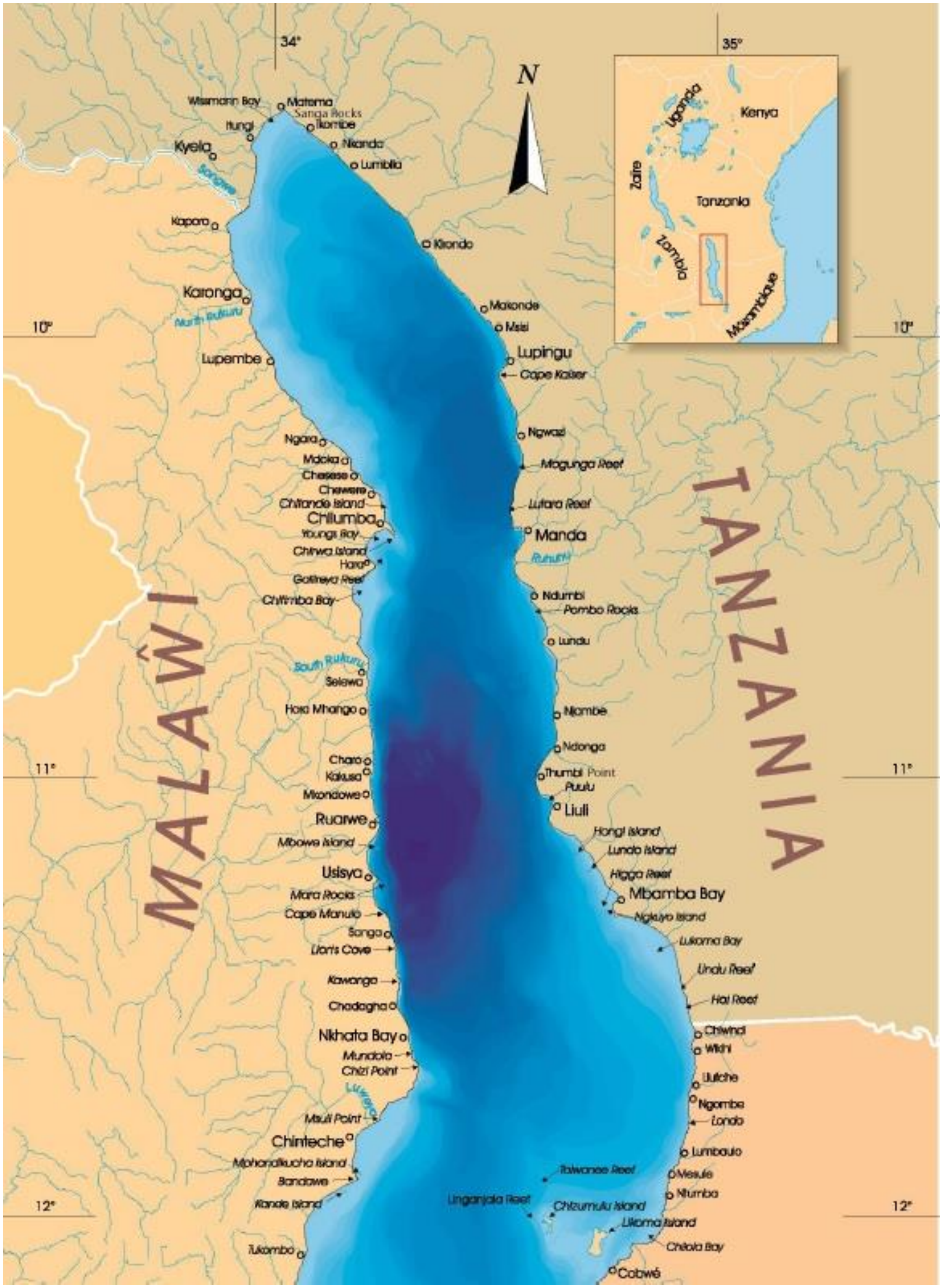

FIGURE 1. Map of the northern half of Lake Malaŵi with notable localities marked, including Likoma Island, Ngara and Gallireya Reef (*Malaŵi Cichlids in their Natural Habitat*, 5th edition).

Methods and Materials

Adult fishes were collected in Lake Malaŵi by SCUBA divers who chased individuals into monofilament block nets (7m x 1m; 1.5cm mesh). Permits required for collection of fishes were acquired from the Malaŵi Department of Fisheries and the Malaŵi Department of Recreation. Collection and processing of fishes followed methods approved by the Animal Use and Care Committee at the Pennsylvania State University (IACUC #24269). Fishes were anesthetized with clove oil, euthanized in 1% formalin, preserved in 10% formalin, and then placed in 70% ethanol for permanent storage in the Pennsylvania State University Fish Museum (PSUFM).

Color and pigmentation patterns for all individuals were recorded in the field at the time of collection by Jay R. Stauffer and Adrianus Konings. These notes, including photographs, are stored at the PSUFM under the catalog numbers provided under species descriptions. Variable color patterns in examined individuals were recorded by placing a slash between the two colors between which the specific patterns varied, i.e. blue/white was used to designate that the color ranges from blue to white. Behavioral notes were also taken at the site of collection.

From our collections, nearly 400 specimens were examined. Twenty-six measurements and 14 counts were taken for each individual following Barel *et al.* (1977) and Konings & Stauffer (2006). Two measurements – standard length and head length – were used for analysis only in the formation of ratios with other measurements, but these two measurements are not considered descriptive or diagnostic. All counts and measurements were made on the left side of the fish except for gill-raker counts, which were taken on the right side. Morphometric data were taken with digital calipers and measured to the nearest 0.01 mm. All rays of the pectoral fin were counted, including the small splinter on the upper edge of the fin. Lateral-line scales were counted from anterior to the hypural plate – counts do not include scales in the overlapping portion of the lower lateral line. Pored lateral-line scales posterior to the hypural plate were counted separately. See Table 1 for a list of measurements and counts taken, as well as abbreviations used. Figure 2 shows most of the 26 measurements taken for each specimen. Full-body CT scans with surface rendering were conducted on each of the holotypes. The angles of the ethmo-vomerine block and its shape were measured and observed using images reconstructed with Avizo 8 (VSG, Burlington, MA) and Dragonfly software, Version 3.6 for Windows, Object Research Systems (ORS) Inc, Montreal, Canada, 2018; software available at http://www.theobjects.com/dragonfly.

Analysis of morphometrics and meristics was conducted using sheared principal component analysis (SPCA) and principal component analysis (PCA), respectively, as described by Humphries *et al.* 1981 and Stauffer *et al.* 1997. Principal component analysis was used to analyze meristic data with the correlation matrix factored. Body-shape differences were analyzed using SPCA with the covariance matrix factored. To illustrate differences in counts and measurements among species, the sheared second principal components of the morphometric data were plotted against the first principal components of the meristic data. The first sheared principal component of the morphometric data accounts for variation of individual size and presents that variation as a percentage. Similarly, the sheared second principal components explain the remaining variation in shape, also expressed as a percentage.

Minimum polygon clusters for each species were drawn. The minimum polygon clusters enclose all points of individuals belonging to the same population or group. An ANOVA ($P<0.05$) was used to determine if differences in minimum polygon clusters were significant along either axis.

TABLE 1. Morphometric and meristic measurements and abbreviations used in morphological analysis.

Morphometric Measurement	**Abbreviation**
Standard length	SL
Head length	HL
Snout length	SNL
Postorbital head length	POHL
Horizontal eye diameter	HED
Vertical eye diameter	VED
Premaxillary depth	PRE
Cheek depth	CD
Lower jaw length	LJL
Head depth	HD
Inter-orbital width	IOWI
Premaxillary pedicel	PMPE
Body depth	BD
Snout to dorsal fin origin	SNDOR
Snout to pelvic fin origin	SNPEL
Dorsal fin base length	DFBL
Anterior dorsal to anterior anal	ADAA
Anterior dorsal to posterior anal	ADPA
Posterior dorsal to anterior anal	PDAA
Posterior dorsal to posterior anal	PDPA
Posterior dorsal to ventral caudal	PDVC
Posterior anal to dorsal caudal	PADC
Anterior dorsal to pelvic-fin origin	ADP2
Posterior dorsal to pelvic-fin origin	PDP2
Caudal peduncle length	CPL
Least caudal peduncle depth	LCPD
Meristic Measurement	**Abbreviation**
Dorsal-fin spines	DSPINES
Dorsal-fin rays	DRAYS
Anal-fin spines	ASPINES
Anal-fin rays	ARAYS
Pectoral-fin rays	P1RAYS
Pelvic-fin rays	P2RAYS
Lateral line scales	LLS
Pored scales caudal	PSPLL
Cheek scale rows	CS
Gill rakers 1st ceratobranchial	GRLOW
Gill rakers 1st epibranchial	GRUP
Teeth outer left lower jaw	TORLLJ
Tooth rows upper jaw	TRU
Tooth rows lower jaw	TRU

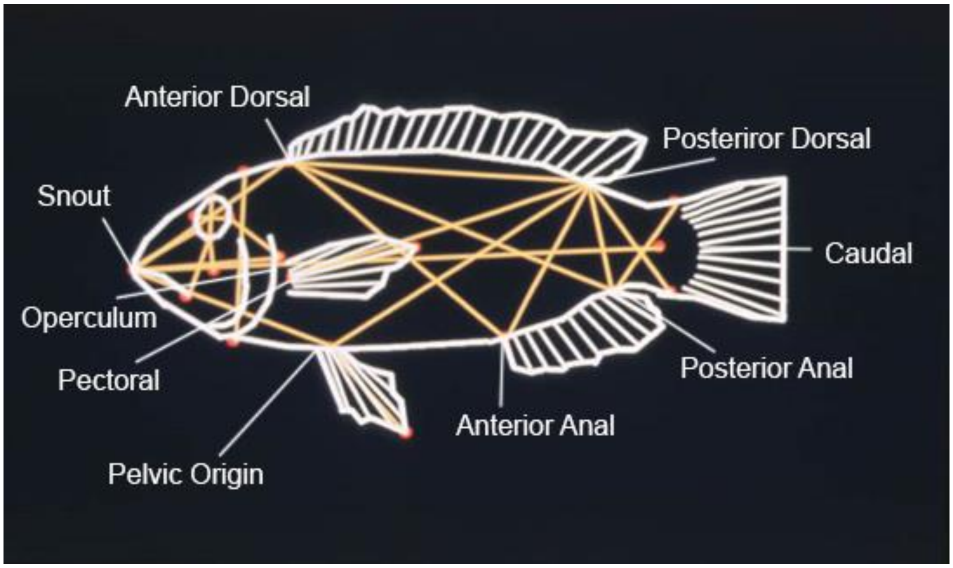

FIGURE 2. Diagram of many of the morphometric measurements taken for each specimen included in this study.

Results/Taxonomy

Of the nearly 400 specimens examined as part of this study, 320 were found to belong to described *Pseudotropheus* and *Metriaclima*. The remaining 80 specimens were found to be members of previously undescribed species, including forty-six specimens from four collections belonging to *P. likoma*, 14 specimens from one collection belonging to *M. ngara*, and 20 specimens from one collection belonging to *M. gallireya*. The diagnosis of these 80 specimens was the result of coloration, behavioral and statistical analysis, including PCA/SPCA and ANOVA, of morphometrics and meristics.

***Pseudotropheus likoma*, new species**
Fig. 3A-B

Holotype. Accession #681, Collection # JRS-02-19-10, adult male, 80.8 mm SL, S 12° 04.677', E 34° 44.883', Mbuzi Island, Lake Malaŵi, Malaŵi, Africa, 19 Feb. 2002, A. F. Konings, J. R. Stauffer Jr. and Stuart M. Grant's crew.

Paratypes. Accession #681, 20, (51.8 mm–80.8 mm SL), same data as holotype; accession #1128, 14, 64.44 mm–76.14 mm SL, Likoma Island, Lake Malaŵi, Malaŵi, Africa, 2 July 1991,

J. R. Stauffer Jr.; accession #743, 6, 63.07 mm–74.23 mm SL, Likoma Island, Lake Malaŵi, Malaŵi, Africa, 2 July 1991, J. R. Stauffer Jr.; accession #2649, 6, 49.84 mm–60.77 mm SL, Jaro Beach, Likoma Island, Lake Malaŵi, Malaŵi, Africa, 17 Feb. 1993, Stuart M. Grant's crew.

Diagnosis. The steep angle of ethmovomerine block (72.09°) with the parasphenoid (Fig. 3) places this species in *Pseudotrpheus*. *Pseudotropheus likoma* is distinguished from other mbuna that reinvaded the sand (e.g., *M. lanisticola*) because only the adults frequent empty snail shells. *Pseudotropheus likoma* is distinguished from *P. livingstoni* by the presence of six distinct vertical bars below the dorsal fin, whereas *P. livingstoni* has four. *Pseudotropheus likoma* is further distinguished from *P. livingstoni* by green highlights on the opercle and anal fin with one orange ocelli, whereas *P. livingstoni* has blue highlights on the opercle and anal fin with 0-6 yellow ocelli.

Description. Morphometric and meristic data in Table 3. Medium-sized mbuna, ovoid body (mean BD 35.37% SL) with greatest depth between third to fifth dorsal spine. Dorsal body profile with gradual curve downward posteriorly, more pronounced towards posterior of dorsal fin and beginning of caudal peduncle; ventral body profile slightly convex to almost straight between pelvic fins and base of anal fin with upward curve to caudal peduncle mirroring dorsally. Dorsal head profile straight between snout tip and interorbital, rounded with smooth curve between interorbital and dorsal-fin origin; horizontal eye diameter (mean 31.87% HL) greater than premaxillary depth (mean 18.54% HL); eye positioned in anterior half of head with posterior orbit margin on or near vertical median of head; short, straight snout with isognathous jaws; teeth in upper jaw in 3–6 rows and 4–6 rows in lower jaw; teeth in outer row bicuspid (some lateral teeth unicuspid), in inner rows tricuspid.

Dorsal fin with XVII or XIX (mode XVIII) spines and 7–9 (mode 8) soft rays. Anal fin with III spines and 7–9 (mode 8) soft rays. First 6 or 7 dorsal-fin spines gradually increasing in length posteriorly with sixth spine about twice as long as first spine; last 12 increasing only slightly in length posteriorly with last spine longest; soft dorsal fin with subacuminate tip, third or fourth ray longest. Anal-fin spines progressively increasing in length posteriorly; fourth or fifth ray longest, length equal to or slightly longer than dorsal fin. Caudal fin subtruncate to emarginate. Pelvic fin reaching to second or third anal-fin spine. Pectoral fin rounded, paddle-shaped, short, reaching vertical through base of 10th or 11th dorsal-fin spine. Flank scales ctenoid with abrupt change to small scales on breast and belly; 28–34 lateral line scales, cheek with 4–5 rows of small scales. Dorsal fin and anal fin scaleless; tiny scales over proximal ¼ of caudal fin.

Head of males brown with light blue interorbital bar; cheek white and with blue outline; white opercle with green highlights and dark brown spot; gular white. Laterally brown dorsally with six brown bars and a brown stripe from the origin of dorsal fin to dorsal point of dorsal fin; brown lateral band over the lateral line from opercle to caudal fin. Laterally lighter ventrally with blue highlights; breast brown and belly white. Dorsal fin light tan with orange lappets. Caudal fin membranes clear. Proximal ¼ of anal fin white and distal ¾ black with white lappets; one orange ocelli. Pelvic fins with white leading edge; first spine white with black distal ¼. Pectoral fins clear.

Head of females brown with no interorbital bar; opercle with green highlights and black spot; gular white. Laterally dorsally same as males. Laterally very light tan ventrally; breast and belly white.

Distribution. *Pseudotropheus likoma* is found near Likoma Island and its surrounding cluster islands (S 12°3'30.24", E 34°44'07.45"), Malaŵi.

Etymology. The specific epithet *likoma* is derived from Likoma Island, the island and surrounding cluster islands near which the type specimens were collected.

Remarks. The morphometrics and meristics of *M. likoma* are both significantly different from *P. livingstoni* (Table 2). While PCA is not used to diagnose and distinguish species, PCA does further support the diagnosis that *P. likoma* is a new species separate from *P. livingstoni* (Fig. 4). Individual size accounted for 92.22% of the variance in the two species, and shape accounted for 1.59% of the variance. The three highest individual morphometric loadings on the sheared second principal components were premaxillary pedicel (-0.47), lower jaw length (-0.46), and caudal peduncle length (-0.43).

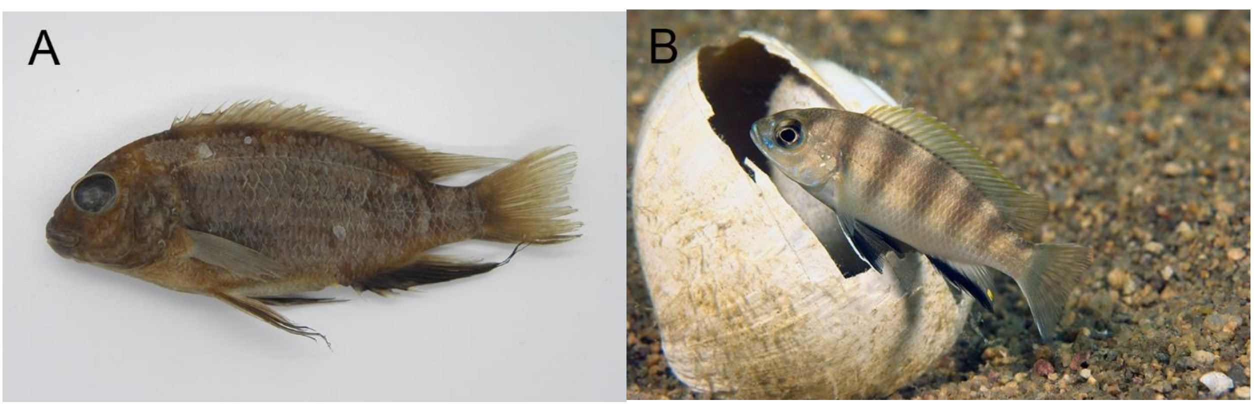

FIGURE 3. *Pseudotropheus likoma*. A. Holotype, Accession #681, adult male, 80.8 mm SL, Mbuzi Island, Lake Malaŵi; B. Male in breeding coloration at type locality.

TABLE 2. ANOVA output for meristic and morphometric data of *P. likoma* and *P. livingstoni*.

PC1 Meristic Data					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	101.7687	101.7687	328.49	<.0001
Error	146	45.23136	0.309804		
Corrected Total	147	147.0001			
SHRD_PC2 Morphometric Data					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.365264	0.365264	194.6	<.0001
Error	146	0.274048	0.001877		
Corrected Total	147	0.639312			

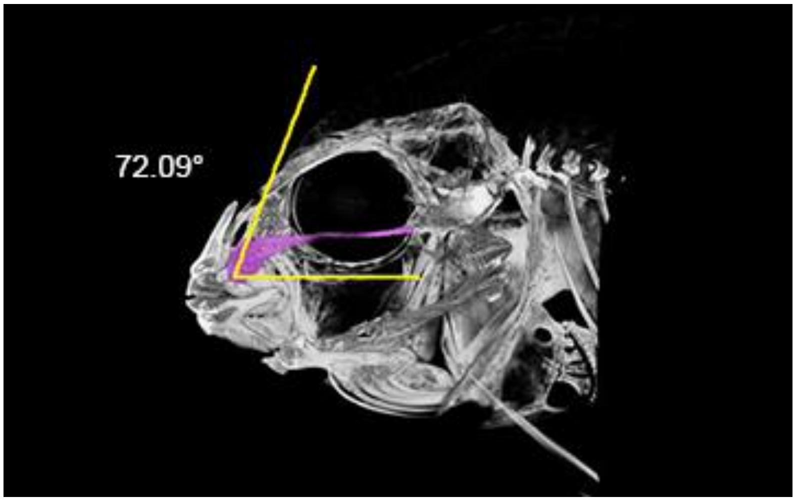

FIGURE 4. Cranium of *Pseudotropheus likoma*, adult male, 80.8 mm SL, Mbuzi Island, Lake Malaŵi; angle of ethmovomerine block is 72.09° with parasphenoid.

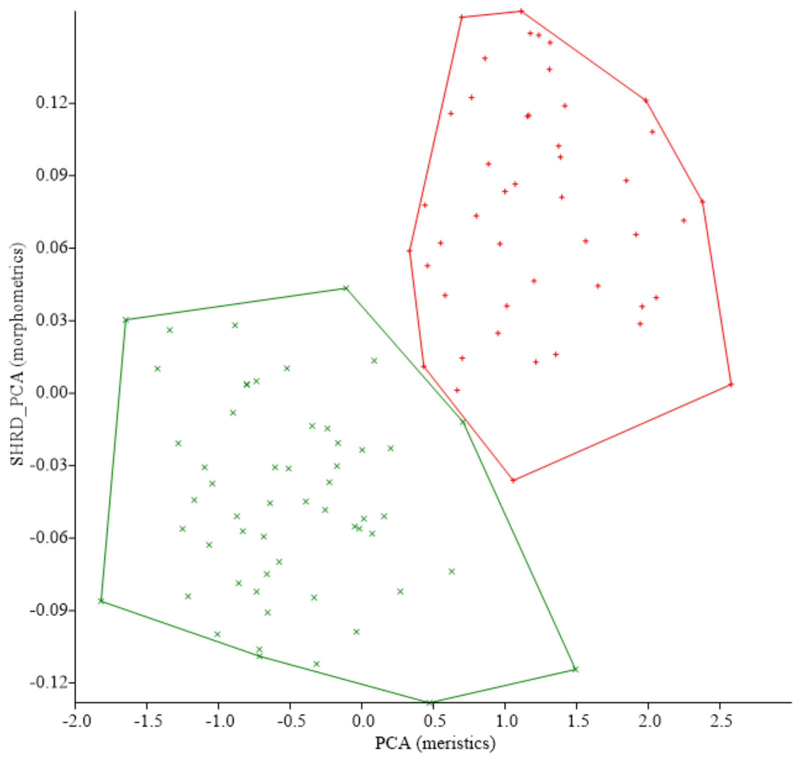

FIGURE 5. Sheared second principal components (morphometric data) plotted against the first principal components (meristic data) of specimens of *Pseudotropheus likoma* from Likoma Island and surrounding cluster islands (+) and specimens of *P. livingstoni* (x). The data points are bounded by minimum polygon convex hulls.

TABLE 3. Morphological and meristic data for *Pseudotropheus likoma* from Likoma Island, Lake Malaŵi, Accession #681, Collection # JRS-02-19-10, holotype; Accession #s 1128, 743 and 2649, n=26. Ranges include holotype.

Variable	Holotype	Mean	Std Dev	Range
Standard length (mm)	80.8	63.79	8.22	46.2 – 80.8
Head length (mm)	23.89	19.69	2.22	14 – 23.9
Percent head length (%)				
Snout length	30.01	28.93	1.89	24 – 33
Postorbital head length	44.83	44.11	2.19	40 – 50
Horizontal eye diameter	31.14	31.87	2.17	23 – 36
Vertical eye diameter	27.84	29.78	1.55	27 – 33
Premaxillary depth	20.80	18.54	1.91	15 – 22
Cheek depth	26.37	24.07	1.77	20 – 29
Lower jaw length	22.06	23.15	2.64	18 – 28
Head depth	102.85	95.46	4.32	87 – 103
Inter-orbital width	30.18	28.39	2.05	25 – 33
Premaxillary pedicel depth	17.12	19.46	2.93	14 – 31
Percent standard length (%)				
Body depth	37.66	35.37	1.76	31 – 39
Snout to dorsal fin origin	36.05	36.04	1.09	34 – 38
Snout to pelvic fin origin	35.92	36.80	1.38	34 – 39
Dorsal fin base length	61.66	59.11	1.43	57 – 62
Anterior dorsal to anterior anal	54.59	52.0	1.52	49 – 56
Anterior dorsal to posterior anal	64.91	63.3	1.40	60 – 66
Posterior dorsal to anterior anal	30.73	30.6	1.09	28 – 32
Posterior dorsal to posterior anal	16.76	16.65	0.85	15 – 18
Posterior dorsal to ventral caudal	17.72	18.72	0.69	17 – 20
Posterior anal to dorsal caudal	20.54	21.15	0.89	19 – 23
Anterior dorsal to pelvic-fin origin	37.59	35.37	1.76	31 – 39
Posterior dorsal to pelvic-fin origin	60.20	57.17	1.62	54 – 61
Caudal peduncle length	13.18	13.41	1.29	11 – 16
Least caudal peduncle depth	13.09	13.65	0.53	13 – 15
Meristics		Mode	Frequency (%)	Range
Dorsal-fin spines	19	18	73.91	17 - 19
Dorsal-fin rays	8	8	67.39	7 – 9
Anal-fin spines	3	3	100	3 – 3
Anal-fin rays	8	8	86.96	7 – 9
Pectoral-fin rays	14	14	56.52	12 – 14
Pelvic-fin rays	6	6	84.78	6 – 7
Lateral line scales	34	31	30.43	28 – 34
Pored scales caudal	2	1	36.96	0 – 3
Cheek scale rows	5	4	78.26	4 – 5
Gill rakers 1st ceratobranchial	11	10	47.83	8 – 11
Gill rakers 1st epibranchial	4	4	84.78	3 – 5
Teeth outer left lower jaw	14	16	21.74	13 - 21
Tooth rows upper jaw	6	5	52.17	3 - 6
Tooth rows lower jaw	5	5	45.65	4 - 6

***Metriaclima ngara*, new species**

Fig. 6A-B

Holotype. Accession #1126, Collection # JRS-00-29-9, adult male, 59.13 mm SL, (no coordinates), Ngara, Lake Malaŵi, Malaŵi, Africa, Jan. 2000, S. Grant's crew.

Paratypes. Accession #1126, 14, (49.61 mm–62.4 mm SL), same data as holotype.

Diagnosis. The moderately sloped vomer (46.42º in holotype) with a swollen rostral tip (Fig. 6) and bicuspid teeth in the anterior portion of the outer row of both upper and lower jaws place this species in *Metriaclima*. It differs from all other *Metriaclima* sp. by living over the sand except for *M. lanisticola*, *Metriaclima pursus.* and *Metriaclima gallireya* n. sp.. It differs from other sand-dwelling *Metriaclima* sp. except *M. gallireya* n. sp. by the presence of a black submarginal bars on the dorsal and anal fins. The interorbital eye width of *M. ngara* is larger than that of *M. gallireya* (31–37% vs. 24-30% HL). Generally, premaxillary depth is greater than that of *M. gallireya* (18–21% vs. 14-19% HL) and distance from the posterior margin of the dorsal fin to the anterior margin of the anal fin is also greater (34–38% vs. 30-35% SL). *Metriaclima ngara* is further distinguished from *M. gallireya* by two light gray interorbital bars, yellow gular, laterally gray with blue scales outlined in pale orange below lateral line, four lateral bars and caudal fin with orange rays and blue membranes, whereas *M. gallireya* has dark brown interorbital bar, brown gular, laterally brown ground with center of scales brown outlined in blue, five to six brown lateral bars and caudal fin with brown rays and blue membranes.

Description. Morphometric and meristic data in Table 5. Medium-sized mbuna, ovoid body (mean BD 38.71% SL) with greatest body depth at about 3^{rd}-4^{th} dorsal spine. Dorsal body profile with gradual curve downward posteriorly with highest point at sixth or seventh dorsal spine, more pronounced towards posterior of dorsal fin and beginning of caudal peduncle; ventral body profile nearly straight between pelvic fins and base of anal fin with slight upward curve to caudal fin. Dorsal head profile round with continuous curve between interorbital and dorsal-fin origin; horizontal eye diameter (mean 30.07% HL) about one and half times greater than premaxillary depth (mean 19.29% HL); posterior orbit margin of eye posterior of vertical median of head; short snout with isognathous jaws; teeth in upper and lower jaws in 2–3 rows (mode 3); teeth in outer row bicuspid, inner rows unicuspid or tricuspid.

Dorsal fin with XVI or XVII (mode XVII) spines and 7–8 (mode 8) soft rays. Anal fin with III spines and 8 soft rays. First 5 or 6 dorsal-fin spines gradually increasing in length posteriorly with sixth spine about twice as long as first spine; last 11 spines increasing only slightly in length posteriorly with last spine longest; soft dorsal fin with rounded to subacuminate tip, second or third ray longest, to approximately ¼ length of caudal fin. Anal-fin spines progressively increasing in length posteriorly; fifth or sixth ray longest, to base of caudal fin, length equal to or slightly longer than dorsal fin. Caudal fin subtruncate to emarginate. Pelvic fin reaching to first anal-fin spine. Pectoral fin rounded, paddle-shaped, short, reaching vertical through base of 8th or 9th dorsal-fin spine. Flank scales ctenoid with abrupt change to small scales on breast and belly; 23–32 (mode 31) lateral line scales, cheek with 4 rows of small scales. Dorsal and anal fins scaleless; tiny scales over proximal ¼ of caudal fin.

Head of males gray with two light gray interorbital bars; black opercle spot; gular yellow. Laterally gray with blue scales outlined in pale orange below lateral line; four bars fade out below lateral line; ventrally white. Dorsal fin clear with orange markings; black submarginal bar. Caudal fin rays orange with blue membranes. Anal fin with black bar encompassing all of spines and angling through rays to encompass 2/3 of distal portion; proximal portion of rays light blue;

one yellow ocelli. Pelvic fins with spines and first two rays black; remaining clear. Pectoral fins clear.

Head of females dark gray with two faint green interorbital bars; ventral ½ pale yellow; black opercle; pale yellow gular. Laterally yellow below lateral line fading to white with light gray bars that disappear below lateral line. Fins same as males; not as intense. Females with ocelli.

Distribution. *Metriaclima ngara* is found on a submerged reef near Ngara (S 10° 14'00.23", E 34° 6'23.73"), Malaŵi.

Etymology. The specific epithet *ngara* is derived from Ngara, the village near which the type specimens were collected.

Remarks. The morphometrics and meristics of *M. ngara* are both significantly different from *M. gallireya* (Table 4). While PCA is not used to diagnose and distinguish species, PCA does further support the diagnosis that *M. ngara* is a new species separate from *M. gallireya* (Fig. 9). Individual size accounted for 86.89% of the variance in the two species, and shape accounted for 6.33% of the variance. The three highest individual morphometric loadings on the sheared second principal components were premaxillary pedicel depth (-0.92), distance from the anterior margin of the dorsal fin to the insertion of the pelvic fin (0.11), and distance from the posterior margin of the dorsal fin to posterior margin of the anal fin (0.11).

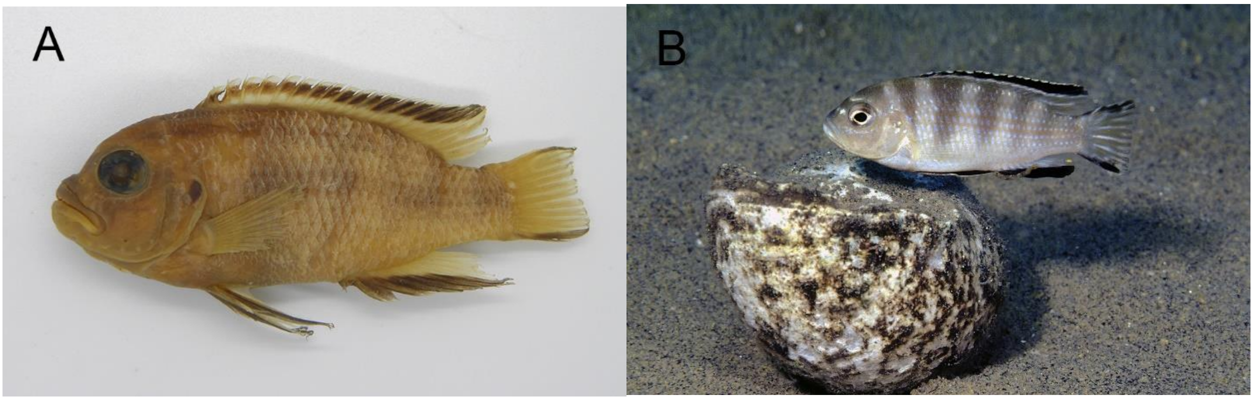

FIGURE 6. *Metriaclima ngara*. A. Holotype, Accession #1126, Collection # JRS-00-29-9, adult male, 59.13 mm SL, Ngara, Lake Malaŵi; B. Male in breeding coloration at type locality.

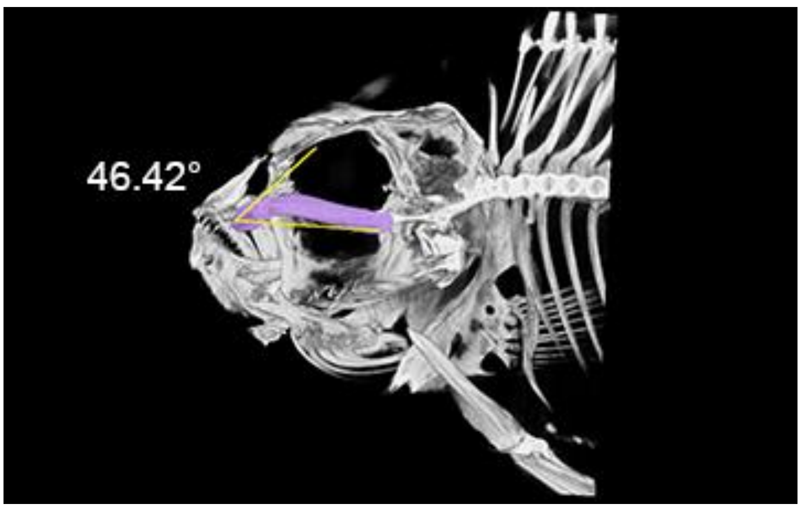

FIGURE 7. Cranium of *Metriaclima ngara*, adult male, 59.13 mm SL, Ngara, Lake Malaŵi; angle of ethmovomerine block is 46.42° with parasphenoid.

TABLE 4. ANOVA output for meristic and morphometric data of *M. ngara* and *M. gallireya*.

PC1 Meristic Data					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	24.83121	24.83121	97.27	<.0001
Error	32	8.168823	0.255276		
Corrected Total	33	33.00003			
SHRD_PC2 Morphometric Data					
Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	0.210581	0.210581	26.68	<.0001
Error	32	0.252578	0.007893		
Corrected Total	33	0.463159			

TABLE 5. Morphological and meristic data for *Metriaclima ngara* from Ngara, Lake Malaŵi, Accession #1126, Collection # JRS-00-29-9 holotype; Accession #1126, n=14. Ranges include holotype.

Variable	Holotype	Mean	Std Dev	Range
Standard length (mm)	59.13	56.59	3.68	49.6 - 62.4
Head length (mm)	19.08	18.71	1.24	17 - 21.4
Percent head length (%)				
Snout length	34.59	34.86	1.23	31 - 36
Postorbital head length	39.52	40.79	1.67	37 - 43
Horizontal eye diameter	30.61	30.07	1.59	27 - 32
Vertical eye diameter	28.93	28	1.47	24 - 30
Premaxillary depth	18.66	19.29	1.14	18 - 21
Cheek depth	35.27	34.57	2.50	30 - 39
Lower jaw length	24.95	26	2.83	21 - 30
Head depth	109.91	104.14	4.55	98 - 113
Inter-orbital width	34.38	33.36	2.06	31 - 37
Premaxillary pedicel depth	23.69	24.07	2.23	20 - 28
Percent standard length (%)				
Body depth	39.08	38.71	0.83	37 - 40
Snout to dorsal fin origin	34.91	35.71	1.33	34 - 38
Snout to pelvic fin origin	38.36	37.5	1.09	36 - 40
Dorsal fin base length	59.82	58.29	1.38	56 - 60
Anterior dorsal to anterior anal	50.06	50.07	0.83	49 - 51
Anterior dorsal to posterior anal	63.45	62.93	1.33	61 - 65
Posterior dorsal to anterior anal	36.61	36	1.24	34 - 38
Posterior dorsal to posterior anal	19.33	19.43	0.85	18 - 20
Posterior dorsal to ventral caudal	21.09	20.57	0.85	19 - 22
Posterior anal to dorsal caudal	25.06	23.21	1.05	21 - 25
Anterior dorsal to pelvic-fin origin	39.37	38.5	0.85	37 - 40
Posterior dorsal to pelvic-fin origin	65.18	61.5	1.40	59 - 65
Caudal peduncle length	14.90	14	0.96	12 - 15
Least caudal peduncle depth	16.25	16.29	0.61	15 - 17
Meristics		Mode	Frequency (%)	Range
Dorsal-fin spines	17	17	71.43	16 - 17
Dorsal-fin rays	8	8	71.43	7 - 8
Anal-fin spines	3	3	100	3 - 3
Anal-fin rays	8	8	100	8 - 8
Pectoral-fin rays	12	14	85.71	12 - 15
Pelvic-fin rays	7	7	85.71	6 - 7
Lateral line scales	31	31	57.14	23 - 32
Pored scales caudal	2	2	50	0 - 2
Cheek scale rows	4	4	100	4 - 4
Gill rakers 1st ceratobranchial	10	11	57.14	9 - 12
Gill rakers 1st epibranchial	5	5	50	4 - 5
Teeth outer left lower jaw	8	7	35.71	4 - 10
Tooth rows upper jaw	3	3	92.86	2 - 3
Tooth rows lower jaw	3	3	64.29	2 - 3

***Metriaclima gallireya*, new species**

Fig. 8A-B

Holotype. Accession #2207, Collection # JRS-08-13-1, adult male, 54.42 mm SL, S 10° 30.055', E 34° 14.104', Gallireya Reef, Lake Malaŵi, Malaŵi, Africa, 15 Jan. 2008, A. F. Konings & J. R. Stauffer Jr. (CB and JW).

Paratypes. Accession #2207, 20, (36.37 mm–54.42 mm SL), same data as holotype.

Diagnosis. The moderately-sloped vomer (49.62º in holotype) with a swollen rostral tip (Fig. 8) and bicuspid teeth in the anterior portion of the outer row of both upper and lower jaws place this species in *Metriaclima*. It differs from all other *Metriaclima* sp. by living over the sand except for *M. lanisticola, Metriaclima pursus.* and *Metriaclima ngara* n. sp. It differs from other sand-dwelling *Metriaclima* sp. except *M. ngara n. sp.* by the presence of black submarginal bars on the dorsal and anal fins. Narrower interorbital eye width than *ngara* (24-30% vs. 31–37% HL). Generally smaller premaxillary depth than *ngara* (14-19% vs. 18–21% HL) and distance from the posterior margin of the dorsal fin to the anterior margin of the anal fin (30-35% vs. 34–38% SL). Also distinguished from *M. ngara* by dark brown interorbital bar, brown gular, laterally brown ground with center of scales brown outlined in blue, five to six brown lateral bars and caudal fin with brown rays and blue membranes, whereas *M. ngara* has two light gray interorbital bars, yellow gular, laterally gray with blue scales outlined in pale orange below lateral line, four lateral bars and caudal fin with orange rays and blue membranes.

Description. Morphometric and meristic data in Table 6. Small to medium-sized mbuna, ovoid body (mean BD 38.6% SL) with greatest depth between the third and fourth dorsal spine. Dorsal body profile with gradual curve downward posteriorly (more pronounced than *M. ngara*) with highest point at 4^{th}-5^{th} spine, steepens towards posterior of dorsal fin and beginning of caudal peduncle; ventral body profile flat between pelvic fins and base of anal fin with slight upward angle to caudal fin. Dorsal head profile round with continuous curve between interorbital and dorsal-fin origin; horizontal eye diameter (mean 31.05% HL) about twice as large as premaxillary depth (mean 16.25% HL); posterior orbit margin of eye posterior of vertical median of head; short snout with isognathous to slightly retrognathous jaws; teeth in upper and lower jaws in 3–4 rows (mode 3); teeth in outer row bicuspid, inner rows unicuspid or tricuspid.

Dorsal fin with XVI or XVIII (mode XVII) spines and 7–9 (mode 8) soft rays. Anal fin with III spines and 7–8 soft rays. First 5 or 6 dorsal-fin spines gradually increasing in length posteriorly with sixth spine about twice as long as first spine; last 13 spines increasing just slightly in length posteriorly with last spine longest; soft dorsal fin with subacuminate tip, second or third ray longest, to approximately one-third to one-half length of caudal fin. Anal-fin spines progressively increasing in length posteriorly; third or fourth ray longest, to ½ of caudal fin, length equal to or slightly longer than dorsal fin. Caudal fin subtruncate to emarginate. Pelvic fin reaching to first anal-fin spine. Pectoral fin rounded, paddle-shaped, short, reaching vertical through base of 10th or 11th dorsal-fin spine. Flank scales ctenoid with abrupt change to small scales on breast and belly; 24–31 (mode 30) lateral line scales, cheek with 4 to 5 rows of small scales. Dorsal and anal fins scaleless; tiny scales over proximal ¼ of caudal fin.

Head of males interorbital brown with dark brown interorbital bar; cheek and preopercle with blue highlights; opercle with blue and green highlights and black spot; gular brown. Laterally brown ground color, center of scales brown outlined in blue; five to six brown bars; breast brown and belly white and brown. Dorsal fin brown with black submarginal bar; orange and brown lappets. Caudal fin with two dorsal and ventral membranes black; brown rays; blue membranes. Anal fin with proximal ¼ gray, distal ¾ black; one yellow ocelli. Pelvic fins with white leading edge; first two membranes black and rest gray. Pectoral fins clear.

Females similar to males but no as intense; breast and belly white.

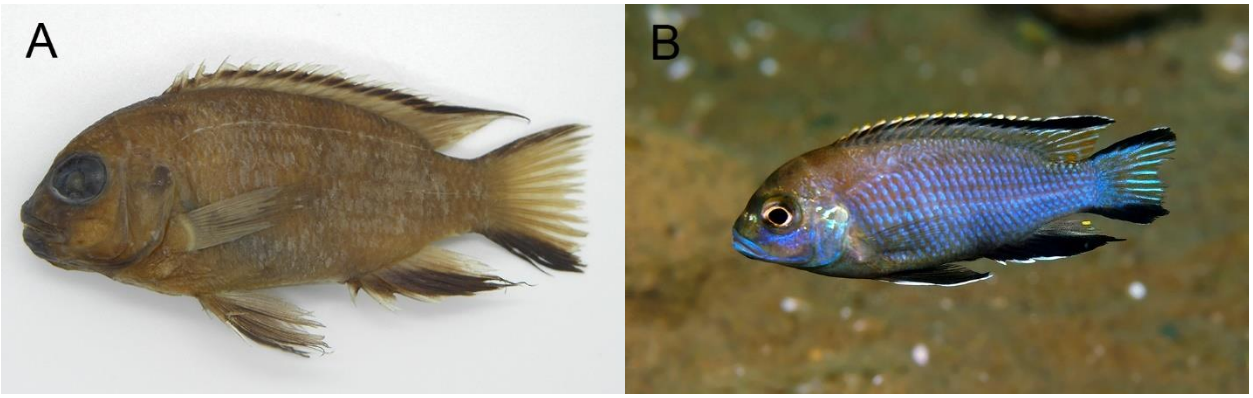

FIGURE 8. *Metriaclima gallireya*. A. Holotype, Accession #2207, Collection # JRS-08-13-1 adult male, 54.42 mm SL, Gallireya Reef, Lake Malaŵi; B. Male in breeding coloration at type locality.

Distribution. *Metriaclima gallireya* is found on Gallireya Reef (S 10° 30.055', E 34° 14.104'), Lake Malaŵi.

Etymology. The specific epithet *gallireya* is derived from Gallireya Reef, a prominent reef in Lake Malaŵi from which type specimens were collected near the village of Kliwawa.

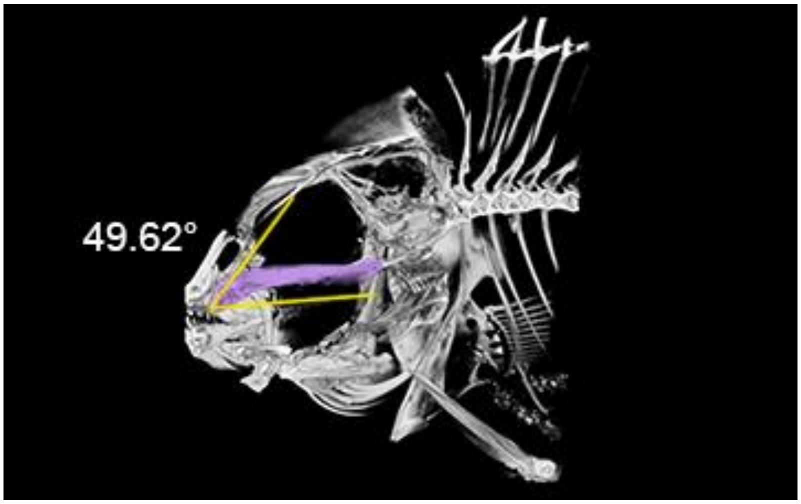

FIGURE 9. Cranium of *Metriaclima gallireya*, adult male, 54.42 mm SL, Gallireya Reef, Lake Malaŵi; angle of ethmovomerine block is 49.62° with parasphenoid.

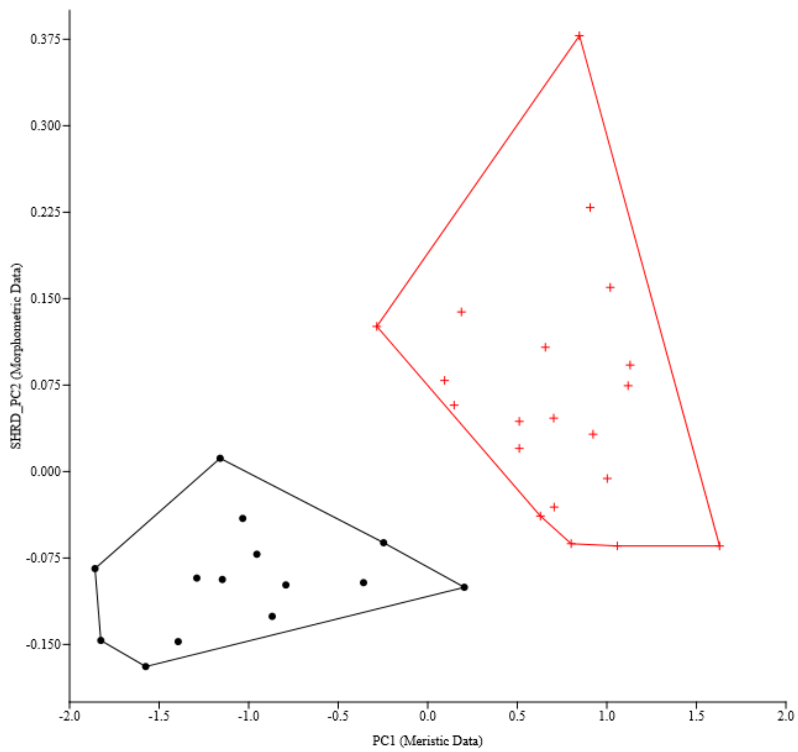

FIGURE 10. Sheared second principal components (morphometric data) plotted against the first principal components (meristic data) of specimens of *Metriaclima ngara* from Ngara (•) and specimens of *Metriaclima gallireya* from Gallireya Reef (+). The data points are bounded by minimum polygon convex hulls.

Remarks. The morphometrics and meristics of *M. gallireya* are both significantly different from *M. ngara* (Table 4). While PCA is not used to diagnose and distinguish species, PCA does further support the diagnosis that *M. gallireya* is a new species separate from *M. ngara* (Fig. 9). Individual size accounted for 86.89% of the variance in the two species, and shape accounted for 6.33% of the variance. The three highest individual morphometric loadings on the sheared second principal components were premaxillary pedicel (-0.92), distance from the anterior margin of the dorsal fin to the insertion of the pelvic fin (0.11), and distance from the posterior margin of the dorsal fin to posterior margin of the anal fin (0.11).

TABLE 6. Morphological and meristic data for *Metriaclima gallireya* from Gallireya Reef, Lake Malaŵi, Accession #2207, Collection # JRS-08-13-1 holotype; PSU 2207, n=20. Ranges include holotype.

Variable	Holotype	Mean	Std Dev	Range
Standard length (mm)	54.42	45.75	4.96	36.4 - 54.4
Head length (mm)	17.67	15.07	1.42	12.4 - 17.7
Percent head length (%)				
Snout length	28.30	30.95	2.26	25 - 35
Postorbital head length	41.94	42.65	1.76	39 - 46
Horizontal eye diameter	32.26	31.05	1.61	28 - 34
Vertical eye diameter	30.79	28.95	1.79	25 - 32
Premaxillary depth	17.88	16.25	1.45	14 - 19
Cheek depth	31.07	26.3	3.57	21 - 34
Lower jaw length	26.88	25.95	3.03	22 - 33
Head depth	104.81	100.05	5.44	91 - 110
Inter-orbital width	26.20	27.30	1.45	24 - 30
Premaxillary pedicel depth	19.19	23.05	5.27	10 - 32
Percent standard length (%)				
Body depth	43.26	38.6	1.79	35 - 43
Snout to dorsal fin origin	39.47	35.65	1.27	33 - 39
Snout to pelvic fin origin	38.85	40.6	1.47	37 - 43
Dorsal fin base length	60.22	57.15	2.16	52 - 60
Anterior dorsal to anterior anal	55.33	51.75	1.71	49 - 55
Anterior dorsal to posterior anal	65.31	62.45	1.79	58 - 65
Posterior dorsal to anterior anal	34.86	32.95	1.39	30 - 35
Posterior dorsal to posterior anal	19.94	18.55	1.00	17 - 20
Posterior dorsal to ventral caudal	20.89	19.25	0.85	18 - 21
Posterior anal to dorsal caudal	23.23	22	0.86	21 - 24
Anterior dorsal to pelvic-fin origin	42.70	38.5	1.76	35 - 43
Posterior dorsal to pelvic-fin origin	61.08	57.45	1.70	55 - 61
Caudal peduncle length	13.62	13.3	0.98	12 - 15
Least caudal peduncle depth	15.78	15.55	0.69	14 - 16
Meristics		Mode	Frequency (%)	Range
Dorsal-fin spines	17	17	80	16 - 18
Dorsal-fin rays	8	8	80	7 - 9
Anal-fin spines	3	3	100	3 - 3
Anal-fin rays	7	8	75	7 - 8
Pectoral-fin rays	14	14	45	12 - 15
Pelvic-fin rays	6	6	90	6 - 7
Lateral line scales	30	30	30	24 - 31
Pored scales caudal	2	1	40	0 - 3
Cheek scale rows	4	4	85	4 - 5
Gill rakers 1st ceratobranchial	10	10	70	9 - 11
Gill rakers 1st epibranchial	5	4	85	3 - 5
Teeth outer left lower jaw	12	10	25	6 - 17
Tooth rows upper jaw	4	3	70	3 - 4
Tooth rows lower jaw	4	3	90	3 - 4

Discussion

Among the 850 or so species of cichlids found in Lake Malaŵi is a highly diverse group of small, rock-dwelling fishes known locally as mbuna. *Metriaclima and Pseudotropheus* are two of the most speciose mbuna genera found in Lake Malaŵi. *Metriaclima* is comprised of at least 75 species, while *Pseudotropheus* is the most diverse and widespread. Most mbuna are found over rocky outcroppings or reefs, but both *Metriaclima* and *Pseuodtropheus* are sand-dwelling mbuna, showing high-fidelity to sandy-bottom habitats. We hypothesize that sandy habitat reinvasion events occurred one at a time; for instance, *Pseudotrepheus* and *Metriaclima* each reinvaded sandy habitats singly and separately. Still, it is possible that one single mbuna reinvasion event occurred initially and speciation of sand-dwelling Pseudotrepheus and Metriaclima occurred thereafter. Detailed genetic studies are still needed to determine the extent and timing mbuna's reinvasion of the sand.

Pseudotropheus originally served as a catch-all genus for newly discovered mbuna species. Still, some species remain rooted in *Pseudotropheus*, although most regard it as polyphyletic. In this study, we described a new species of *Pseudotropheus, P. likoma*. The placement of *P. likoma* in the genera *Pseudotropheus* is supported by the close relationship we discovered between *P. likoma* and *P. livingstoni* with respect to size and shape, the steep angle of ethmovomerine block (72.09°) with the parasphenoid, and the dissociation from snail shells in adults.

Metriaclima was removed from *Pseudotropheus* and was comprised of the *Pseudotropheus zebra* complex by Stauffer et al. 1997 and Konings & Stauffer 2006. *Metriaclima* contains many geographically narrow populations with high-fidelity to specific habitat landmarks, such as single reefs or islands, and it is likely this narrow habitat selection preference has led to the high richness of species in *Metriaclima.* Often, only minute differences in male breeding coloration distinguish the many *Metriaclima* species, and, as a result, color as a species delimiter has been adopted by cichlid taxonomists, specifically for species within Lake Malaŵi. The swollen rostral tip of the ethmo-vomerine block distinguishes *Metriaclima* from *Pseudotropheus*, and the feeding behavior of *Metriaclima* distinguishes the genus from *Pseudotropheus* even further.

We described two new *Metriaclima* species that are found in sandy habitats: *M. ngara* and *M. gallireya*. Both species show high-fidelity to specific habitats, with *M. ngara* found on a submerged reef near the village of Ngara, Malaŵi, and *M. gallireya* found on Gallireya Reef near the village of Kliwawa, Malaŵi. Both species exhibit a moderately-sloped vomer with a swollen rostral tip, placing them squarely in *Metriaclima. M. ngara* and *M. gallireya* are distinguished from other *Metriaclima* by living over sandy bottoms, with the exception of *M. lanisiticola* and *M. pursus*. Like other sand-dwelling *Metriaclima*, *M. ngara* and *M. gallireya* are associated with *lanisti* shells. *M. ngara* and *M. gallireya* are distinguished from other sand-dwelling *Metriaclima* by coloration. Specifically*, M. ngara* and *M. gallireya* are distinguished by the presence of black submarginal bars on the dorsal and anal fins, and *M. ngara* and *M. gallireya* are distinguished from each other by morphological and coloration differences.

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