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Descriptions of two new shell-dwelling species of *Metriaclima* (Cichlidae) from Lake Malaŵi, Africa

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Abstract

Metriaclima is the most speciose genus of rock-dwelling fishes (mbuna) found in Lake Malaŵi with 32 described species and with about 40 recognized forms that still await formal description. The genus is comprised of many geographically narrow populations restricted to specific habitat landmarks, such as reefs or islands. A few species have taken to the open sandy habitat where empty gastropod shells provide shelter. Two species of such shell-dwellers are here described as new. A combination of a black submarginal band in the dorsal and anal fins and five or fewer bars on the flank distinguishes *Metriaclima ngarae* **sp. n.** and *M. gallireyae* **sp. n.** from all other species of *Metriaclima*. *Metriaclima ngarae* **sp. n.** differs from *M. gallireyae* by a greater interorbital width and by a greater ratio of the snout length in the distance between snout tip and pelvic fin origin. Adult males of *M. gallireyae* have a blue-brown overall coloration obscuring the bar pattern on the flank while males of *M. ngarae* and those of the closely related *M. lanisticola* retain the bar pattern and have a coloration very similar to that of females.

Key words: shell-dwelling cichlids, gastropod shells

Introduction

Lake Malaŵi, one of the three great lakes of Africa (lakes Malaŵi, Victoria, and Tanganyika), lies in the East African countries of Malaŵi, Tanzania, and Mozambique. Some 80% of the world's cichlids are found in Africa, and the majority of those are found in the African Great Lakes (Snoeks 2001, Stauffer *et al.* 2007). Within this diverse assemblage of fishes from Lake Malaŵi, the small and colorful rock-dwelling cichlids are referred to as mbuna in the local vernacular. Although not formally described, the mbuna share the following characters: 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 which is non-functional; and 4) possession of true ocelli on the anal fin (Fryer 1959). The mbuna are mostly associated with rocky habitats, but a small group of species occurs on sandy substrates (Fryer 1959; Fryer & Iles 1972; Ribbink *et al.* 1983; Stauffer 1991).

Lake Malaŵi harbors an estimated 850 haplochromine species of cichlids alone, making it the most speciose lake in the world (Konings 2016). Still, only slightly more than half of Malaŵian cichlid species have been formally described while new species await their description and earlier descriptions need revisions (Stauffer *et al.* 2013). Discrimination among cichlid species of Lake Malaŵi can be difficult, because visual differences among species may be very small (Konings 2016) and because morphological characters may be prone to convergence (Kocher *et al.* 1993) and/or are phenotypically flexible (Stauffer & van Snik Gray 2004). In conjunction with their morphological attributes, behavioral traits of these species are important diagnostic tools in distinguishing the multitude of species (Barlow 2002; Stauffer *et al.* 2002). Thus, 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 the main characteristics for delimiting species. Specifically, cichlid males of

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most rock-dwelling species express bright, dramatic coloration, which is thought to be an important mate-selection factor and a potential reproductive barrier among different populations. Male coloration of mbuna populations vary (sometimes slightly) by location, but very little variation may be exhibited within a population (Black 2010). Visually similar species in Lake Malaŵi are sometimes distinguished by feeding techniques, and species may vary significantly in mouth structure, dentition, and/or number of gillrakers (Stauffer *et al.* 2007; Konings *et al.* 2021). Morphology alone, just like coloration and behavior, is often not enough to delimit species due to recent and rapid speciation that has led to the incredible diversity and similarity in morphological and genetic traits. For instance, Won *et al.* (2005) found evidence that three sympatric *Tropheops* species from southern Malaŵi may have diverged from each other within the last 17,000 years.

Lake Malaŵi is home to 14 genera of mbuna, with *Metriaclima* likely the most speciose genus, possibly comprising at least 75 species (Stauffer *et al.* 2013). The species currently assigned to *Metriaclima* were previously grouped in the catch-all genus *Pseudotropheus*. Members of that genus have been re-evaluated numerous times and the 16 described species that currently remain in the genus still form a polyphyletic group with only a handful of species closely related to the type, *Pseudotropheus williamsi* Günther.

Stauffer et al (1997) diagnosed *Metriaclima*, and this diagnosis was expanded by Konings & Stauffer (2006). Condé & Géry (1999) claimed that *Metriaclima* should be regarded as a junior synonym of *Maylandia* Meyer & Foerster (1984); however, Meyer & Foerster (1984) failed to supply a character in which their subgenus *Maylandia*, defined by its type species *M. greshakei* Meyer & Förster, is distinct from *Pseudotropheus*. Characters were given for a so-called zebra complex but *M. greshakei* was not considered part of that complex. The subgenus was thus not diagnosed according to the requirements of Article 13.1.1 of the Code and was therefore regarded a *nomen nudum* by Stauffer *et al.* (1997) and subsequent authors (Konings & Geerts 1999, Geerts 2002, Stauffer & Kellogg 2002).

Originally, Stauffer *et al.* (1997) provided three morphological characteristics 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 at a 45° angle to a line from the tip of the snout to the hypural plate. Konings & Stauffer (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 in upper and lower jaw furthest apart; and 7) the placement of 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 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.

The feeding behavior of *Metriaclima* spp. distinguishes the genus from *Pseudotropheus* even further. *Metriaclima* spp. feed at a perpendicular angle to the substrate by abducting its jaws to a nearly 180° angle, which is not observed in *Pseudotropheus* (Konings & Stauffer 2006). The two species described herein are aligned with *Metriaclima lanisticola* (Burgess), and all three occur in sandy habitats and display a life-long association with empty gastropod shells.

Methods and materials

Adult fishes were collected in Lake Malaŵi (Fig. 1) 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 Parks. 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. These notes, including photographs, are stored at the PSUFM under the catalog numbers provided. Variable color patterns were recorded by placing a slash between the two colors between which the specific patterns varied, e.g., blue/white was used to designate that the color ranges from blue to white. Behavioral notes were also taken at the site of collection.

Twenty-six measurements and 14 counts were taken for each individual following Barel *et al.* (1977) and Konings & Stauffer (2006). 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 0.1 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 and upper lateral lines. Pored lateral-line scales posterior to the hypural plate were counted separately. 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 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.

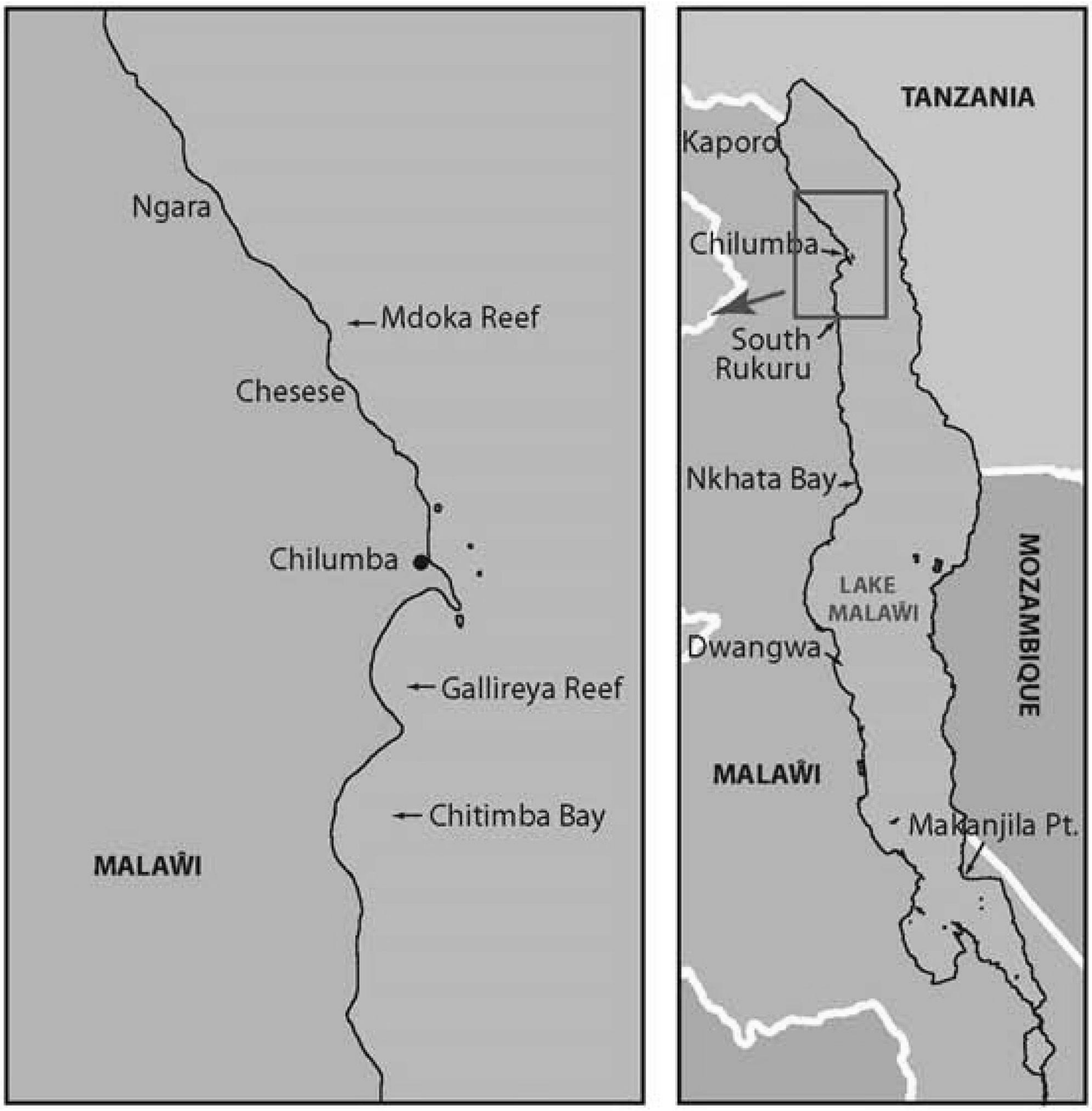

FIGURE 1. Map of Lake Malaŵi with the localities marked that are mentioned in the text.

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 accounted for variation of individual size. The sheared second principal components account for variation in shape, independent of size.

Results

***Metriaclima ngarae*, new species**
Figures 2, 3, 4; Table 1

Pseudotropheus lanisticola (in part), Konings 1989
Pseudotropheus livingstonii (in part), Konings 1995
Metriaclima livingstonii (in part), Konings 2001
Metriaclima sp. 'lanisticola north' Konings 2007

Holotype. PSU 13365, adult male, 59.1 mm SL, (10.233397 S, 34.106592 E) Ngara, Lake Malaŵi, Malaŵi, Africa, Jan. 2000, S. Grant's crew.

Paratypes. PSU 13366, 14, (49.6 mm–62.4 mm SL), data as for holotype.

Diagnosis. The moderately sloped vomer (45.4º in holotype) with a swollen rostral tip (Fig. 3) and bicuspid teeth in the anterior portion of the outer row of both upper and lower jaws place this species in *Metriaclima*. The presence of a black submarginal band (Fig. 4) in the dorsal and anal fin distinguishes *M. ngarae* from most other species in *Metriaclima*, except for *M. phaeos* (Stauffer, Bowers, Kellogg, & McKaye), *M. lundoense* Stauffer, Black, & Konings, *M. nigrodorsalis* Stauffer, Black, & Konings, *M. koningsi* Stauffer, *M. gallireyae* n. sp., and from some populations of *M. zebra* (Boulenger), *M. pulpican* Tawil, and *M. usisyae* Li, Konings, & Stauffer. It differs from all of these except *M. gallireyae* by the number of vertical bars below the dorsal fin which is 4-5 for *M. ngarae* and 6-10 for the other species or none at all for *M. koningsi*. It differs from *M. gallireyae* by a greater interorbital width (30.7–37.4% vs. 23.6–29.7% HL) and by a greater ratio of the snout length in the distance between snout tip and pelvic fin origin (28.7–32.8% vs. 20.6–27.8% SNP2). On average, the ratio of premaxillary pedicel length in snout length is smaller in *M. ngarae* at 35.1% vs. 44.6 %SNL in *M. gallireyae* (ranges 20.3–45.2 vs. 33.1–62.7 %SNL). Males of *M. ngarae* have a color pattern similar to that of females but males of *M. gallireyae* are dark brown to blue without visible bar pattern. Female *M. ngarae* have a similar color pattern to those of *M. gallireyae* but the bars on the flank are less prominent and do not extend to the abdomen.

FIGURE 2. *Metriaclima ngarae*. Holotype, PSU 13365, adult male, 59.1 mm SL, Ngara, Lake Malaŵi.

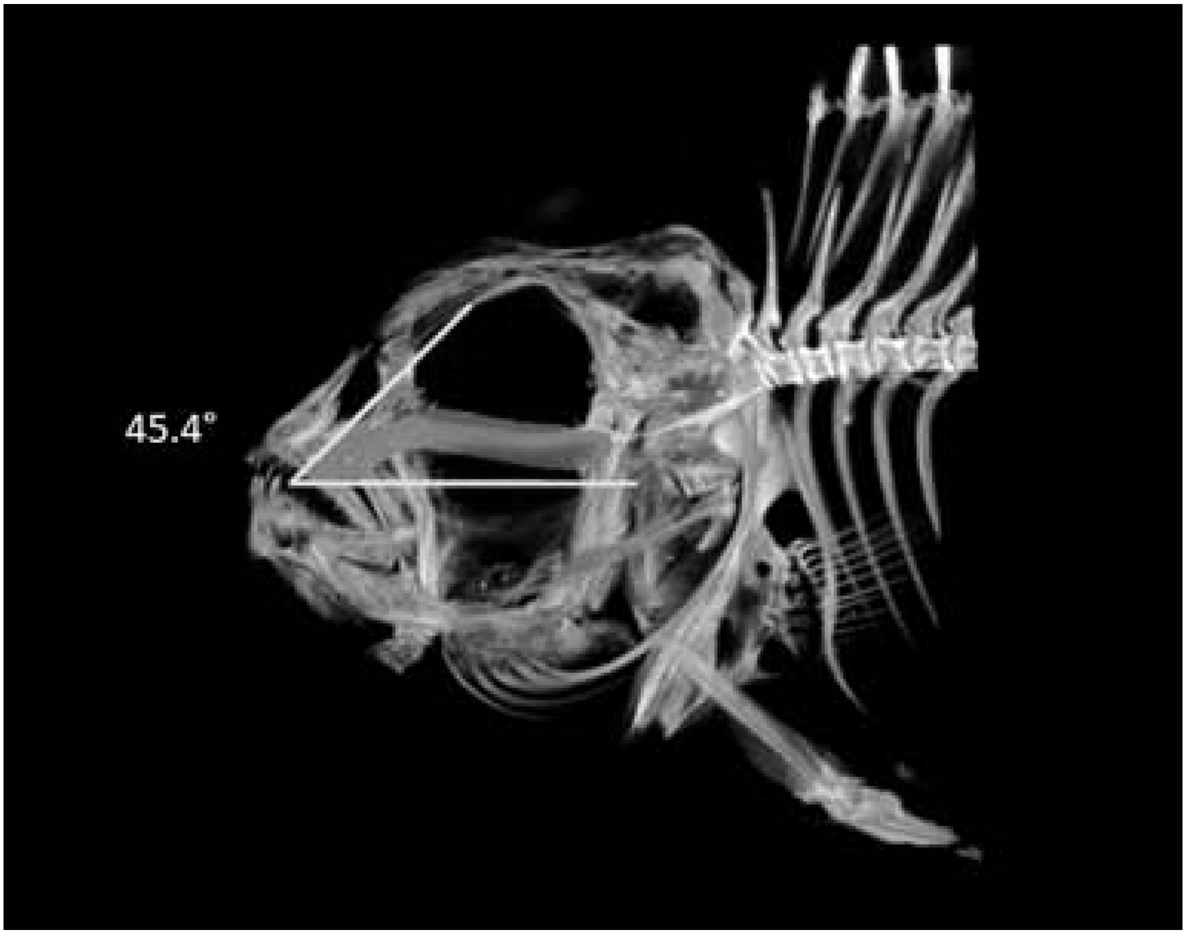

FIGURE 3. CT scan of the cranium of *Metriaclima ngarae* Holotype, PSU 13365, adult male, 59.1 mm SL, Ngara, Lake Malaŵi; angle of ethmovomerine block is 46.4° with parasphenoid.

Description. Morphometric and meristic data in Table 1. Small-sized mbuna, ovoid body (mean BD 38.7% SL) with greatest body depth at about 3rd and 4th dorsal-fin spine. Dorsal body profile with gradual curve downward posteriorly with highest point at 6th or 7th dorsal-fin spine, more pronounced towards posterior end of dorsal fin and beginning 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; 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) rays. Anal fin with III spines and 8 rays. First 5–6 dorsal-fin spines gradually longer posteriorly with 6th spine about twice as long as first; last 11 spines only slightly greater in length posteriorly with last spine longest; soft dorsal fin with rounded to subacuminate tip, second or third ray longest, to approximately ¼ length caudal fin. Anal-fin spines progressively longer posteriorly; 5th or 6th anal-fin ray longest, tip to base of caudal fin in females and to ½ length of caudal fin in males, equal to or slightly further posterior than tip dorsal fin. Caudal fin subtruncate to emarginate. Pectoral fin rounded, paddle-shaped, short, extending to vertical through base of 8th or 9th dorsal-fin spine. Flank scales ctenoid with abrupt change to small scales on breast and belly; 30–32 (mode 31) lateral-line scales, cheek with 4 rows of small scales. Tiny scales over proximal ¼ of caudal fin.

Head of males gray with two light gray interorbital bars; black opercular spot; throat yellow. Flank gray with light blue spots; 4–6 light bars below lateral line; ventrally white. Dorsal fin clear with orange markings, black submarginal band and white lappets. Caudal-fin rays orange with blue membranes. Anal fin with black marginal band encompassing all spines and through rays over 2/3 of distal portion fin; proximal portion of rays light blue; one yellow ocellus. Pelvic fin with spine and first two rays black; remaining clear. Pectoral fin clear.

TABLE 1. Morphological and meristic data for *Metriaclima ngarae* from Ngara, Lake Malaŵi, PSU 13365, 13366, n=14. Ranges include holotype.

Variable	Holotype	Mean	Std Dev	Range
Standard length (mm)	59.1	56.6	3.7	49.6–62.4
Head length (mm)	19.1	18.7	1.2	17.0–21.4
Percent head length (%)				
Snout length	34.6	34.9	1.2	30.8–36.4
Postorbital head length	39.5	40.8	1.7	36.8–42.7
Horizontal eye diameter	30.6	30.1	1.6	26.7–32.3
Vertical eye diameter	28.9	28.0	1.5	24.4–29.9
Preorbital depth	18.7	19.3	1.1	17.9–21.2
Cheek depth	35.3	34.6	2.5	30.3–38.6
Lower jaw length	25.0	26.0	2.8	20.7–30.4
Head depth	109.9	104.1	4.6	98.5–113.0
Inter-orbital width	34.4	33.4	2.1	30.7–37.4
Premaxillary pedicel length	15.0	12.2	2.9	7.0–15.8
Percent standard length (%)				
Head length	32.3	33.1	0.9	32.0–34.5
Body depth	39.1	38.7	0.8	37.1–40.1
Snout to dorsal fin origin	34.9	35.7	1.3	33.9–37.7
Snout to pelvic fin origin	38.4	37.5	1.1	36.3–39.9
Dorsal fin base length	59.8	58.3	1.4	56.0–60.2
Anterior dorsal to anterior anal	50.1	50.1	0.8	48.8–51.5
Anterior dorsal to posterior anal	63.5	62.9	1.3	60.8–64.6
Posterior dorsal to anterior anal	36.6	36.0	1.2	34.2–37.7
Posterior dorsal to posterior anal	19.3	19.4	0.9	18.1–20.3
Posterior dorsal to ventral caudal	21.1	20.6	0.9	19.3–22.3
Posterior anal to dorsal caudal	25.1	23.2	1.1	20.6–25.1
Anterior dorsal to pelvic-fin origin	39.4	38.5	0.9	37.5–40.2
Posterior dorsal to pelvic-fin origin	65.2	61.5	1.4	58.7–65.2
Caudal peduncle length	14.9	14.0	1.0	11.8–15.4
Least caudal peduncle depth	16.3	16.2	0.6	15.5–17.3
Meristics		Mode	Frequency (%)	Range
Dorsal-fin spines	17	17	71.4	16–17
Dorsal-fin rays	8	8	71.4	7–8
Anal-fin spines	3	3	100.0	3–3
Anal-fin rays	8	8	100.0	8–8
Pectoral-fin rays	12	14	85.7	12–15
Pelvic-fin rays	7	7	85.7	6–7
Lateral line scales	32	31	57.1	30–32
Pored scales caudal	2	2	50.0	0–2
Cheek scale rows	4	4	100.0	4–4
Gill rakers 1st ceratobranchial	10	11	57.1	9–12
Gill rakers 1st epibranchial	5	5	50.0	4–5
Teeth outer left lower jaw	8	7	35.7	4–10
Tooth rows upper jaw	3	3	92.9	2–3
Tooth rows lower jaw	3	3	64.3	2–3

Head of females dark gray with two faint green interorbital bars; ventral half pale yellow; black opercular spot; pale yellow throat. Flank yellowish, white below lateral line with light gray bars above lateral line. Fin coloration same as males, not as intense.

Distribution. *Metriaclima ngarae* is found on submerged reefs near Ngara (10.233397 S, 34.106592 E) and Mdoka (10.280608 S, 34.179156 E), and has also been reported from Chesese (10.280608 S, 34.179756 E) and Kaporo (9.731972 S, 33.94415 E), Malaŵi (Fig. 1).

Field observations. *Metriaclima ngarae* is most often encountered near empty shells of the gastropod *Lanistes nyassanus* Dohrn that lie scattered on the sandy bottom at a depth ranging between 10–25 m (Fig. 4). Most observations occurred near rocky habitats, but it was also found at a depth of about 20 m near the outflow of the Songwe River that forms the border between Malawi and Tanzania, with no known rocky reefs within 30 km. No stomach analyses were performed but individuals were observed picking at targeted sites on the sand as well as combing the algal matrix covering the empty shells, small rocks, and other objects that lie on the open sand. Most individuals encountered were solitary and always in association with an empty shell of *Lanistes nyassanus* into which it would retreat when threatened. Mouth-brooding females stay near their shell and probably release their offspring inside such shells as well.

Etymology. The specific epithet *ngarae* in the genitive of Ngara, Malawi, where the specimens were collected.

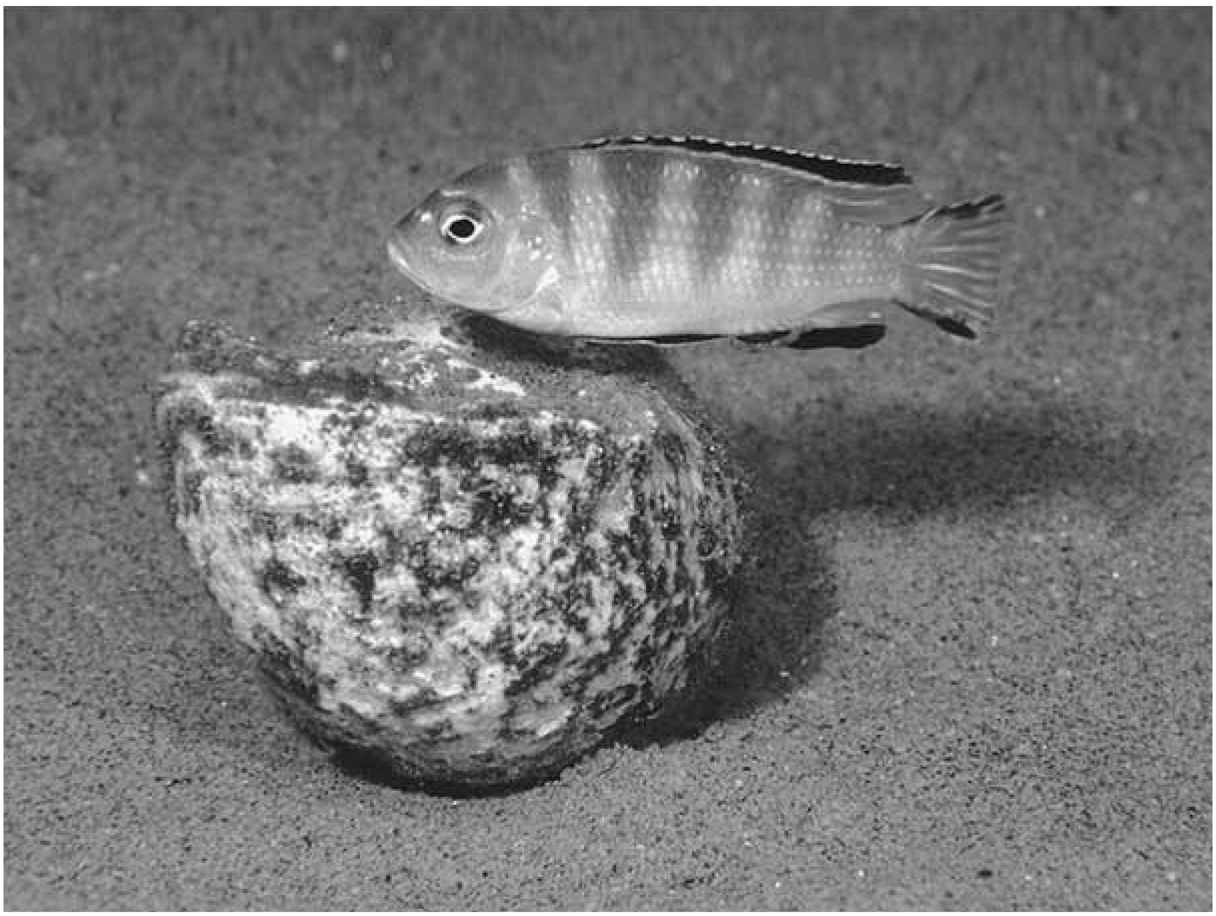

FIGURE 4. A male *Metriaclima ngarae* at a submerged reef near Ngara (10.233397 S, 34.106592 E).

***Metriaclima gallireyae*, new species**

Figures 5, 6, 7; Tables 2

Pseudotropheus lanisticola (in part), Konings 1989
Pseudotropheus livingstonii (in part), Konings 1995

Metriaclima livingstonii (in part), Konings 2001
Metriaclima sp. 'lanisticola north' Konings 2007

Holotype. PSU 13370, adult male, 54.4 mm SL, (10.500153 S, 34.233362 E), Gallireya Reef, Lake Malaŵi, Malaŵi, Africa, 15 Jan. 2008, A. F. Konings & J. R. Stauffer Jr.

Paratypes. PSU 13371, 20, (36.4–54.4 mm SL), data as for holotype.

Diagnosis. The moderately sloped vomer (49.6º 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*. The presence of a black submarginal band in the dorsal and anal fin, and 4–5 bars below the dorsal distinguishes *M. gallireyae* from most other species in *Metriaclima*, except for *M. ngarae.* It differs from *M. ngarae* by a smaller interorbital width (30.7–37.4% vs. 23.6–29.7% HL) and by a smaller ratio of the snout length in the distance between snout tip and pelvic fin origin (20.6–27.8% vs. 28.7–32.8% SNP2). On average the ratio of premaxillary pedicel length in snout length is greater in *M. gallireyae* at 44.6% vs. 35.1 %SNL in *M. ngarae* (ranges 33.1–62.7 vs. 20.3–45.2 %SNL). Mature males of *M. gallireyae* have a dark brown to blue coloration on flank (Fig. 7) on which no bar pattern is visible. Male *M. ngarae* resemble females and display 4–5 dark bars on a light-colored flank. Female *M. gallireyae* have a similar color pattern to those of *M. ngarae* but the bars on the flank are more prominent and extend to the abdomen.

FIGURE 5. *Metriaclima gallireyae*. Holotype, PSU 13370, adult male, 54.4 mm SL, Gallireya Reef, Lake Malaŵi.

Description. Morphometric and meristic data in Table 2. Small mbuna with ovoid body (mean BD 38.6% SL) with greatest depth between the 3rd and 4th dorsal spine. Dorsal body profile with gradual curve downward posteriorly (more pronounced than in *M. ngarae*) with highest point between the 4th and 5th spine, less deep towards posterior end of dorsal fin and beginning of caudal peduncle; ventral body profile flat between pelvic fins and origin of anal fin with slight upward angle to caudal fin. Dorsal head profile round with continuous curve between interorbital and dorsal-fin origin; 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) rays. Anal fin with III spines and 7–8 rays. First 5–6 dorsal-fin spines gradually longer posteriorly with sixth spine about twice as long as first spine; posterior 13 spines slightly longer posteriorly with last spine longest; soft dorsal fin with subacuminate tip, 2nd or 3rd ray longest, extending to approximately 1/3–1/2 length of caudal fin. Anal-fin spines progressively longer posteriorly; 3rd or 4th ray longest, extending to halfway caudal fin, equal to or slightly further posterior than tip of 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 small scales on breast and belly; 29–32 (mode 30) lateral-line scales, cheek with 4–5 rows of small scales. Small scales over proximal ¼ of caudal fin.

Head of male brown with dark brown interorbital bar; cheek and preopercle with blue highlights; opercle with blue and green highlights and black spot; throat brown (Fig. 7). Flank dark brown to blue (in territorial males), center of scales brown with blue outline; 4–5 brown bars, obscured in fully mature males; breast and belly black. Dorsal fin brown with black submarginal bar; orange and brown lappets, with orange pigmentation in membranes of rayed portion. Caudal fin with black dorsal and ventral margin; brown rays; blue membranes. Anal fin with proximal ¼ gray, distal ¾ black; one yellow ocellus. Pelvic fin black with white leading edge. Pectoral fin with clear membranes and gray rays.

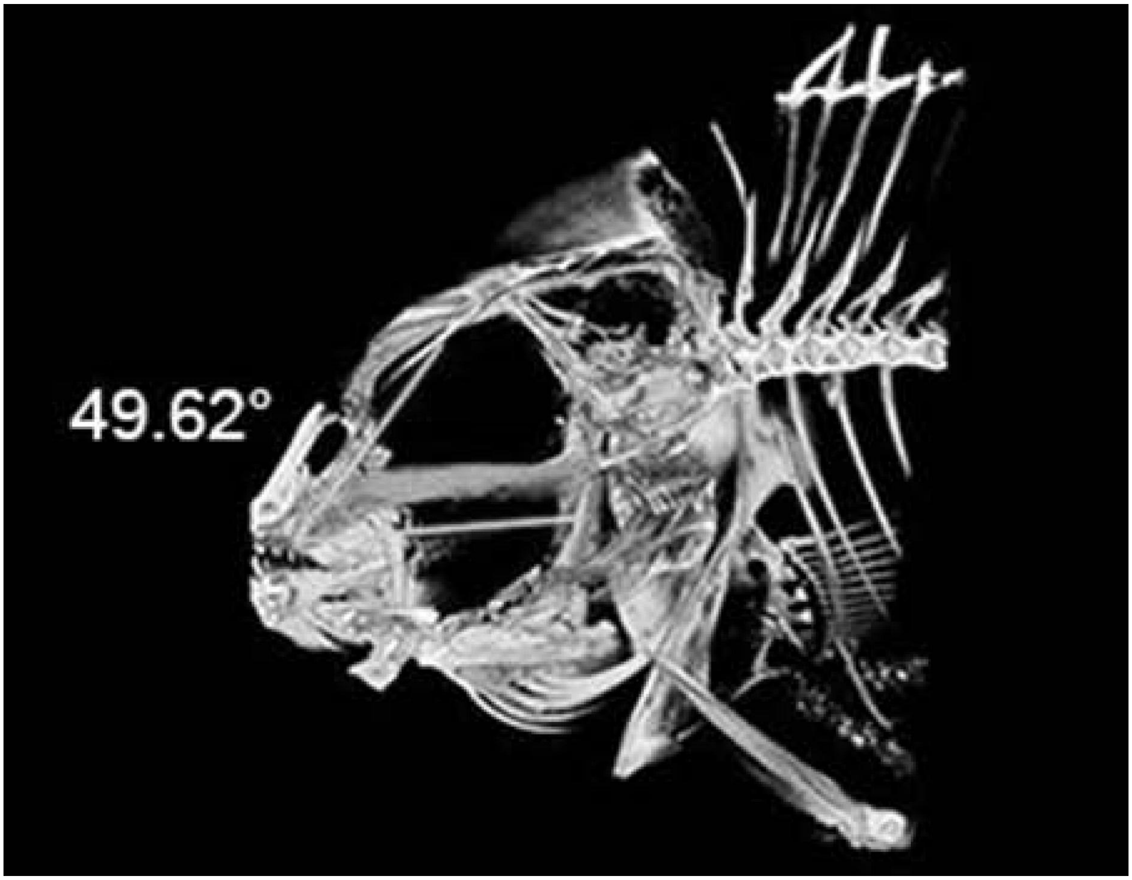

FIGURE 6. CT scan of the cranium of *Metriaclima gallireyae*. Holotype, PSU 13370, adult male, 54.4 mm SL, Gallireya Reef, Lake Malaŵi; angle of ethmovomerine block is 49.6° with parasphenoid.

Distribution. *Metriaclima gallireyae* is found on Gallireya Reef (10.500153 S, 34.233362 E), Youngs Bay and in Chitimba Bay (10.581122 S, 34.23692 Lake Malaŵi, Malaŵi (Fig. 1).

Field observations. The population density of *Metriaclima gallireyae* is much higher than that of *M. ngarae* and is often seen in large groups of up to 20 individuals in the vicinity of empty shells of *L. nyassanus*. Both sites where this small species was observed contained either many football-sized (lava?) rocks (Gallireya Reef) or large slabs of sandstone (Chitimba Bay) that may provide additional shelter to individuals that were not able to secure an empty shell for protection. The depth range at Gallireya Reef is about 8–12 m while the reef (almost solely consisting of sandstone slabs) in Chitimba Bay is at a depth of about 20–25 m. Pure sandy habitats in the area of these two reefs were not visited other than near shore (shallower than 5 m) where *M. gallireyae* was absent.

No stomach analyses were performed but individuals were observed picking from the rocks and slabs, particularly from patches that showed less sediment cover. Repeated application of the fully opened mouth to a sediment-free spot on a rock suggests that it combs the algal matrix for loose strands of (blue-green) algae. Females and immatures were often seen in small foraging groups mainly feeding from plankton in the water column close (<20cm) to the sandy bottom.

TABLE 2. Morphological and meristic data for *Metriaclima gallireyae* from Gallireya Reef, Lake Malaŵi, PSU 13370, 13371, n=20. Ranges include holotype.

Variable	Holotype	Mean	Std Dev	Range
Standard length (mm)	54.4	45.8	5.0	36.4–54.4
Head length (mm)	17.7	15.1	1.4	12.4–17 .7
Percent head length (%)				
Snout length	28.3	31.0	2.3	26.2–35.0
Postorbital head length	41.9	42.7	1.8	39.0–46.0
Horizontal eye diameter	32.3	31.1	1.6	28.5–34.2
Vertical eye diameter	30.8	29.0	1.8	25.1–32.4
Preorbital depth	17.9	16.3	1.5	14.1–18.9
Cheek depth	31.1	26.3	3.6	21.1–33.5
Lower jaw length	26.9	26.0	3.0	21.6–33.5
Head depth	104.8	100.1	5.4	91.3–109.7
Inter-orbital width	26.2	27.3	1.5	23.6–29.7
Premaxillary pedicel length	15.7	13.7	1.7	10.9–16.4
Percent standard length (%)				
Head length	32.7	33.0	0.8	31.5–34.4
Body depth	43.3	38.6	1.8	34.9–43.3
Snout to dorsal fin origin	39.5	35.7	1.3	32.6–39.5
Snout to pelvic fin origin	38.9	40.6	1.5	37.4–42.5
Dorsal fin base length	60.2	57.2	2.2	52.4–60.2
Anterior dorsal to anterior anal	55.3	51.8	1.7	48.6–55.3
Anterior dorsal to posterior anal	65.3	62.5	1.8	58.0–65.3
Posterior dorsal to anterior anal	34.9	33.0	1.4	30.2–35.0
Posterior dorsal to posterior anal	19.9	18.6	1.0	17.0–19.9
Posterior dorsal to ventral caudal	20.9	19.3	0.9	17.5–20.9
Posterior anal to dorsal caudal	23.2	22.0	0.9	21.0–23.8
Anterior dorsal to pelvic-fin origin	42.7	38.5	1.8	35.0–42.7
Posterior dorsal to pelvic-fin origin	61.1	57.5	1.7	54.7–61.1
Caudal peduncle length	13.6	13.3	1.0	11.5–14.8
Least caudal peduncle depth	15.8	15.6	0.7	14.4–16.3
Meristics		Mode	Frequency (%)	Range
Dorsal-fin spines	17	17	80.0	16–18
Dorsal-fin rays	8	8	80.0	7–9
Anal-fin spines	3	3	100.0	3–3
Anal-fin rays	7	8	75.0	7–8
Pectoral-fin rays	14	14	45.0	12–15
Pelvic-fin rays	6	6	90.0	6–7
Lateral line scales	30	30	40.0	29–32
Pored scales caudal	2	1	40.0	0–3
Cheek scale rows	4	4	85.0	4–5
Gill rakers 1st ceratobranchial	10	10	70.0	9–11
Gill rakers 1st epibranchial	5	4	85.0	3–5
Teeth outer left lower jaw	12	10	25.0	6–17
Tooth rows upper jaw	4	3	70.0	3–4
Tooth rows lower jaw	4	3	90.0.	3–4

Mature males protect an empty shell as their territory but mouth-brooding females at Gallireya Reef were frequently encountered among the rocks of the habitat. Mouth-brooding females in Chitimba Bay were mostly seen near their shell.

Etymology. The specific epithet *gallireyae* is a genitive of Gallireya Reef, the local name for a reef in Youngs Bay, Lake Malaŵi.

Remarks. There was complete separation of the minimum polygon clusters when the sheared second principal components (SPCA2) of the morphometric data were plotted against the first principal components (PC1) of the meristic data for *M. ngarae* and *M. gallireyae* (Fig. 8). The first principal component (size variable) of the morphometric data explained 87.8% of the observed variance and SPCA2 explained 5.4%. Variables that had the highest loadings on SPCA2 were the premaxillary pedicel length (0.89), snout length (-0.24), and cheek depth (-0.21). The first principal component of the meristic data explained 24.7% of the variance. Variables with the highest loadings on the first principal components of the meristic data were pored lateral-line scales posterior to the hypural plate (0.50), number of tooth rows on the upper jaw (0.44), and tooth rows on the lower jaw (0.28).

FIGURE 7. A male *Metriaclima gallireyae* at Gallireya Reef (10.500153 S, 34.233362 E), Lake Malaŵi.

Discussion

Most mbuna species occur in rocky habitats of outcroppings and reefs, but the two new *Metriaclima* species described herein show high affinity for sandy habitats where empty shells of *L. nyassanus* provide shelter. *Metriaclima* contains many geographically narrow populations with high-fidelity to specific habitat landmarks, such as single reefs or islands, and it is likely that this narrow habitat preference has led to the richness of species in *Metriaclima.*

The two new species are undoubtedly closely related to *M. lanisticola* as they show the similar morphology, habitat preference, and affinity for empty shells of *L. nyassanus*. *Metriaclima lanisticola*, described from the population at Chembe in the southern part of the lake, has never been encountered further north than Dwangwa (12.584128S, 34.260919E) along the western shore and Makanjila Point along the eastern. South of these two locations it is a very common cichlid of slow-grading, flat sandy habitats that provide shelter in the form of empty shells. *Metriaclima ngarae* and *M. gallireyae* described herein appear to have a restricted distribution in the northern part of the lake and no shell-dwelling *Metriaclima* has been reported from the 220 km (straight line) of shoreline in between the southernmost population of *M. gallireyae* and the northernmost of *M. lanisticola*. The only shell-dwelling mbuna found along the eastern shores north of Makanjila Point is *Pseudotropheus livingstonii* and only juveniles of that species use empty shells as shelter. It appears that the three *Metriaclima* species need extensive flat sandy habitat with a very gradual shelving incline where sufficient numbers of empty snail shells are available to support a population. The shoreline along the eastern side of the lake drops to greater depths at a much greater angle than is the case along most of the western side, but between Nkhata Bay and the outflow of the South Rukuru River on the west side the coast is equally steep sloping. The absence of shell-dwelling *Metriaclima* in these parts of the lake is probably a direct consequence of the lack of extensive flat sandy habitat.

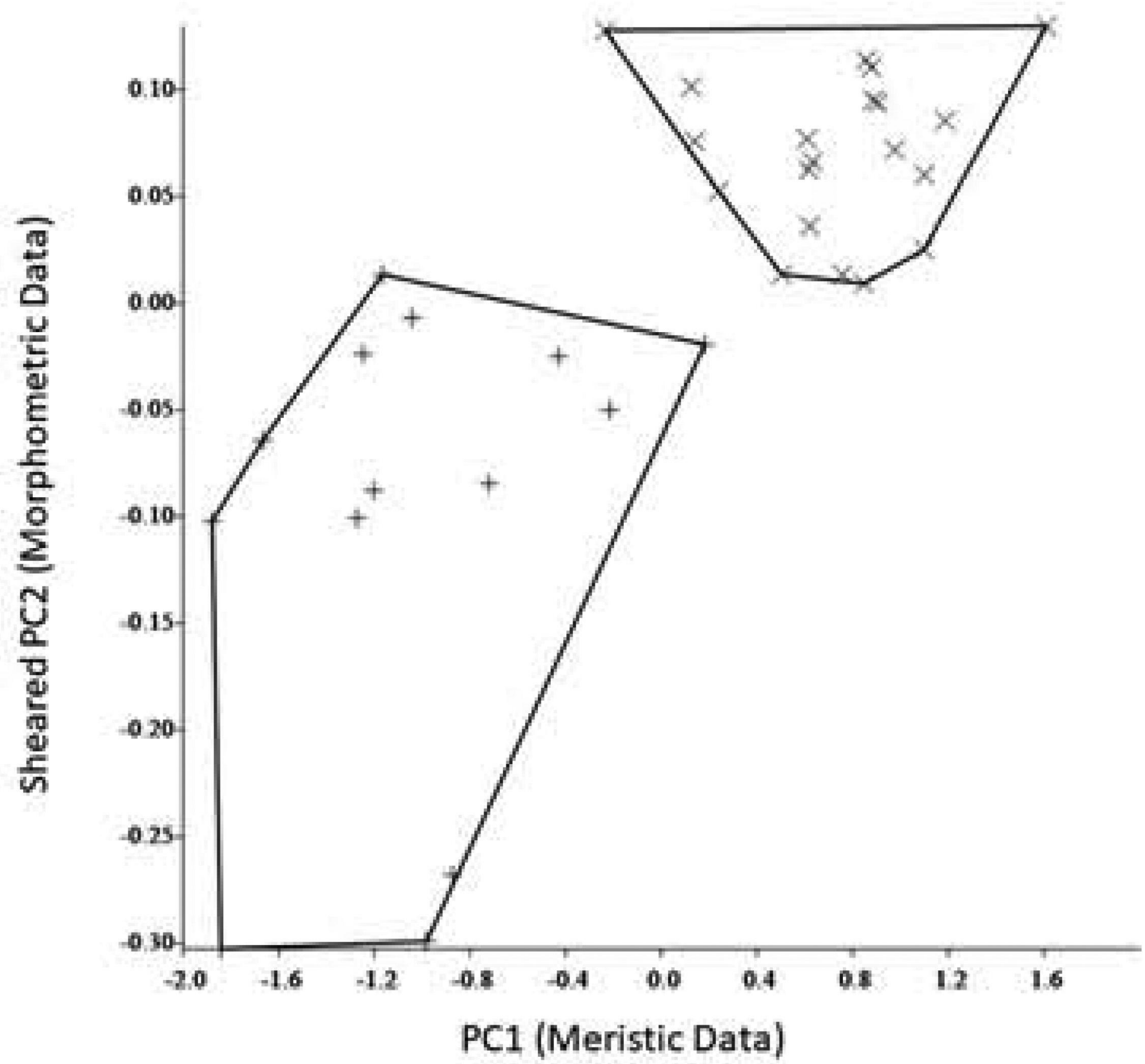

FIGURE 8. Sheared second principal components (morphometric data) plotted against the first principal components (meristic data) of 14 specimens of *Metriaclima ngarae* from Ngara (x) and 20 specimens of *Metriaclima gallireyae* from Gallireya Reef (+).

Initially we assumed that the northern shell-dwellers would represent a single species but the combination of morphological differences and those in male breeding coloration made us decide to treat these as two separate taxa which are geographically separated by a steep-sloping shoreline of about 25 km in length. *Metriaclima ngarae* and

M. gallireyae, in all stages of development, are easily distinguished from those of *M. lanisticola* by the bold black bands in the dorsal and anal fins which are lacking in *M. lanisticola*. Our decision to regard these two populations as two different species precludes the possibility to regard them as geographical populations of *M. lanisticola,* the nearest population of which is more than 220 km away. 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.

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