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Descriptions of five new species of *Metriaclima* (Teleostei: Cichlidae) from Lake Malaŵi, Africa

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Abstract

Lake Malaŵi is known for its endemic haplochromine species flock, most notably the rock-dwelling cichlids known as mbuna. One of the larger genera of mbuna is *Metriaclima*, a group consisting of 31 described species (including the five described herein) and approximately 45 recognized unique populations. *Metriaclima* is diagnosed by its feeding behavior and several morphological characteristics including the angle of the vomer and the presence of bicuspid teeth in the outer row of both the upper and lower jaws. *Metriaclima zebra*, the type species for the genus, was described based on a single specimen. While the collection location of this holotype is not known, based on the travel records of its collector, it is likely that the specimen originated from Likoma Island. The holotype was therefore compared to specimens from several localities around this island and was found to be morphologically indistinguishable from some of these.

This study includes the morphological analysis of 496 specimens of *Metriaclima* belonging to 31 collections from Lake Malaŵi. Morphometric differences were analyzed and the relationships among several distinguishable populations of *Metriaclima zebra* were investigated.

Our study further resulted in the description of the following five new species belonging to the *M. zebra* species complex: *M. pambazuko, M. lundoense, M. midomo, M. tarakiki,* and *M. nigrodorsalis.* These species were distinguished and described based on color patterns, morphometric, meristic, and ecological differences. These new species were compared with and distinguished from nearby populations of *Metriaclima* having similar pigmentation patterns and/or similar ecological niches. An artificial dichotomous key to the described species of *Metriaclima* is presented.

Key words: Mbuna, zebra cichlid, pigmentation patterns

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Introduction

The cichlid fishes of East Africa represent the largest and best-known case of explosive radiation in modern vertebrates. This radiation is concentrated in the three Great Lakes of Africa – lakes Tanganyika, Malaŵi, and Victoria. At present, the Lake Malaŵi radiation represents the greatest number of endemic species of the three lakes, making it the most speciose lake in the world (Greenwood 1974). Lake Malaŵi contains five species of the tilapiine tribe and some 850 haplochromine cichlid species, approximately 400 of which have been described (Konings 2007). The endemic Malaŵi haplochromine cichlid species were originally thought to be monophyletic (Kornfield *et al.* 1985; Meyer *et al.* 1990; Kornfield 1991; Moran *et al.* 1994), but recent studies by Joyce *et al.* (2011) revealed that Lake Malawi was repeatedly colonized by at least two different haplochromine ancestors and that the mbuna possibly arose from hybrid populations.

The driving mechanisms for the explosive radiation of the haplochromine cichlids are unknown. The two earliest suggested methods of speciation are allopatric speciation (Fryer 1959; Fryer & Iles 1972; Greenwood 1984), which may have resulted from lake level fluctuations, and sympatric speciation driven by intrinsic isolating mechanisms (Turner & Burrows 1995; Oppen *et al.* 1998; Takahashi *et al.* 2001; Genner & Turner 2005). The relatively young age of about 0.3–0.5 MYA (Genner *et al.* 2007) of the mbuna species flock, comprising of an estimated 250 species, suggests that some mode of divergence other than the traditionally accepted model of allopatry has operated in Lake Malaŵi. Sexual selection has long been argued as a mechanism that might drive speciation (Seehausen & van Alphen 1999; Seehausen *et al.* 1999; Kellogg *et al.* 2000; Turner 2000). Speciation by sexual selection on variation in male breeding coloration has been proposed to explain the rapid evolution of rock-dwelling haplochromine cichlids (Turner & Burrows 1995; Van Doorn *et al.* 1998; Seehausen & van Alphen 1999, Kidd *et al.* 2006). Seehausen *et al.* (1999) suggested the force of sexual selection has allowed distinctive male breeding coloration to arise and evolve quickly. Thus, many morphologically and genetically similar species have been separated based on breeding coloration and behavioral characteristics (Ribbink *et al.* 1983; Stauffer *et al.* 1993; Stauffer *et al.* 1997).

Live coloration is an important characteristic that cichlid taxonomists use when describing species and in many cases male coloration is the primary trait used to delimit species (e.g., Marsh 1983; Ribbink *et al.* 1983; Bowers & Stauffer 1993, Stauffer *et al.* 1995, 1997). Coloration is an important attribute for intraspecific interactions and may act as a reproductive barrier without concordant morphological differences (Meyer 1993). While non-visual cues (e.g., olfactory cues) were important for species recognition of *M. emmiltos* (Plenderleith *et al.* 2005), Kidd *et al.* (2006) found that female *M. zebra* and *M. benetos* can identify conspecific males using only visual clues.

In the last 25 years, the use of coloration in species delimitation, particularly within lakes Malaŵi and Victoria, has been adopted, based on the assumption that male breeding colors are important in mate recognition and thus act as prezygotic barriers to gene flow (Ribbink *et al.* 1983; Seehausen 1996; Konings 2007). Studies of cichlid fishes in lakes Malaŵi and Victoria have emphasized the importance of male courtship colors in the diagnosis of species (e.g. Ribbink *et al.* 1983; Seehausen 1996; Turner 1996). However, Knight & Turner (2004), using mate choice experiments, showed that color differences between allopatric morphs is not an absolute character in determining specific status. Ciccotto *et al.* (2011) have tried to link a difference in color pattern to an additional morphological difference of neighboring populations or morphs, in order to determine or estimate heterospecificity.

Lake Malaŵi is well known for its endemic, small, rock-dwelling haplochromine cichlid fishes known as mbuna. Although Joyce *et al.* (2011) found that they were not unequivocally resolved as a monophyletic group within the Lake Malaŵi species flock, Genner & Turner (2012) showed support for their monophyly. Morphologically, they are characterized by the possession of many small scales in the chest region with an abrupt transition to larger scales on the flank, a reduced left ovary (Trewavas 1935; Fryer 1959), and a relatively small number of true ocelli in the anal fin (Oliver & Arnegard 2010).

Boulenger (1899) originally described *Metriaclima zebra* in the genus *Tilapia* based on a single specimen (BMNH 1891.12.17.7). Regan (1922) later moved *M. zebra* to the newly formed genus *Pseudotropheus*. Stauffer *et al.* (1997) elevated the members of the *P. zebra* species complex (Ribbink *et al.* 1983) to a newly diagnosed genus, *Metriaclima*.

The characters that currently diagnose *Metriaclima* include: a moderately-sloped ethmo-vomerine bloc with a swollen rostral trip (angle with parasphenoid between 35 and 50°), the presence of bicuspid teeth in the anterior portion of the outer row of the upper and lower jaws, the lower jaw at a 45º angle to the body axis (a line from the tip of the snout to the middle of the caudal peduncle), a lower jaw often slightly longer and thicker than the upper jaw, a portion of the upper dental arcade normally exposed when the mouth is closed, and with the jaws abducted to a near 180º angle during feeding so that the body is aligned at a perpendicular angle to the substrate (Stauffer *et al.* 1997; Konings & Stauffer 2006). Konings & Stauffer (2006) recognized three morphologically similar but phenotypically different assemblages within the genus, i.e., *M. zebra* group, *M. flavifemina* group, *M. aurora* group (see Cicotto *et al.* 2011). Both the *flavifemina* group and the *aurora* group are found in the intermediate habitat along the coast of Lake Malaŵi, where the transition between rocks and sand occurs and are distinguished from one another by the presence or absence of a black band in the dorsal fins of males (Cicotto *et al.* 2011). Males hold territories mainly over the sand near rocks and excavate beneath rocks to construct their spawning burrow. These species are most commonly found at depths of 3–20 m. The members of the *flavifemina* group are characterized by their habitat preference (sand-rock interface), the presence of a black submarginal band in the dorsal fin, and by a brown coloration of most females with a yellow margin in the dorsal, anal, and caudal fins and without (or only faintly present) vertical bars.

In the preparation of this manuscript we encountered a lapsus calami in the description of *Pseudotropheus pursus* Stauffer 1991. In the original publication, under the heading etymology the meaning of the specific epithet was given as: “The name pursus, from the Latin meaning clean, was chosen to reflect the cleaning behavior of this species.” This is clear evidence of an inadvertent error and according to rule 32.5.1. of the International Code of Zoological Nomenclature, it must be corrected. The Latin for “clean” is “purus” and we correct the name of this taxon to *Metriaclima purum* (Stauffer 1991).

The genus *Metriaclima* currently includes the following 26 formally described species (in alphabetical order): *M. aurora* (Burgess), *M. barlowi* (McKaye & Stauffer), *M. benetos* Stauffer, Bowers, Kellogg, & McKaye, *M. callainos* (Stauffer & Hert), *M. chrysomallos* Stauffer, Bowers, Kellogg, & McKaye , *M. cyneusmarginatum* Stauffer, Bowers, Kellogg, & McKaye, *M. emmiltos* Stauffer, Bowers, Kellogg, & McKaye, *M. estherae* (Konings), *M. fainzilberi* (Staeck), *M. flavifemina* Konings & Stauffer, *M. glaucos* Ciccotto, Konings & Stauffer, *M. greshakei* (Meyer & Foerster), *M. hajomaylandi* (Meyer & Schartl), *M. lanisticola* (Burgess), *M. lombardoi* (Burgess), *M. mbenjii* Stauffer, Bowers, Kellogg, & McKaye, *M. mossambicum* Ciccotto, Konings, & Stauffer, *M. nkhunguense* Ciccotto, Konings, & Stauffer, *M. phaeos* Stauffer, Bowers, Kellogg, & McKaye, *M. purum* (Stauffer), *M. pulpican* (Tawil), *M. pyrsonotos* Stauffer, Bowers, Kellogg, & McKaye, *M. sciasma* Ciccotto, Konings, & Stauffer, *M. xanstomachus* (Stauffer & Boltz), *M. xanthos* Ciccotto, Konings, & Stauffer, and *M. zebra* (Boulenger).

Metriaclima may possibly be the most species-rich of all mbuna species complexes as Konings (2007) recognizes at least 75 different forms within the genus. This genus contains many species with a narrow geographical distribution, often endemic to a single island or reef. Such species tend to differ from each other principally in one or more elements of the male breeding coloration. Species richness of *Metriaclima* may be attributed to the restriction of these species to rocky habitats and to the force of allopatric speciation, but also to male-male aggression that was argued by Pauers *et al.* (2008) to be an important diversifying force in the speciation of mbuna.

Many populations of mbuna distributed throughout Lake Malaŵi that are blue-black barred (BB) have been identified as *M. zebra*, which is the type species of *Metriaclima*. The breeding males of *M. zebra* can be distinguished from all other members of *Metriaclima* except from *M. callainos* on the basis of the following color traits: light blue ground coloration with or without distinct black lateral bars, light blue dorsal fin lacking certain pigmentation (the absence of the extension of lateral bars, a dark submarginal or marginal band, or yellow ocellated spots on the trailing part of the dorsal fin), and a light-blue anal fin. Females of *M. zebra* are distinguished from most other members of *Metriaclima* by having a gray/blue to blue/brown ground color and lacking yellow pigment in the unpaired fins.

Metriaclima zebra was described based on a single specimen and the precise location for this holotype was not recorded. Stauffer *et al.* (1997) had compared the holotype with six populations of the putative *M. zebra* from the southern part of the lake and three from the northwestern shore and although they found broad overlap between these nine populations, the holotype did not seem to be congruent with any of them. Initially they were tempted to restrict the name *M. zebra* to the single type and propose a new name for the other populations. Ultimately, they chose to preserve the name *M. zebra*, because of its wide usage in both the scientific and popular literature, and regarded the holotype as being atypical.

The holotype of *M. zebra* was collected by Miss M.E. Woodward and given to the British Museum of Natural History (London) by Miss McLaughlin in 1891. The type locality was recorded as Lake Nyassa. These two women were missionaries who resided on Likoma Island, Lake Malaŵi, Malaŵi from 1888 onward (Anderson-Morshead 1897). For this reason, Konings (2007) hypothesized that the holotype of *M. zebra* was collected at Likoma Island. Here we compare the holotype with various populations collected around Likoma Island. The further purpose of this paper is to describe an additional three new species of *Metriaclima* in the blue-black barred *zebra* group and two new species in the *flavifemina* group.

Methods and materials

Adult fishes (excluding materials borrowed from the Natural History Museum, London) were collected by SCUBA divers, who chased them into a monofilament net (7m x 1m; 1.5 cm mesh). Necessary permits for the collection of fishes were acquired from the governments of Malaŵi, Mozambique, and Tanzania. Fishes were collected and processed under the approval of the Animal Use and Care Committee at Pennsylvania State University (IACUC #24269). Fishes were anesthetized with clove oil and euthanized in 4% formalin, pinned in trays so that their bodies were flat and all fins extended, preserved in 10% formalin, and placed in 70% ethanol for permanent storage in the Pennsylvania State University Fish Museum (PSU). Color notes and pigmentation patterns were recorded in the field at the time of capture for both territorial and non-territorial males, females, and juveniles. If the color patterns were variable in individuals examined, such variation was 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 including feeding angles and habitat were also recorded *in situ*.

A total of 496 specimens in 31 collections belonging to the *M. zebra* complex was examined as part of this study. The selected collections are distributed throughout the lake (Fig. 1). Twenty-four measurements and 14 counts follow Barel *et al.* (1977) and Konings & Stauffer (2006). When possible, 20 individuals were measured per collection. All counts and measurements were made on the left side of the fish except for gill-raker counts, which were performed on the right side.

Morphological data were analyzed using principal component analysis (PCA) and sheared principal component analysis (SPCA) (Humphries *et al.* 1981; Stauffer *et al.* 1997). Meristic data were analyzed using PCA with the correlation matrix factored. Differences in body shape were analyzed using SPCA with the covariance matrix factored (Humphries *et al.* 1981; Bookstein *et al.* 1985). 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 components plots. The minimum polygon clusters that showed the most separation were used. A MANOVA ($P<0.05$) was used to determine if two minimum polygon clusters were significantly different along one or both axes. If more than two groups were included in the analysis and the mean multivariate scores of the clusters were significantly different along one axis, a Duncan's multiple range test ($P<0.05$) was used to determine which clusters differed from each other on that axis.

Results

Metriaclima zebra (Boulenger)

Figs. 2A & B

Holotype. BMNH 1891.12.17.7, holotype, male, 83.7 mm SL, Malawi: "Lake Nyassa", M.E. Woodward, 1891.

Other material. PSU 10632, 10, 70.3–86.0 mm SL, Malawi, Likoma Island, Madimba, 12° 3.708' S, 34° 44.746' E, Konings & Stauffer Jr., 11 Jan 2008. PSU 10633, 10, 73.0–92.1 mm SL, Malawi, Likoma Island, White Rock, 12° 4.133' S, 34° 44.559'E, Konings & Stauffer Jr., 11 Jan 2008. PSU 10681, 5, 70.8–80.4 mm SL, Malawi, Likoma Island, Membe Point, 12° 03.514' S, 34° 45.148' E, Konings, Stauffer Jr. & Kocher, 3 Feb 2005. PSU 10680, 3, 68.9–75.5 mm SL, Malawi, Likoma Island, Maingano Island, 12° 02.621' S, 34° 45.366' E.

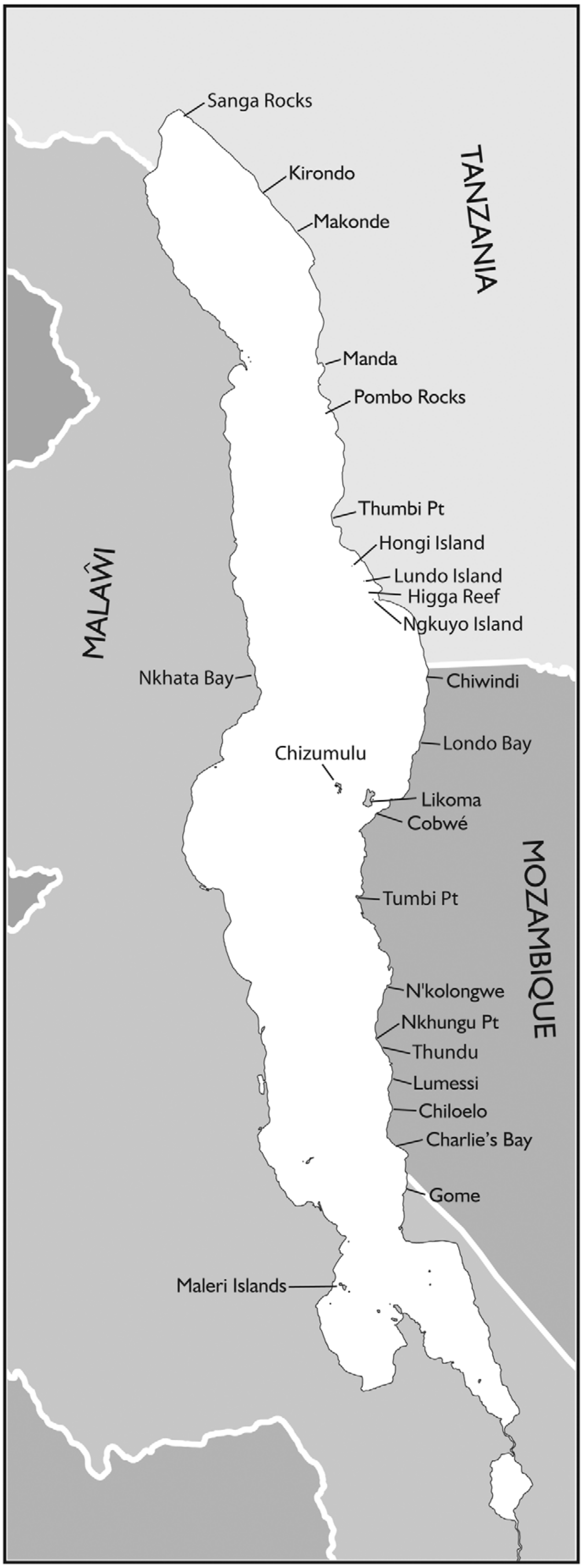

FIGURE 1. Map of Lake Malaŵi with localities mentioned in the text.

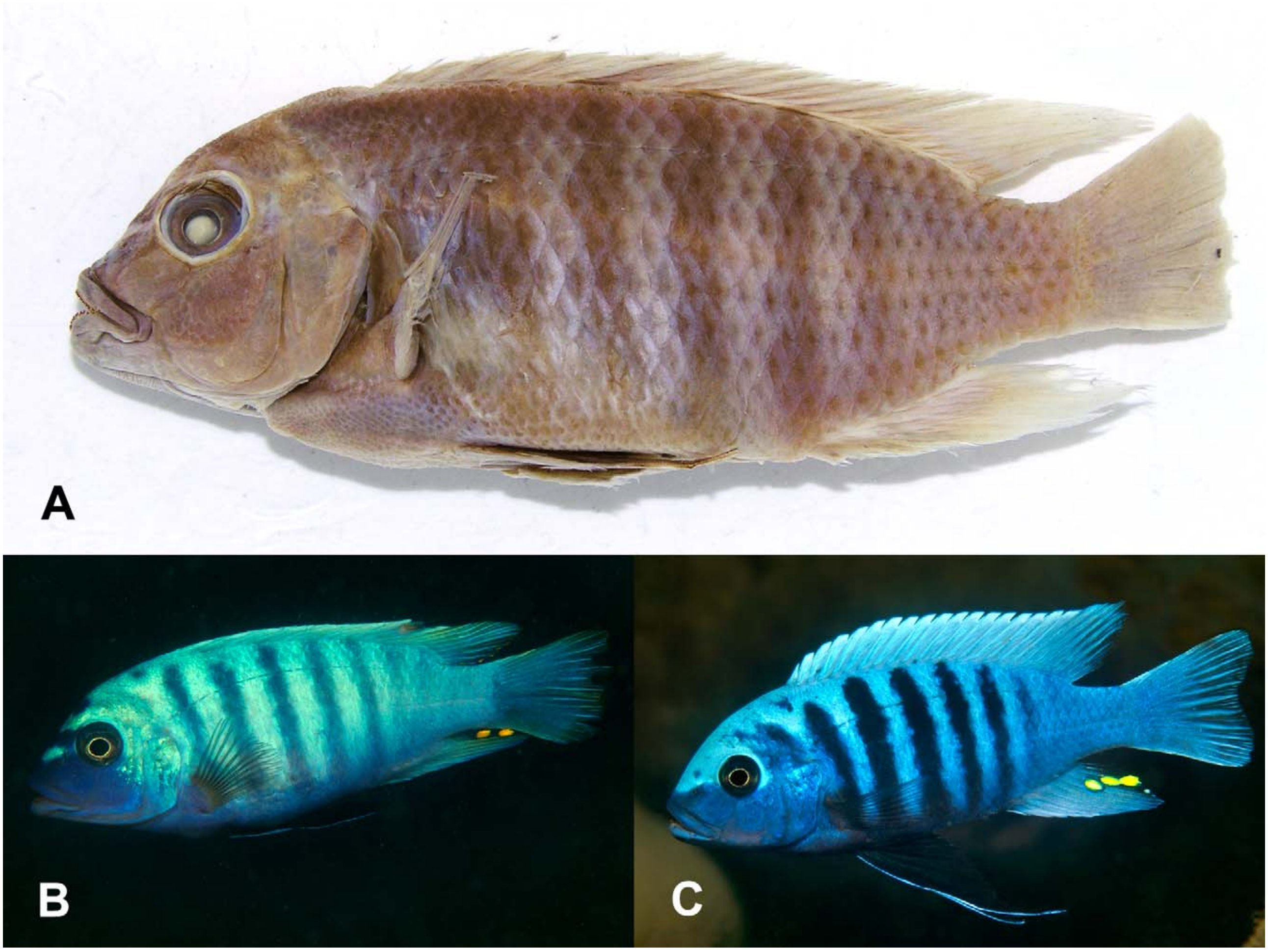

FIGURE 2. A. *Metriaclima zebra*, holotype, BMNH 1891.12.17.7, 83.7 mm SL, Malawi: "Lake Nyassa"; B. *M. zebra*, male in breeding coloration (approx. 85 mm SL) at Madimba, Likoma Island, Malawi; C. *M. zebra*, male (approx. 70 mm SL) Makonde, Tanzania.

TABLE 1. Morphometric and meristic data for *Metriaclima zebra*; holotype, our collections from Likoma Island (Madimba (n=10), White Rock (n=10), Membe Point (n=5), and Maingano Island (n=3). Ranges include the holotype. An asterisk indicates a character not determined in that particular series.

	Holotype	Mean	Madimba range	White Rock range	Maingano Range	Membe Point range
Standard length, mm	83.7	78.8	70.3–86.0	73.0–92.1	68.9–75.5	70.8–80.4
Head length, mm	26.8	25.4	21.8–27.1	23.8–30.0	21.8–23.8	21.0–25.0
Percent standard length						
Head length	32.1	32.2	30.5–33.1	31.1–34.7	31.5–32.6	29.7–31.4
Body depth	38.5	37.3	35.5–38.8	36.7–40.8	36.5–38.7	35.1–37.6
Snout to dorsal	33.1	35.0	31.6–37.1	33.1–36.4	33.7–36.6	31.8–33.5
Snout to pelvic	45.2	38.8	37.8–41.7	40.3–43.4	38.9–42.2	38.7–41.7
Dorsal–fin base length	57.3	61.6	60.5–64.7	59.9–63.9	60.2–63.4	60.8–63.1
Anterior dorsal to anterior anal	51.2	52.3	53.1–57.6	53.6–58.3	53.5–54.6	53.8–56.4
Anterior dorsal to posterior anal	61.0	65.4	64.8–66.8	61.3–65.7	65.0–66.4	63.8–67.8
Posterior dorsal to anterior anal	31.2	32.2	30.3–34.3	30.2–33.7	32.1–32.7	31.7–32.3
Posterior dorsal to posterior anal	17.5	17.4	15.4–17.3	15.0–17.2	16.4–17.0	14.6–16.5

......*continued on the next page*

TABLE 1. (Continued)

	Holotype	Mean	Madimba range	White Rock range	Maingano Range	Membe Point range
Posterior dorsal to ventral caudal	20.1	19.7	16.6–19.2	17.4–19.8	18.2–19.7	16.3–19.4
Posterior anal to dorsal caudal	22.4	21.6	17.9–20.6	18.4–21.6	18.5–19.9	18.6–21.5
Anterior dorsal to pelvic-fin origin	38.4	37.6	36.2–42.4	38.0–42.0	38.5–41.0	37.7–40.6
Posterior dorsal to pelvic-fin origin	57.6	58.1	57.1–62.6	56.5–63.4	55.0–59.1	57.3–59.9
Caudal-peduncle length	15.0	13.9	12.6–15.1	12.5–15.6	14.3–16.6	13.4–15.0
Least caudal-peduncle depth	13.4	13.7	11.5–13.2	11.9–13.6	13.2–13.9	11.8–13.5
Pectoral-fin length	23.3	23.7	35.0–39.0	37.0–41.0	*	*
Pelvic-fin length	41.9	31.1	32.0–37.0	33.0–36.0	*	*
Percent head length						
Snout length	39.7	35.8	29.5–36.9	31.5–37.7	30.2–35.1	33.1–34.8
Postorbital head length	37.0	42.1	36.9–42.5	35.6–40.6	37.1–42.1	37.1–41.1
Horizontal eye diameter	28.7	27.3	27.3–32.6	28.6–32.5	30.6–31.9	29.4–31.9
Vertical eye diameter	28.2	26.8	28.6–33.8	28.4–34.4	32.0–34.0	30.3–34.2
Head depth	96.7	93.6	90.4–105.1	98.4–112.6	96.9–106.3	92.1–99.1
Preorbital depth	21.2	22.5	19.8–24.4	20.4–24.4	21.8–22.8	21.1–23.8
Cheek depth	22.7	25.0	24.2–31.7	23.2–35.0	27.6–29.3	27.0–31.8
Lower-jaw length	36.3	35.4	38.2–51.7	33.7–44.6	36.4–39.2	32.8–37.5
Meristics	**Holotype**	**Mode**	**Madimba**	**White Rock**	**Maingano**	**Membe Point**
Dorsal-fin spines	17	17	17–18	17–18	17–18	17–18
Dorsal-fin rays	10	9	8–10	8–9	8–9	8–9
Anal-fin spines	3	3	3	3	3–4	3
Anal-fin rays	8	7	7–8	7–8	7–8	8–9
Pectoral-fin rays	14	14	12–13	12–13	13	12–14
Pelvic-fin rays	5	5	5	5	5	5
Lateral-line scales	32	32	31–34	30–32	31–32	31–33
Pored scales post lateral line	2	2	0–1	0–1	2	2–3
Cheek-scale rows	4	4	4–5	4–5	4	4–5
Gillrakers 1st ceratobranchial	12	11	11–13	10–13	10–12	11–12
Gillrakers 1st epibranchial	3	3	2–3	2–3	3	3
Teeth in outer series of left lower jaw	9	9–10	9–11	9–11	10–12	10–12
Tooth rows in upper jaw	5	4	3–4	3–4	4	3
Tooth rows in lower jaw	4	4	3–4	3–4	4	3–4

A morphological description of *M. zebra* has been given by Konings & Stauffer (2006). A multivariate analysis of morphometric and meristic data of the holotype and four populations of *M. zebra* from Likoma Island (Table 1; Fig. 3) shows that the holotype is morphologically indistinguishable from the population at Madimba. Although, morphologically, the holotype was also congruent with *M. zebra* from nearby Chizumulu Island (data not shown), it is improbable that the holotype was collected there. *M. zebra* from Chizumulu Island either have a blue snout without black interorbital stripes (often referred to as “blaze”) or have an entirely light-colored body without lateral bars whereas the holotype has dark interorbital stripes on the snout and has distinct bars, similar to freshly collected *M. zebra* from Likoma Island.

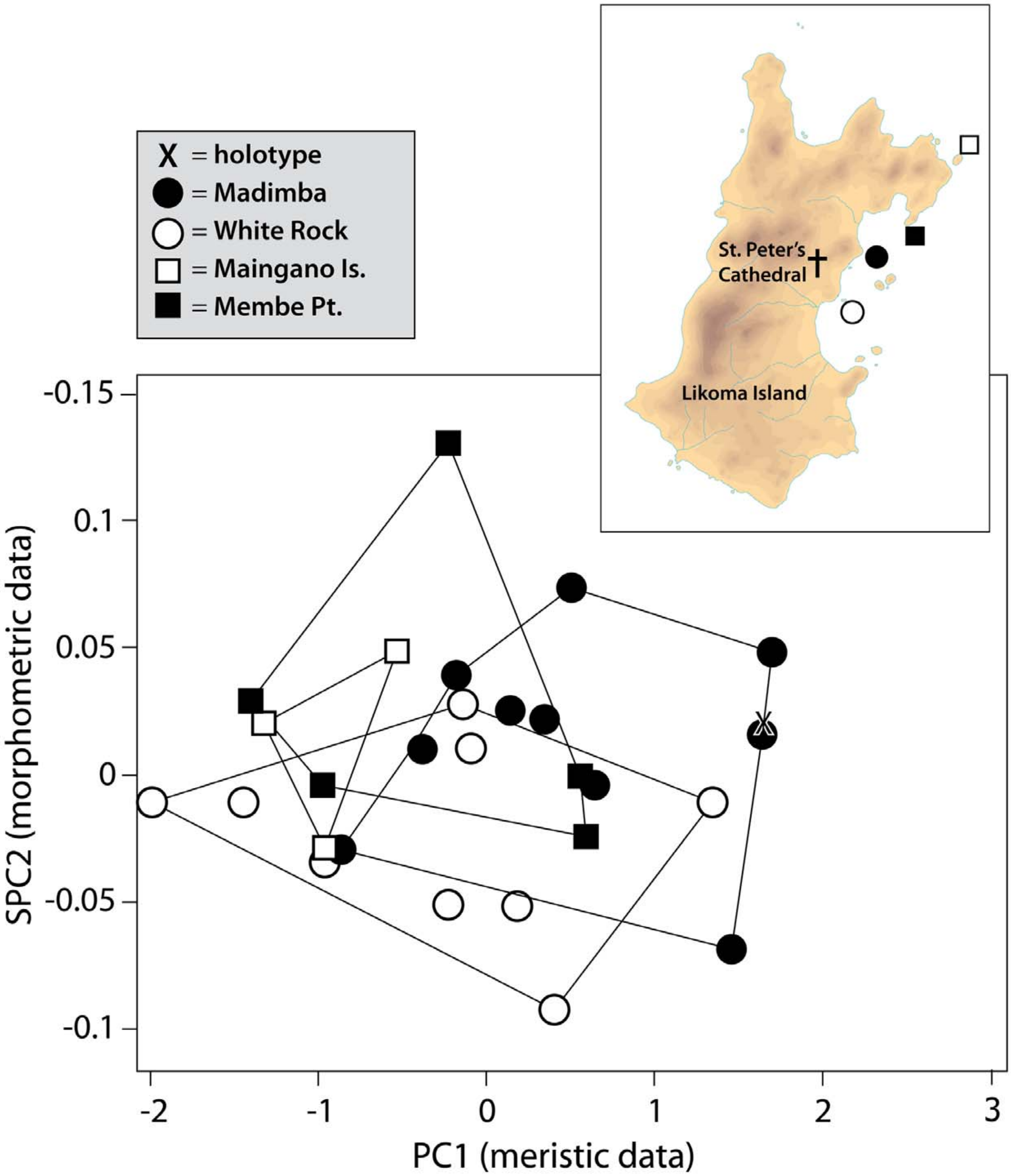

FIGURE 3. Plot of the first principal component of the meristic data (PC1) and the sheared second principal component of the morphometric data (PC2) of *M. zebra* holotype, and from four populations of *M. zebra* around Likoma Island. The cross indicates the position of the University Mission of Central Africa in 1891 when the holotype was collected by one of its missionaries.

Metriacl

***Metriaclima pambazuko*, new species**
Fig. 4A–C

Metriaclima sp. 'red top londo' Konings 2007

Holotype. PSU 4900, adult male, 61.3 mm SL, 11° 49.552' E 34°56.292', Londo Bay, Lake Malaŵi, Mozambique, Africa, Konings & Stauffer Jr., 23 Feb 2006.

Paratypes. PSU 4901, 19, (51.9–73.2 mm SL), same data as holotype; PSU 4902, 19, 59.3–75.9 mm SL, Hongi, Lake Malaŵi, Tanzania, Konings & Stauffer Jr., 28 Jan 2004; PSU 4903, 18, AMNH 257793, 2, 61.8–74.7 mm SL, Lundo Island, Lake Malaŵi, Tanzania, Konings & Stauffer Jr., 29 Jan 2004.

Diagnosis. The presence of bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws and a moderately-sloped (37° in one uncatalogued specimen) ethmo-vomerine block with a swollen rostral tip place this species in *Metriaclima*. The yellow/orange dorsal fin of males in combination with distinct black bars on a blue ground color and the absence of a yellow chin distinguish this species from all other members of the genus except for *M. emmiltos* and *M. pyrsonotos*. The lateral bars of male *M. pambazuko* infiltrate the proximal portion of the dorsal fin and can form a solid band in males of the Lundo population, while the lateral bars of most males of *M. emmiltos* and *M. pyrsonotos* stop at the base of the dorsal fin. In some individuals of the latter species narrow bar extensions are visible in the dorsal fin but none have been encountered with black membranes in the soft-rayed part of the dorsal, which is another character of the color pattern of *M. pambazuko*. Also the anal fin of male *M. pambazuko* is darker and often black, while that of most male *M. pyrsonotos* and *M. emmiltos* is light blue.

Female *M. pambazuko* have a light brown to beige ground color while those of *M. emmiltos* and *M. pyrsonotos* are dark brown to blue-brown. *M. pambazuko* has more teeth in the outer row of the left lower jaw than *M. emmiltos* and *M. pyrsonotos* (13–23 vs. 8–12 and 4–10 resp.) and differs further from *M. emmiltos* by a larger distance between snout and pelvic-fin origin (35.3–44.2 % vs. 22.8–32.8 % SL).

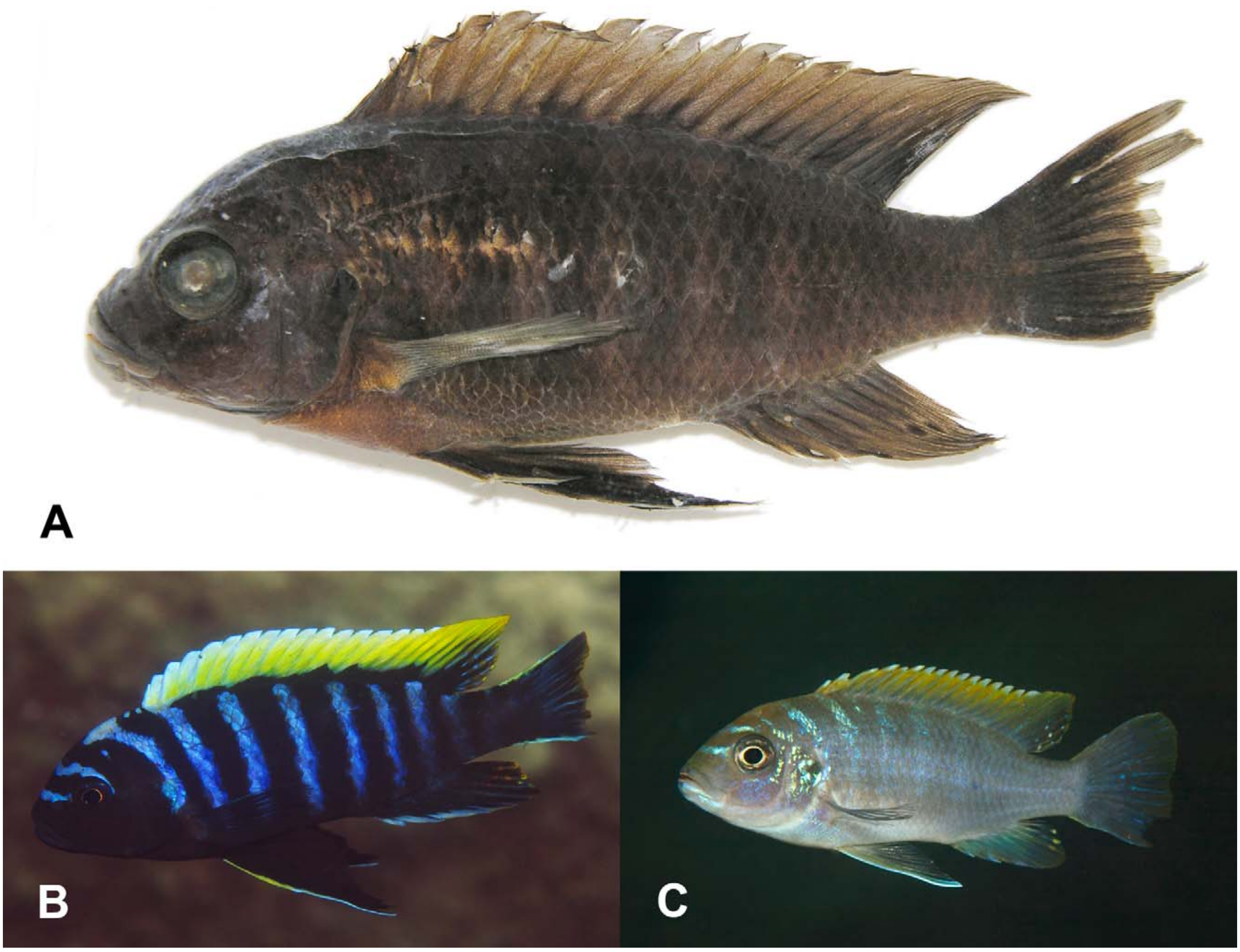

FIGURE 4. *Metriaclima pambazuko*. A. Holotype, PSU 4900, adult male, 61.3 mm SL, Mozambique: Londo Bay; B. Male in breeding coloration (approx. 70 mm SL) at Hongi Island, Tanzania; C. Female (approx. 55 mm SL) in Londo Bay, Mozambique.

TABLE 2. Morphometric and meristic data for *Metriaclima pambazuko* from Londo Bay, Mozambique (PSU 4900–4901); Lundo Island, Tanzania (PSU 4903); and Hongi, Tanzania (PSU 4902). Ranges include the holotype.

Metriaclima pambazuko	Holotype	Mean	Londo Bay range	Hongi Island range	Lundo Island range
Standard length, mm	61.3	64.3	51.9–73.2	59.3–75.9	61.8–74.7
Head length, mm	19.5	20.4	16.8–23.2	18.6–24.0	19.6–23.8
Percent standard length					
Head length	31.8	31.7	31.7	31.3	31.8
Body depth	31.2	32.1	30.5–33.5	28.9–33.0	30.6–35.6
Snout to dorsal	33.3	33.3	31.5–35.7	32.2–35.1	30.4–36.2
Snout to pelvic	38.3	38.0	35.3–39.1	35.9–39.8	36.1–44.2
Dorsal-fin base length	59.4	60.2	58.8–62.7	58.3–62.6	56.8–63.7
Anterior dorsal to anterior anal	50.1	49.4	46.9–52.4	46.6–52.7	47.3–52.3
Anterior dorsal to posterior anal	62.3	62.7	61.8–64.7	61.2–65.3	59.4–66.6
Posterior dorsal to anterior anal	29.1	29.8	28.7–32.3	27.0–30.4	27.7–31.1
Posterior dorsal to posterior anal	15.9	16.2	15.4–17.3	14.9–17.0	15.0–17.9
Posterior dorsal to ventral caudal	18.4	18.3	17.4–19.6	16.5–19.0	16.8–20.9
Posterior anal to dorsal caudal	22.4	22.1	21.0–23.7	21.2–23.1	20.0–23.3
Anterior dorsal to pelvic-fin origin	36.3	35.6	33.6–37.9	32.1–37.2	32.4–38.6
Posterior dorsal to pelvic-fin origin	57.7	56.9	55.8–59.6	55.3–60.3	52.4–58.4
Caudal-peduncle length	14.6	15.0	14.2–17.4	13.0–16.3	12.8–17.2
Least caudal-peduncle depth	10.9	11.2	10.5–12.0	10.2–11.5	10.3–12.4
Percent head length					
Snout length	31.4	33.9	30.1–36.0	31.8–35.8	30.8–37.9
Postorbital head length	39.3	40.0	38.4–43.3	38.3–42.1	37.3–41.7
Horizontal eye diameter	37.0	36.7	35.3–40.8	33.0–39.9	31.2–37.9
Vertical eye diameter	35.4	35.9	35.0–41.3	32.4–38.3	32.1–37.8
Head depth	81.4	84.3	78.2–88.5	76.2–90.1	81.7–92.4
Preorbital depth	22.1	20.7	18.9–22.7	18.6–22.2	18.5–22.7
Cheek depth	24.3	25.3	22.5–30.8	22.3–26.4	22.8–29.3
Lower-jaw length	36.9	37.2	34.4–40.2	35.4–40.0	36.1–40.1
Meristics	**Holotype**	**Mode**	**Londo Bay**	**Hongi Island**	**Lundo Island**
Dorsal-fin spines	16	17	16–17	16–18	16–18
Dorsal-fin rays	10	9	8–10	8–10	8–10
Anal-fin spines	3	3	3	3	3
Anal-fin rays	8	8	7–8	7–8	7–8
Pectoral-fin rays	14	14	13–14	14–15	14–15
Pelvic-fin rays	5	5	5	5	5
Lateral-line scales	31	31	30–32	29–32	29–32
Pored scales post lateral line	1	1	0–1	0–1	0–1
Cheek-scale rows	4	4	4–6	3–5	3–5
Gillrakers 1st ceratobranchial	12	12	11–14	11–18	11–13
Gillrakers 1st epibranchial	3	3	2–3	2–4	2–4
Teeth in outer series of left lower jaw	20	17	16–22	17–23	12–22
Tooth rows in upper jaw	3	3	3	3–4	2–4
Tooth rows in lower jaw	3	3	3–4	3–4	2–3

Description. Morphometric and meristic data in Table 2. Moderate compact species (mean BD 32.1% SL) with greatest body depth at about base of fifth dorsal spine. Dorsal body profile with gradual curve to caudal peduncle; ventral body profile slightly convex with similar, mirrored curve upward to caudal fin. Dorsal head profile straight between snout tip and interorbital, making about 45° angle with body axis, then rounding to dorsal fin origin; eye (mean 36.7% HL) almost twice depth preorbital and positioned in anterior half of head with posterior orbit margin on or slightly posterior of vertical median of head. Snout short with isognathous jaws; teeth on lower jaw in 2–4 rows with outer row bicuspid (some lateral teeth unicuspid) and inner rows tricuspid.

Dorsal fin with XVI or XVIII (mode XVII) spines and 8–10 (mode 9) soft rays. Anal fin with III spines and 7 or 8 (mode 8) soft rays. First 3 or 4 dorsal-fin spines gradually increasing in length posteriorly with first spine about ½ length of fourth spine; last 14 spines slightly increasing in length posteriorly with last spine longest; soft dorsal fin with rounded or subacuminate tip, third or fourth ray longest, about to middle of caudal fin in males and to base of caudal fin in females. Anal-fin spines progressively increasing in length posteriorly; fourth or fifth ray longest, length to almost middle of caudal fin in some males, to about base of caudal in females, length slightly shorter than dorsal fin. Caudal fin subtruncate to emarginate. Pelvic fin not reaching anal fin in females; length in males to first anal-fin rays. Pectoral fin rounded, paddle-shaped, short, reaching vertical through base of 10^{th} or 11^{th} dorsal-fin spine.

Flank scales large, ctenoid; abrupt difference to small scales on breast and belly; cheek with 3–6 rows of small scales. Dorsal and anal fins scaleless; tiny scales over proximal ¾ of caudal fin.

Live breeding males with blue ground coloration and 5–7 distinct black bars. Caudal peduncle blue/black; breast dark blue/black; belly gray/black. Head black with two blue interorbital bars; opercular spot gray-green/black; throat black. Dorsal fin proximally blue/gray/black and distally yellow (Lundo Island population) to orange/red (Londo Bay population); lateral bars extended onto proximal dorsal fin; dorsal fin with light-blue/white lappets in spinous portion. Caudal fin gray/black with wide, orange distal margin; proximal half of caudal-fin membranes black, distal half blue/gray. Anal fin black with 3–5 orange/yellow ocelli in rayed portion, with light-blue/white narrow margin. Pectoral fin with black/gray rays and clear membranes. Pelvic fin with narrow blue, white, or yellow leading edge; remainder black.

Females with gray-blue or light-brown ground coloration and 4–6 gray bars; lateral scales brown with blue center. Caudal peduncle beige/brown; belly and breast white/gray. Head brown/gray; opercle with blue/green highlights; black opercular spot; throat gray. Dorsal fin proximally gray and distally orange/brown. Caudal-fin rays gray; membranes clear. Anal fin gray without ocelli or with very small yellow/orange spots. Pectoral fins with gray rays and clear membranes. Pelvic fins with first two membranes black/gray, remainder clear.

Distribution. *Metriaclima pambazuko* is known from Lundo and Hongi islands in Tanzania and from Londo Bay in Mozambique (Fig. 1).

Etymology. The name *pambazuko,* from Swahili, means dawn or sunrise to note the orange/red dorsal fin of males, alluding to the orange/red sky of daybreak.

Remarks. The coloration of *M. pambazuko* most closely resembles that of *Cynotilapia zebroides* (formerly known as *C. afra*, but this turned out to be a different species (see Tawil 2011)), but the presence of bicuspid teeth in the anterior portion of the outer row of both the upper and lower jaws distinguishes members of *Metriaclima* from those of *Cynotilapia*, a genus characterized by widely spaced, unicuspid teeth in the outer jaws. *Cynotilapia zebroides* and *M. pambazuko* are sympatric in Londo Bay, Mozambique, as well as at the two islands, Lundo and Hongi, in Tanzania.

Metriaclima lundoense new species

Fig. 5A–C

Pseudotropheus 'Black Dorsal Tanzania', Spreinat 1994
Pseudotropheus sp. 'black dorsal shauri', Konings 1995
Maylandia phaeos (non Stauffer *et al.*), Schraml 1998
Metriaclima sp. 'black dorsal cobalt', Konings 2001
Metriaclima sp. 'black dorsal lundo', Konings 2007

Holotype. PSU 4910, adult male, 81.5 mm SL, 11°13.438’ S, 34°44.076’ E, Lundo Island, Lake Malaŵi, Tanzania, Africa, A. F. Konings & J. R. Stauffer Jr. 28 Jan. 2004

Paratypes. PSU 4911, 17, AMNH 257794, 2 (63.2–83.4 mm), same data as holotype.

Diagnosis. The presence of bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws and a moderately sloped ethmo-vomerine block with a swollen rostral tip place this species in *Metriaclima*. The presence of a dark submarginal band in the dorsal fin in combination with distinct black lateral bars on a blue ground color in the male distinguish *M. lundoense* from all other member of the genus except from *M. phaeos* and *M. cyneusmarginatus* and some populations of *M. flavifemina, M. fainzilberi,* and *M. zebra*. Males of *M. phaeos, M. flavifemina, M. cyneusmarginatus*, and *M. zebra* that have a black band in the dorsal fin, all have lateral bars which extend onto the dorsal fin, a trait not found in *M. lundoense.* Male *M. lundoense* are distinguished from those of *M. fainzilberi* by a black band in the anal fin which is absent in the latter species. Female *M. lundoense* are distinguished from all other female *Metriaclima,* except from those of *M. nigrodorsalis,* by the presence of a black submarginal band in the dorsal fin. Female *M. lundoense* cannot reliably be differentiated from those of *M. nigrodorsalis*.

Description. Morphometric and meristic data in Table 3. Moderate elongate species (mean BD 30.1% SL) with greatest body depth at about base of eighth dorsal spine. Dorsal body profile with gradual curve to caudal peduncle with highest point at about eighth dorsal-fin spine; ventral body profile between pelvic and anal fin flat to slightly convex with upward curve to caudal fin. Dorsal head profile straight to slightly concave between snout tip and interorbital, making about 50–60° angle with body axis, then rounding to dorsal fin origin; eye (mean 36.2% HL) about one and a half times depth of preorbital. Snout in ¾ of anterior half of head with posterior orbit margin posterior of vertical median of head. Snout short with isognathous to slightly retrognathous jaws; teeth on lower jaw in 3 or 4 rows with outer row bicuspid (some lateral teeth unicuspid) and inner rows tricuspid.

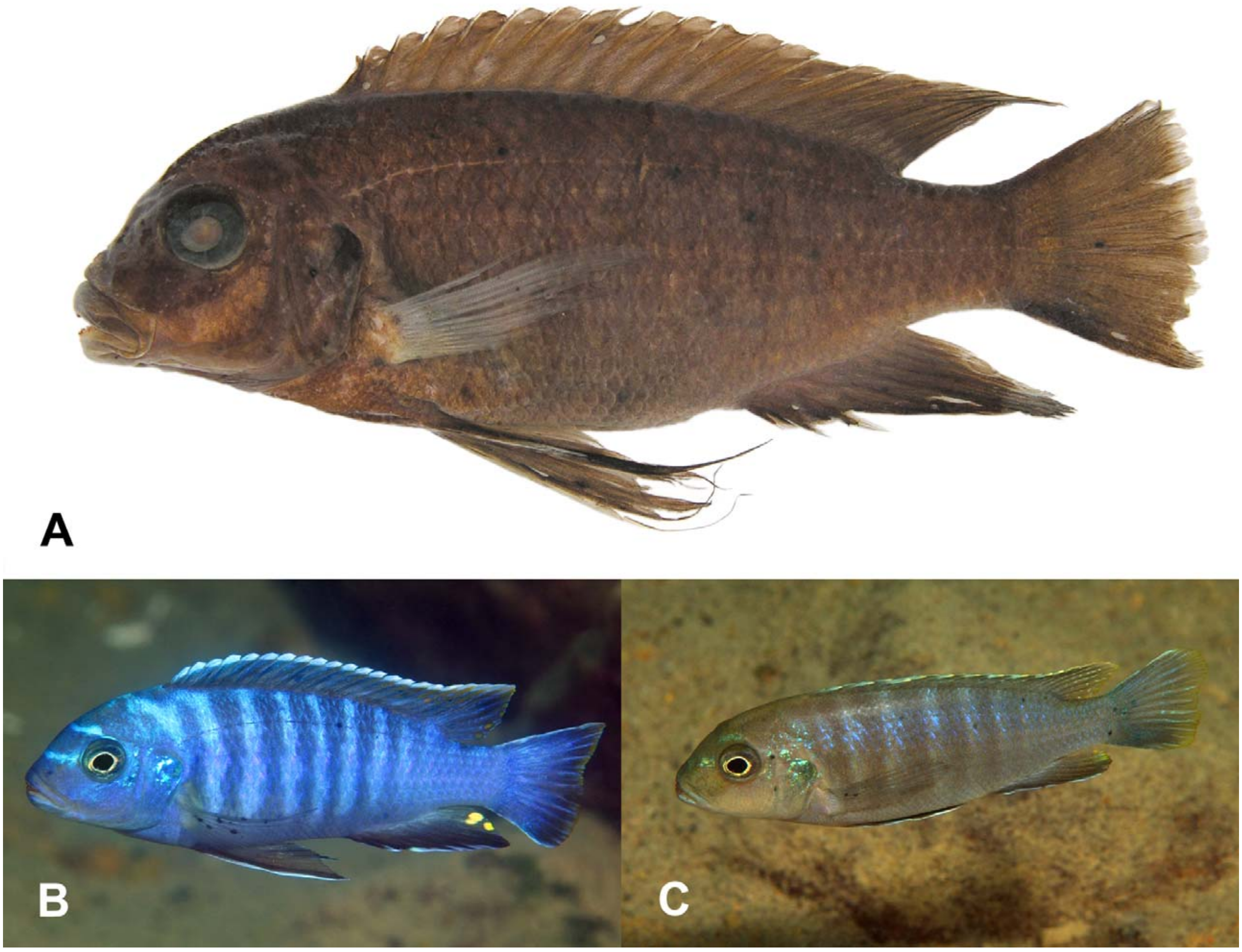

FIGURE 5. *Metriaclima lundoense*. A. Holotype, PSU 4910, adult male, 81.5 mm SL, Tanzania: Lundo Island; B. Male in breeding coloration (approx. 80 mm SL) at Lundo Island, Tanzania; C. Female (approx. 70 mm SL) at Lundo Island, Tanzania.

TABLE 3. Morphometric and meristic values for *Metriaclima lundoense* from Lundo Island, Tanzania (PSU 4910–4911). Ranges include the holotype.

Metriaclima lundoense	Holotype	Mean	Range
Standard length, mm	81.5	74.6	63.2–83.4
Head length, mm	25.6	23.6	19.5–25.6
Percent standard length			
Head length	31.8	31.7	30.5–32.9
Body depth	31.2	30.1	28.8–31.6
Snout to dorsal	34.8	33.8	32.4–35.9
Snout to pelvic	39.3	40.0	36.8–44.2
Dorsal-fin base length	59.8	59.7	57.2–62.2
Anterior dorsal to anterior anal	53.7	50.4	48.5–53.7
Anterior dorsal to posterior anal	63.8	62.3	59.6–65.3
Posterior dorsal to anterior anal	28.7	28.1	25.8–29.8
Posterior dorsal to posterior anal	15.5	15.0	13.8–16.6
Posterior dorsal to ventral caudal	18.4	17.8	16.6–18.5
Posterior anal to dorsal caudal	20.3	20.3	18.5–22.2
Anterior dorsal to pelvic-fin origin	35.5	34.6	32.6–37.6
Posterior dorsal to pelvic-fin origin	56.7	57.0	53.1–59.2
Caudal-peduncle length	13.2	13.4	12.2–15.1
Least caudal-peduncle depth	11.5	10.9	9.4–11.6
Percent head length			
Snout length	39.9	36.8	33.1–39.9
Postorbital head length	39.2	38.3	37.1–40.8
Horizontal eye diameter	35.1	36.2	34.2–40.4
Vertical eye diameter	33.8	35.7	33.2–38.3
Head depth	79.2	79.2	75.5–84.2
Preorbital depth	21.5	21.1	19.3–24.8
Cheek depth	24.6	24.4	20.0–28.1
Lower-jaw length	31.2	33.6	30.6–35.9
Meristics	**Holotype**	**Mode**	**Range**
Dorsal-fin spines	17	18	17–19
Dorsal-fin rays	9	9	8–10
Anal-fin spines	3	3	3–3
Anal-fin rays	8	8	8–9
Pectoral-fin rays	15	15	14–15
Pelvic-fin rays	5	5	5
Lateral-line scales	31	31	30–32
Pored scales post lateral line	0	1	0–1
Cheek-scale rows	4	5	4–6
Gillrakers 1st ceratobranchial	12	11	11–12
Gillrakers 1st epibranchial	2	3	2–4
Teeth in outer series of left lower jaw	14	14	12–20
Tooth rows in upper jaw	3	3	3–4
Tooth rows in lower jaw	3	3	3–4

Dorsal fin with XVII–XIX (mode XVIII) spines and 8–10 (mode 9) rays. Anal fin with III spines and 7 or 8 (mode 8) rays. First 3 or 4 dorsal spines gradually longer posteriorly with first spine about ½ length of fourth spine; last 14 spines slightly longer posteriorly with last spine longest; dorsal-fin rays with subacuminate tip, third or fourth ray longest, about to middle of caudal fin in males and to base of caudal fin in females. Anal-fin spines progressively longer posteriorly; fourth or fifth ray longest, length to almost middle caudal fin in some males, to about base of caudal in females. Caudal fin subtruncate to emarginate. Pelvic fin not to anal fin in females; length in males to third anal-fin spine. Pectoral fin rounded, paddle-shaped, short, to vertical through base of 11th or 12th dorsal spine.

Flank scales large, ctenoid; abrupt difference to small scales on breast and belly; cheek with 4–6 rows of small scales. Dorsal-fin and anal-fin rays with narrow proximal margin of tiny scales; tiny scales over proximal 75–90% of caudal fin.

Males with blue flank and 7–10 narrow, black bars; breast and belly blue; caudal peduncle blue. Head dark blue/purple with blue/green highlights; dark blue opercle spot; 2 light-blue interorbital bars; blue throat. Dorsal fin proximally blue with black submarginal band, sometimes over most of fin, white lappets, and with small yellow spots in rayed part. Caudal fin with light-blue/gray rays and orange tips; blue membranes. Anal fin black with narrow blue proximal margin and white lappets; 2 or 3 yellow ocelli. Pectoral fin clear. Pelvic fin with white/blue leading edge; anterior dark brown/black, posterior light brown/gray.

Females with light-brown ground coloration and blue and green highlights; occasionally with faint brown bars; belly and breast white/gray. Head light brown with green highlights; gray/black opercle spot; interorbital green/brown; throat white. Dorsal fin proximally light brown; narrow black submarginal band; white lappets with orange tips. Caudal and anal fins gray/brown. Pectoral fin clear. Anal and pelvic fins with first few membranes black and remainder clear; occasionally with white leading edge.

Distribution. *Metriaclima lundoense* is known only from Lundo Island, Lake Malaŵi, Tanzania (Fig. 1).

Etymology. The name refers to Lundo Island, the only known location for this species.

Metriaclima midomo, new species

Fig. 6A–C

Metriaclima cf. *zebra*, Konings 2007

Holotype. PSU 4912, adult male, 69.5 mm SL, 11°08.0827' S, 34°38.792' E, Lundo Island, Lake Malaŵi, Tanzania, Africa, A. F. Konings & J. R. Stauffer Jr., 28 Jan. 2004.

Paratypes. PSU 4913, 16, AMNH 257795, 2, (66.3–98.3 mm SL), same data as holotype.

Diagnosis. The presence of bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws and a moderately-sloped ethmo-vomerine block with a swollen rostral tip place this species in *Metriaclima*. The blue ground color with distinct black bars, absence of dark pigmentation on a light blue dorsal fin distinguishes *M. midomo* from all other members of the genus except for *M. xanstomachus*, *M. hajomaylandi*, *M. fainzilberi*, and *M. zebra*. The bright yellow throat of male *M. xanstomachus* and of some *M. fainzilberi*, and the orange/yellow head, throat, and chest of male *M. hajomaylandi* distinguish these species from *M. midomo*. *Metriaclima midomo* is distinguished from *M. fainzilberi* and *M. zebra* by the number of tooth rows in the lower jaw: 7–11 in *M. midomo* versus 3–5 in *M. zebra* and 3–6 in *M. fainzilberi*. The presence of bicuspid teeth on the outer rows of the oral jaws distinguishes *M. midomo* from members of *Petrotilapia* to which it has a striking resemblance.

Description. Morphometric and meristic data in Table 4. Fairly deep-bodied species (mean BD 35.4% SL) with greatest body depth at about base of 6th or 7th dorsal spine. Dorsal body profile with gradual taper to caudal peduncle with highest point at about sixth dorsal spine; ventral body profile between pelvic and anal fin slightly convex with upward curve to caudal fin. Head short and deep with dorsal head profile concave to almost straight between snout tip and interorbital, making about 50˚ angle with body axis; then round above orbit to dorsal-fin origin; eye (mean 34.6% HL) about one and a half times depth of preorbital and in about ¾ in anterior half of head with posterior orbit margin posterior of vertical median of head. Snout short with large isognathous to slightly prognathous jaws with teeth exposed reminiscent of species of *Petrotilapia*; teeth on lower jaw in 7–11 rows with outer row bicuspid and inner rows tricuspid.

TABLE 4. Morphometric and meristic values for *Metriaclima midomo* from Lundo Island, Tanzania (PSU 4912–4913; n=19). Ranges include the holotype.

Variable	Holotype	Mean	Range
Standard length, mm	69.5	77.4	66.3–98.3
Head length, mm	22.6	24.8	21.9–32.0
Percent standard length			
Head length	32.5	31.2	29.8–32.0
Body depth	36.3	35.4	34.0–37.7
Snout to dorsal	34.2	34.0	31.8–36.3
Snout to pelvic	39.1	40.3	37.3–41.9
Dorsal-fin base length	61.9	61.1	57.7–64.4
Anterior dorsal to anterior anal	52.0	52.5	49.8–55.6
Anterior dorsal to posterior anal	64.8	63.6	60.3–66.4
Posterior dorsal to anterior anal	29.2	29.2	27.0–30.7
Posterior dorsal to posterior anal	15.8	15.9	15.2–16.8
Posterior dorsal to ventral caudal	18.2	18.5	16.6–19.8
Posterior anal to dorsal caudal	22.8	21.3	19.5–23.5
Anterior dorsal to pelvic-fin origin	39.3	39.0	36.0–42.7
Posterior dorsal to pelvic-fin origin	59.0	57.8	54.7–60.4
Caudal-peduncle length	13.6	14.1	11.2–16.8
Least caudal-peduncle depth	11.5	11.1	10.0–12.2
Percent head length			
Snout length	34.9	38.0	34.9–41.3
Postorbital head length	40.1	38.9	35.6–40.3
Horizontal eye diameter	34.4	34.6	32.1–36.4
Vertical eye diameter	36.3	35.0	33.8–36.6
Head depth	88.1	90.6	86.9–96.0
Preorbital depth	22.7	23.4	20.7–26.0
Cheek depth	29.8	29.6	27.5–34.3
Lower-jaw length	33.8	36.9	33.7–39.5
Meristics	Holotype	Mode	Range
Dorsal-fin spines	17	17	17–18
Dorsal-fin rays	9	9	8–10
Anal-fin spines	3	3	3
Anal-fin rays	8	8	7–8
Pectoral-fin rays	15	15	14–15
Pelvic-fin rays	5	5	5
Lateral-line scales	31	31	29–32
Pored scales post lateral line	2	1	0–2
Cheek-scale rows	4	5	3–6
Gillrakers 1st ceratobranchial	12	11	10–12
Gillrakers 1st epibranchial	2	2	2–3
Teeth in outer series of left lower jaw	30	26	23–32
Tooth rows in upper jaw	8	7	6–8
Tooth rows in lower jaw	10	10	7–11

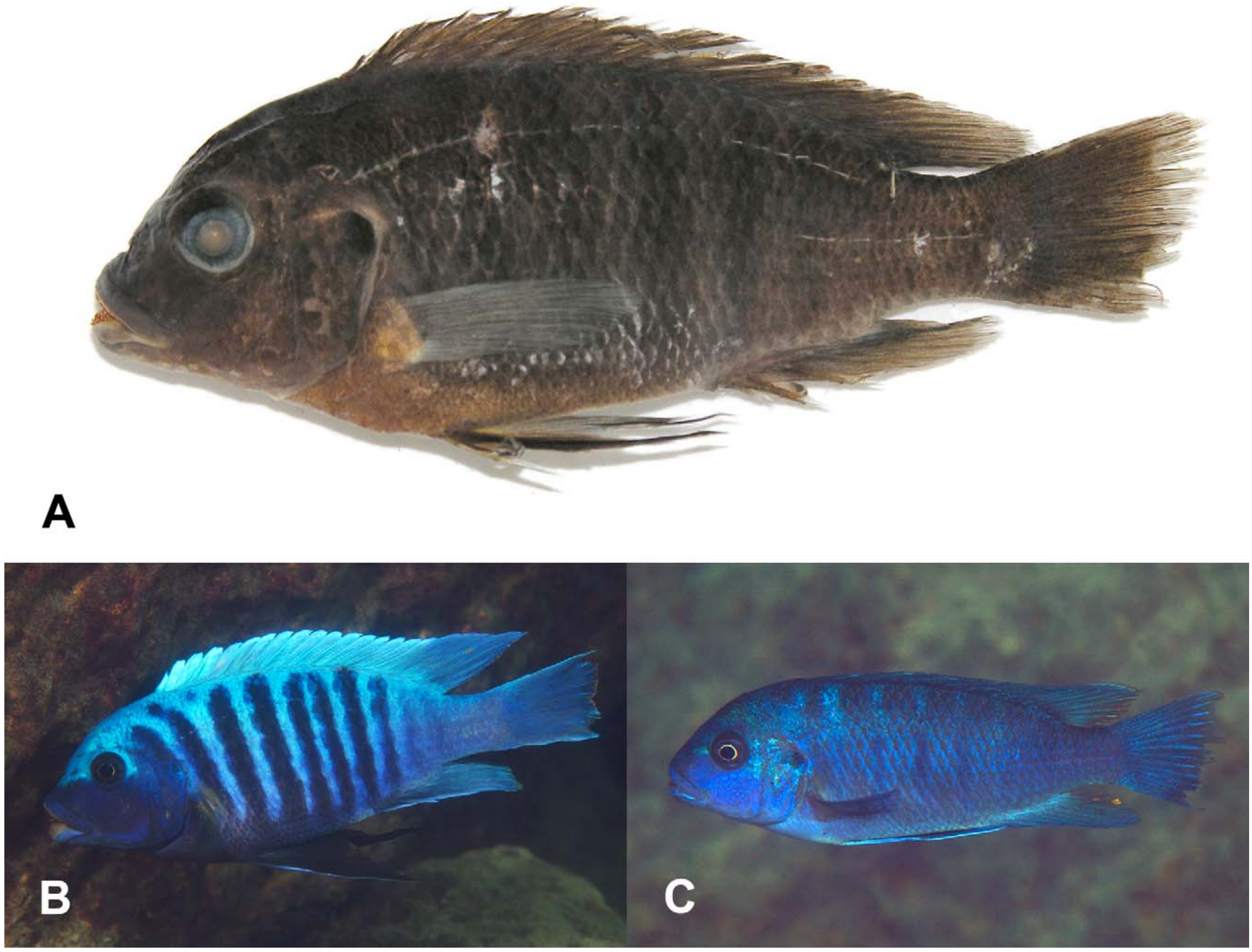

FIGURE 6. *Metriaclima midomo*. A. Holotype, PSU 4912, adult male, 69.5 mm SL, Tanzania: Lundo Island; B. Male in breeding coloration (approx. 80 mm SL) at Lundo Island, Tanzania; C. Female (approx. 70 mm SL) at Lundo Island, Tanzania.

Dorsal fin with XVII or XVIII (mode XVII) spines and 8–10 (mode 9) rays. Anal fin with III spines and 7 or 8 (mode 8) rays. First 2–4 dorsal spines gradually longer posteriorly with first spine about ½ length of fourth spine; last 13 spines slightly longer posteriorly with last spine longest; rayed portion of dorsal fin with subacuminate tip, third or fourth ray longest, about to ¼ to ½ of caudal fin. Anal spines progressively longer posteriorly; fourth or fifth ray longest, length to almost middle caudal fin in some males, to about ¼ caudal in females. Caudal fin subtruncate to emarginate. Pelvic fin to anal fin in females; length in males to first anal-fin rays. Pectoral fin rounded, paddle-shaped, short, to vertical through base of 11^{th} or 12^{th} dorsal spine.

Flank scales large, ctenoid; abrupt shift to small scales on breast and belly; cheek with 3–6 rows of small scales. Dorsal and anal fins scaleless; tiny scales over proximal ¾ of caudal fin.

Males with blue flank, green highlights, and 5–9 black lateral bars. Head with light blue opercle and green highlights; gray opercle spot; cheek, preorbital and preopercle dark blue/gray; throat blue; interorbital and occipital light blue with one dark-blue interorbital band. Dorsal fin light blue with orange spots on posterior margin. Caudal fin blue/dark-blue with narrow upper and lower margin light blue. Anal fin light blue/white with 0–5 yellow ocelli on posterior margin. Pectoral fin with gray rays and clear membranes. Pelvic fin black with blue/white leading edge.

Females blue ground coloration with green highlights and 5–7 faint bars; belly and breast blue/white; caudal peduncle blue/gray. Opercle, preopercle, and interorbital green with blue highlights; black opercular spot; cheek, and preorbital blue/gray; throat white. Dorsal, caudal, and anal fins gray; 0–2 ocelli on posterior margin anal fin. Pectoral fin with gray rays and clear membranes. Pelvic fin with first two membranes blue/gray; remainder clear.

Distribution. *Metriaclima midomo* is known from Lundo Island, Lake Malaŵi, Tanzania (Fig. 1). Lundo Island is inhabited by at least four other members of *Metriaclima – M. fainzilberi*, *M. pambazuko*, *M. lundoense*, and an undescribed species *M.* sp. ‘msobo heteropictus’. These can be distinguished by the male color pattern — male *M. fainzilberi* and *M. pambazuko* have a red/orange dorsal fin, while that of *M. midomo*, *M. lundoense* and *M.* sp. ‘msobo heteropictus’ is blue. The anal fin of *M. pambazuko* is black while that of male *M. fainzilberi* is blue. The dorsal fin of *M. lundoense* and of some male *M.* sp. ‘msobo heteropictus’ has a black submarginal band, which is lacking in *M. midomo*. The occipital region of *M.* sp. ‘msobo heteropictus’ is light blue and has two black interorbital bars while that of *M. midomo* lacks interorbital bars and that of *M. lundoense* is dark blue.

Etymology. The name *midomo*, from Swahili, means lips to note the enlarged lips.

***Metriaclima tarakiki*, new species**

Fig. 7A–C

Pseudotropheus 'Zebra Mbamba Bay Kompakt', Spreinat 1994
Metriaclima sp. 'zebra slim', Konings 2001

Holotype. PSU 4914, adult male, 115.2 mm SL, 11°18.380’ S, 34°44.791’ E, Higga Reef, Lake Malaŵi, Tanzania, Africa, A. F. Konings & J. R. Stauffer Jr., 13 Feb. 2005.

Paratypes. PSU 4915, 11, 72.2–119.3 mm SL, same data as holotype; PSU 4916, 18, AMNH 257796, 2, (75.9–96.8 mm SL), Ngkuyo Island, Lake Malaŵi, Tanzania, A. F. Konings & J. R. Stauffer Jr., 29 Jan. 2004.

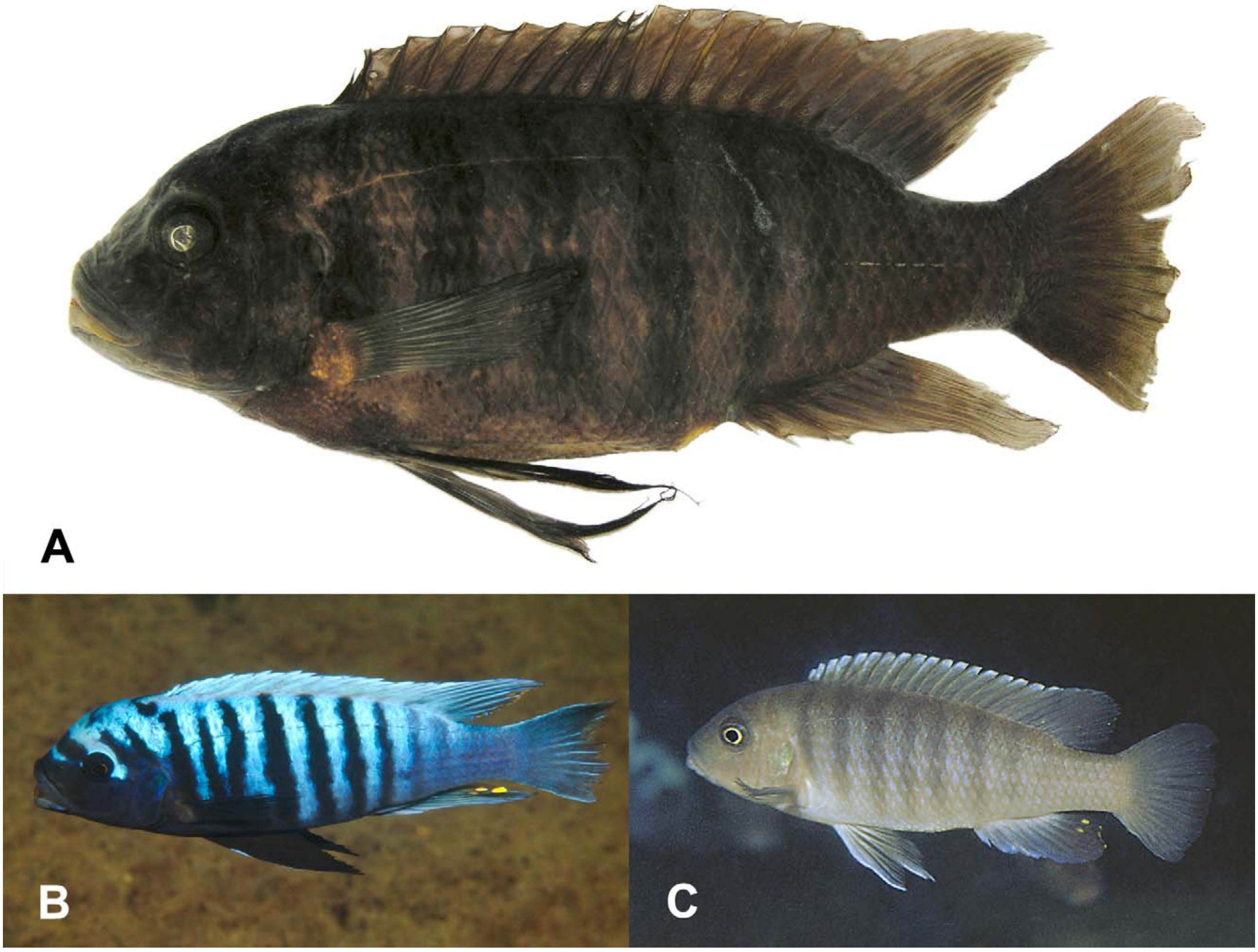

FIGURE 7. *Metriaclima tarakiki*. A. Holotype, PSU 4914, adult male, 115.2 mm SL, Tanzania: Higga Reef; B. Male in breeding coloration (approx. 110 mm SL) at Higga Reef, Tanzania; C. Female (approx. 90 mm SL) at Higga Reef, Tanzania.

TABLE 5. Morphometric and meristic values for *Metriaclima tarakiki* from Higga Reef, Tanzania (PSU 4914, holotype; PSU 4915, n=11) and Ngkuyo, Tanzania (PSU 4916, n=20). Ranges include the holotype.

Metriaclima tarakiki	Holotype	Mean	Higga Reef Range	Ngkuyo Island Range
Standard length, mm	115.2	90.0	72.2–119.3	75.9–96.8
Head length, mm	34.0	26.6	21.9–35.8	21.7–28.1
Percent standard length				
Head length	33.9	33.8	33.8	34.0
Body depth	32.9	28.8	28.2–32.9	25.8–29.1
Snout to dorsal	31.3	30.9	28.5–32.7	29.4–33.0
Snout to pelvic	36.4	36.5	35.3–39.3	34.7–39.0
Dorsal-fin base length	61.7	59.9	59.4–61.8	56.7–62.4
Anterior dorsal to anterior anal	51.9	48.4	47.6–51.9	45.8–50.0
Anterior dorsal to posterior anal	63.5	61.6	60.9–63.9	59.5–63.7
Posterior dorsal to anterior anal	30.4	27.7	26.6–30.8	25.3–29.0
Posterior dorsal to posterior anal	17.0	15.3	15.4–17.0	13.2–15.5
Posterior dorsal to ventral caudal	20.2	18.8	18.5–20.2	16.4–20.5
Posterior anal to dorsal caudal	22.8	21.6	20.6–22.8	20.3–22.6
Anterior dorsal to pelvic-fin origin	35.6	31.7	31.9–36.0	28.1–33.1
Posterior dorsal to pelvic-fin origin	61.9	58.5	56.9–62.0	56.0–59.5
Caudal-peduncle length	15.0	15.4	13.7–15.5	14.7–17.5
Least caudal-peduncle depth	12.3	10.8	10.7–12.3	9.7–11.5
Percent head length				
Snout length	39.8	37.5	37.1–42.2	32.9–39.9
Postorbital head length	39.1	38.7	37.7–40.6	36.0–40.8
Horizontal eye diameter	27.2	32.5	27.2–35.0	30.6–36.3
Vertical eye diameter	28.4	32.6	28.2–33.5	30.2–36.5
Head depth	90.6	81.9	77.4–96.4	73.3–85.1
Preorbital depth	23.5	22.5	20.5–25.1	20.8–23.2
Cheek depth	29.9	26.5	23.7–30.8	23.3–29.2
Lower-jaw length	35.2	37.1	35.0–39.7	34.8–38.9
Meristics	Holotype	Mode	Higga Reef	Ngkuyo Island
Dorsal-fin spines	18	18	18	17–19
Dorsal-fin rays	8	9	8–9	8–10
Anal-fin spines	3	3	3–4	3–3
Anal-fin rays	8	8	8	8–9
Pectoral-fin rays	15	14	14–15	14–15
Pelvic-fin rays	5	5	5	5
Lateral-line scales	31	32	31–32	32–33
Pored scales post lateral line	0	1	0–2	1–2
Cheek-scale rows	5	4	4–5	4–5
Gillrakers 1st ceratobranchial	11	11	11–12	10–12
Gillrakers 1st epibranchial	2	3	2–3	2–3
Teeth in outer series of left lower jaw	27	24–25	24–31	20–28
Tooth rows in upper jaw	6	6	5–7	4–8
Tooth rows in lower jaw	8	7	7–8	5–8

Diagnosis. The presence of bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws and a moderately sloped ethmo-vomerine block with a swollen rostral tip place this species in *Metriaclima*. Male *M. tarakiki* are distinguished from those of the other members of *Metriaclima* by the blue ground color with distinct black bars, the extension of the lateral bars onto the blue dorsal fin, the blue anal fin, and the absence of a dark submarginal band in the dorsal fin or yellow pigment on the body. While some males of *M. zebra* and *M. fainzilberi* exhibit extension of the lateral bars into the dorsal fin, these extensions fuse into a broad submarginal band, which is not observed in males of *M. tarakiki*. Male and female *M. tarakiki* are further distinguished from *M. zebra* by a shallower body as expressed in the distance between the dorsal fin origin and pelvic fin which ranges from 28.1–36.0% SL in *M. tarakiki* and from 34.2–40.7% SL in *M. zebra* populations from the Tanzanian shores and from Chiwindi in Mozambique. On average *M. tarakiki* has more tooth rows on the lower jaw (range 5–8) than *M. zebra* (range 3–5).

Description. Morphometric and meristic data in Table 5. Moderately elongate species (mean BD 28.8% SL) with greatest body depth at about base of 6th dorsal spine. Dorsal body profile with slight curve to caudal peduncle with highest point at about sixth dorsal spine; ventral body profile between pelvic and anal fin slightly convex with upward curve to caudal fin. Dorsal head profile straight to slightly concave between snout tip and interorbital, making about 45° angle with body axis, then round above orbit to dorsal-fin origin; eye (mean 32.5% HL) about one and a half times depth of preorbital and present for ¾ in anterior half of head with posterior orbit margin posterior of vertical median of head. Snout short with isognathous to slightly prognathous jaws; teeth on lower jaw in 5–8 rows with outer row bicuspid and inner rows tricuspid.

Dorsal fin with XVII–XIX (mode XVIII) spines and 8–10 (mode 9) rays. Anal fin with III spines and 8 or 9 (mode 8) rays. First 4 or 5 dorsal spines gradually increasing in length posteriorly with first spine about ½ length of fourth spine; last 13 spines slightly longer posteriorly with last spine longest; dorsal-fin rays with subacuminate tip in males, round in females, third or fourth ray longest, about to middle of caudal fin in males and to base of caudal fin in females. Anal spines longer posteriorly; fourth or fifth ray longest, length to about ¼ caudal fin in some males, to about base if caudal fin in females. Caudal fin subtruncate to emarginate. Pelvic fin not to anal pore in females; length in males about to anal fin. Pectoral fin rounded, paddle-shaped, short, to vertical through base of 9th or 10th dorsal-fin spine.

Flank scales large, ctenoid; abrupt difference to small scales on breast and belly; cheek with 4 or 5 rows of small scales. Dorsal-fin rays and anal fin with narrow proximal margin of tiny scales; tiny scales over proximal 90% of caudal fin.

Breeding males with blue/white flank and 7–9 black lateral bars; caudal peduncle blue/gray; belly gray; breast dark gray. Head blue/black with two blue interorbital bars; throat blue/gray; opercle with light blue and green highlights. Dorsal fin blue to white-blue with some lateral bars on proximal portion of dorsal fin; usually with white marginal band. Proximal 2/3 of caudal fin gray/blue and distal 1/3 dark gray. Anal fin blue/gray; posterior margin clear in some individuals; 2–8 yellow ocelli. Pectoral fin with gray rays and clear membranes. Pelvic fin black/dark gray with white leading edge.

Females light brown or orange blotch (OB). Non-OB females with brown flank; center of flank scales blue; belly and breast white/beige. Head light brown; blue/black opercular spot; light brown/white throat. Dorsal fin dark gray or brown with white/light-blue distal margin. Proximal ½ of caudal fin gray/ brown and distal ½ light brown to clear. Pectoral fin with gray rays and clear membranes. Pelvic fin with white leading edge, gray rays and clear membranes.

Orange blotch (OB) females with yellow-gray/orange flank with irregular black blotches; belly white with black blotches; breast yellow with black blotches. Head gray-yellow/orange with black blotches; throat white with black blotches; opercle with blue/green highlights. Dorsal, caudal, and anal fins gray-yellow with black blotches. Pectoral fins with yellow/black rays and clear membranes with black blotches.

Distribution. *Metriaclima tarakiki* is known from Ngkuyo Island and Higga Reef, Lake Malaŵi, Tanzania.

Etymology. The name *tarakiki*, from Swahili, means slim or slender to note the elongate body shape of this species.

Remarks. *Metriaclima tarakiki* exhibits polychromatism with OB females and males present in both known populations (see Konings 2001; Figure 14 for OB female at Higga Reef).

***Metriaclima nigrodorsalis*, new species**
Fig. 8A–E

Pseudotropheus sp. 'black dorsal chiloelo', Konings 1995
Pseudotropheus sp. 'black dorsal nkhungu', Konings 1995
Pseudotropheus sp. 'black dorsal nkolongwe', Konings 1995
Pseudotropheus sp. 'black dorsal thundu', Konings 1995

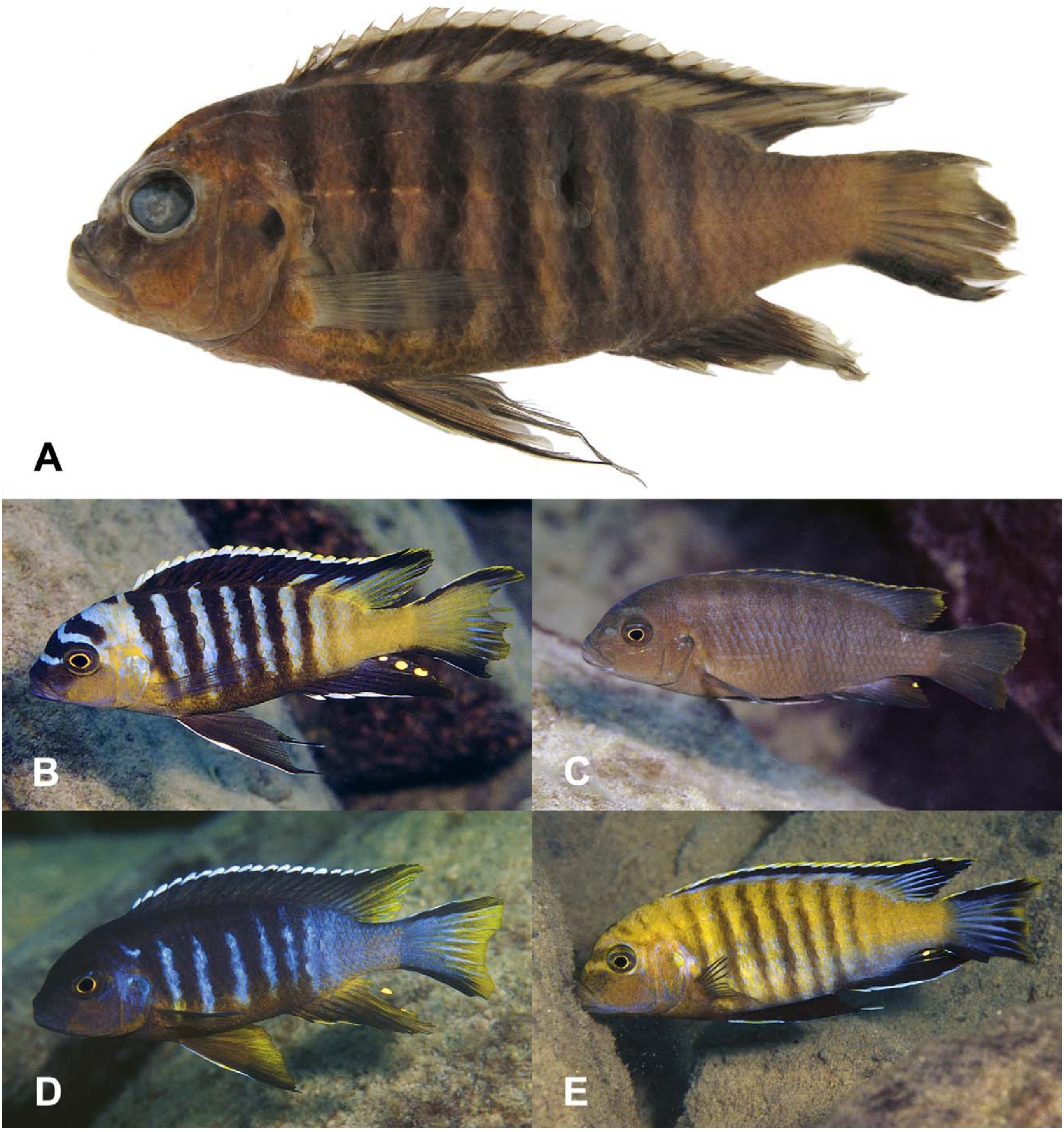

FIGURE 8. *Metriaclima nigrodorsalis*. A. Holotype, PSU 4904, adult male, 75.8 mm SL, Mozambique: N'kolongwe; B. Male in breeding coloration (approx. 75 mm SL) at N'kolongwe, Mozambique; C. Female (approx. 70 mm SL) at N'kolongwe; D. Male in breeding coloration (approx. 75 mm SL) at Chiloelo, Mozambique; E. Male in breeding coloration (approx. 80 mm SL) at Nkhungu Point, Mozambique.

Holotype. PSU 4904, adult male, 75.83 mm SL, 12 °47.671' S, 34°47.159' E, N'kolongwe, Lake Malaŵi, Mozambique, Africa, A. F. Konings & J. R. Stauffer Jr., 16 Feb. 2002.

Paratypes. PSU 4905, 17, AMNH 257797, 2 (66.5–78.7 mm SL), same collection data as for holotype; PSU 4906, 20, (63.8–81.6 mm SL), Charlie's Bay, Lake Malaŵi, Mozambique, A. F. Konings & J. R. Stauffer Jr., Feb. 2002; PSU 4907, 20, (65.4–83.3 mm SL), Nkhungu Point, Lake Malaŵi, Mozambique, A. F. Konings & J. R. Stauffer Jr., 15 Feb. 2002; PSU 4908, 20, (55.3–76.1 mm SL), Thundu, Lake Malaŵi, Mozambique, A. F. Konings & J. R. Stauffer Jr., 14 Feb. 2002; PSU 4909, 8, (60.8–71.7 mm SL), Chiloelo, Lake Malaŵi, Mozambique, A. F. Konings & J. R. Stauffer Jr., 1 Mar. 2006.

Diagnosis. The presence of bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws and a moderately sloped ethmo-vomerine block with a swollen rostral tip place this species in *Metriaclima*. The presence of a black submarginal band in the dorsal fin in combination with distinct black lateral bars on a blue and/or yellow flank and with yellow pigment on the cheek and breast distinguish males of this species from those of all other members of the genus except from those of the Maleri Island population of *M. flavifemina*. *Metriaclima nigrodorsalis* can be distinguished from *M. flavifemina* by a deeper cheek expressed as a percentage of body depth – range 25.3–32.0% BD in *M. nigrodorsalis* vs. 20.3–24.8% BD in *M. flavifemina* from Maleri Island. Female *M. nigrodorsalis* are distinguished from all other female *Metriaclima*, except from those of *M. lundoense*, by the presence of a black submarginal band in the dorsal fin. Female *M. nigrodorsalis* cannot reliably be distinguished from those of *M. lundoense*.

Description. Morphometric and meristic data in Table 6. Moderately compact species (mean BD 31.9% SL) with greatest body depth at about base of ninth 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 slightly convex between pelvic and anal fin then rounded to caudal fin. Dorsal head profile concave to straight between snout tip and interorbital, with about 55˚ angle with body axis, then round to dorsal-fin origin; eye (mean 36.8% HL) about 1½ times depth preorbital and in ¾ of anterior half head with posterior ¼ orbit posterior of vertical median head. Snout short with isognathous to slightly prognathous jaws; teeth on lower jaw in 3–5 rows with outer row bicuspid and inner rows tricuspid.

TABLE 6. Morphometric and meristic values for *Metriaclima nigrodorsalis* from N'kolongwe, Mozambique (PSU 4904, holotype; PSU 4905, n=18); Charlie's Bay, Mozambique (PSU 4906, n=20); Nkhungu, Mozambique (PSU 4907, n=20); Thundu, Mozambique (PSU 4908, n=20); and Chiloelo, Mozambique (PSU 4909, n=8). Ranges include the holotype.

Variable	Holotype	Mean	N'kolongwe	Charlie's Bay	Nkhungu	Thundu	Chiloelo
Standard length, mm	78.7	71.6	66.5–78.7	63.8–81.6	65.4–83.3	55.3–76.1	60.8–71.7
Head length, mm	24.0	22.0	20.1–25.2	19.8–25.0	19.6–25.2	17.7–23.3	19.0–22.9
Percent standard length							
Head length	32.8	32.5	30.8–33.7	30.5–33.5	32.1–34.2	31.2–34.6	30.3–32.1
Body depth	31.4	31.9	31.3–36.0	29.6–34.4	30.1–33.4	30.0–33.4	30.6–33.5
Snout to dorsal	33.2	33.4	32.5–35.5	30.0–34.2	31.5–35.5	32.5–35.2	32.2–35.3
Snout to pelvic	36.7	37.8	35.7–40.1	35.3–42.8	35.3–38.3	36.1–39.3	36.6–42.1
Dorsal-fin base length	60.7	61.6	59.0–64.7	58.4–65.6	60.2–64.8	57.9–63.9	57.9–64.4
Anterior dorsal to anterior anal	54.3	51.8	50.1–54.3	49.1–53.4	49.9–53.8	48.6–53.2	50.0–53.0
Anterior dorsal to posterior anal	65.7	64.4	61.7–68.8	61.4–66.6	63.0–66.7	61.3–66.3	60.8–65.7
Posterior dorsal to anterior anal	30.9	29.9	27.9–32.2	28.7–31.4	28.4–31.7	27.6–31.0	28.5–31.3
Posterior dorsal to posterior anal	15.6	16.4	15.6–17.7	15.7–17.3	15.2–17.9	15.1–17.3	15.1–16.8
Posterior dorsal to ventral caudal	18.8	18.4	17.4–19.4	17.2–20.6	16.3–19.6	17.4–19.2	18.0–20.0
Posterior anal to dorsal caudal	21.7	21.5	20.0–22.9	17.8–22.6	19.8–23.4	20.1–23.0	20.4–23.5
Anterior dorsal to pelvic-fin origin	34.8	36.4	34.8–39.6	35.1–37.9	34.7–37.9	34.6–38.4	34.9–38.0
Posterior dorsal to pelvic-fin origin	59.4	58.9	56.8–60.7	55.8–61.7	55.3–61.7	57.4–61.7	56.5–59.1

......*continued on the next page*

TABLE 6. (Continued)

Variable	Holotype	Mean	N'kolongwe	Charlie's Bay	Nkhungu	Thundu	Chiloelo
Caudal-peduncle length	13.9	14.4	13.2–15.2	13.2–15.3	13.1–16.3	13.2–16.1	12.3–16.9
Least caudal-peduncle depth	12.0	11.5	10.5–12.8	10.4–12.4	10.2–12.2	10.5–12.4	10.7–12.0
Percent head length							
Snout length	36.1	34.1	31.0–36.1	30.0–37.2	32.3–38.9	29.9–37.3	28.8–37.1
Postorbital head length	38.8	39.6	36.9–41.2	36.0–41.9	38.5–41.4	36.9–41.8	37.9–42.1
Horizontal eye diameter	34.9	36.7	34.9–40.3	34.8–38.1	33.9–37.0	34.6–39.3	34.5–39.2
Vertical eye diameter	35.5	36.6	35.5–40.1	34.0–37.7	34.0–36.9	35.3–39.5	35.4–39.2
Head depth	88.0	84.6	78.4–89.4	79.9–89.2	77.9–91.1	77.9–90.5	79.7–90.1
Preorbital depth	22.7	21.9	21.1–26.0	20.6–24.4	20.2–24.4	19.1–23.4	19.5–22.6
Cheek depth	28.7	27.7	26.0–32.9	25.3–33.7	25.4–31.8	23.4–28.6	24.4–29.2
Lower-jaw length	33.8	34.2	33.2–35.8	30.3–36.3	33.0–36.5	33.3–36.9	31.2–35.5
Meristics	**Holotype**	**Mode**	**N'kolongwe**	**Charlie's Bay**	**Nkhungu**	**Thundu**	**Chiloelo**
Dorsal-fin spines	18	18	17–19	17–19	17–19	17–19	18–19
Dorsal-fin rays	9	9	8–9	8–9	8–10	8–10	8–8
Anal-fin spines	3	3	3	3	3	3	3
Anal-fin rays	9	8	7–9	7–9	7–9	7–9	7–8
Pectoral-fin rays	15	14	14–15	14–15	14–15	13–15	14–15
Pelvic–fin rays	5	5	5	5	5	5	5
Lateral–line scales	31	31	30–32	30–32	31–32	30–32	30–31
Pored scales post lateral line	1	1	0–1	0–1	0–1	0–1	0–1
Cheek–scale rows	5	5	4–5	4–6	4–6	4–6	4–6
Gillrakers 1st ceratobranchial	12	11	11–13	11–12	10–12	10–13	11–12
Gillrakers 1st epibranchial	2	3	2–4	2–4	2–4	3–4	2–3
Teeth in outer series of left lower jaw	22	21	14–24	20–24	17–26	16–24	18–23
Tooth rows in upper jaw	4	4	3–4	3–5	3–4	3–5	3–4
Tooth rows in lower jaw	4	4	3–4	4–5	3–5	3–5	3–4

Dorsal fin with XVII–XIX (mode XVIII) spines and 8–10 (mode 9) rays. Anal fin with III spines and 7–9 (mode 8) rays. First 5 or 6 dorsal-fin spines gradually longer in length posteriorly with first spine about ½ length of fourth spine; last 12 dorsal-fin spines slightly increasing in length posteriorly with last spine longest; soft dorsal with subacuminate tip, third or fourth ray longest, reaching to about ¼ of caudal fin in males and to base caudal fin in females. Anal-fin spines progressively longer posteriorly; fourth or fifth ray longest, length to almost middle caudal fin in some males, to about base caudal in females. Caudal fin subtruncate to emarginate. Pelvic fin not to anal fin in females; length in males to first anal-fin rays. Pectoral fin rounded, paddle-shaped, to vertical through base of 12th or 13th dorsal spine.

Flank scales large, ctenoid; abrupt difference to small scales on breast and belly; cheek with 4–6 rows of small scales. Rayed portions dorsal and anal fins with few tiny scales in proximal margin; tiny scales over proximal ¾ of caudal fin.

Color notes —N'kolongwe population (Fig. 8B)**.** Males with light blue flank and 6–9 black bars; belly yellow; caudal peduncle yellow/brown. Interorbital light blue with 1 or 2 black interorbital bars; cheek and preopercle dark brown; dark blue gray opercle with black opercle spot. Dorsal fin proximally yellow/orange with extensions of lateral bars; black/gray submarginal band; white/light-blue lappets; posterior 5 rays orange/brown with light-blue membrane. Caudal fin yellow/brown with dorsal and ventral margin black. Anal fin black with 2 or 3 yellow ocelli in posterior margin. Pectoral fin with black rays and clear membranes. Pelvic fin black with white leading edge.

Females (Fig. 8C) with bluish brown flank and 6–9 dark brown lateral bars; center of lateral scales brown; caudal peduncle brown. Head brown with 1–2 faint blue interorbital bars; green/blue highlights on opercle; throat gray/brown. Dorsal fin brown with darker submarginal band; orange/yellow lappets. Caudal fin dark brown with blue spots on membranes; orange/yellow posterior margin. Anal fin dark brown/yellow, with no or just a single small yellow spot in posterior margin. Pectoral fin with gray rays and clear membranes. Pelvic fin with white leading edge, black rays, and clear membranes.

—Chiloelo and Charlie's Bay population (Fig. 8D). Breeding males with dark blue flank and 6–9 lateral bars; belly dark gray/yellow. Interorbital black/dark blue with blue interorbital bars sometimes present; cheek with blue and yellow markings; throat gray. Dorsal fin black with gray/yellow trailing part; white lappets. Caudal fin blue with wide yellow posterior margin and black dorsal and ventral margins. Anal fin black with yellow/gray posterior margin and 2–6 ocelli. Pectoral fin with black rays and clear membranes. Pelvic fin black with blue/white leading edge and yellow posterior margin.

Females with brown/beige flank and 7–9 gray lateral bars; brown/orange spot on anterior portion of scales. Head dark gray with 2 light gray/green interorbital bars; cheek light gray; lower jaw with blue highlights; branchiostegal membranes bluish gray; blue opercle spot. Dorsal fin brown/dark gray with white lappets and dark submarginal band sometimes present. Caudal fin gray with black ventral and dorsal margin. Anal fin gray fading to yellow with 1 or 2 small yellow spots in posterior margin. Pectoral fin with gray rays and clear membranes. Pelvic fin gray with white leading edge.

—Thundu population. Breeding males with light-blue flank and 6–9 gray/black lateral bars; caudal peduncle blue/gray; belly gray/yellow. Interorbital brown/orange with 1–2 light-blue interorbital bars; cheek brown with yellow highlights; throat brown/orange; dark green opercle spot. Dorsal fin light blue and yellow highlights with black submarginal band, white marginal band, and orange lappets. Caudal fin with black dorsal and ventral margins with light-blue/yellow edge, orange rays, and blue membranes. Anal fin light blue with wide black submarginal band, often over 90% of fin, and white/light-blue lappets, 1–6 orange/yellow ocelli in posterior margin. Pectoral fin with blue/gray rays and clear membranes. Pelvic fin black with white leading edge.

Females with light-brown ground color and 7–9 faint dark-brown bars; white belly. Head brown/beige with white/light brown throat; with occasional black opercle spot. Dorsal fin brown with light blue spots in membrane; white lappets with orange/yellow tips. Caudal fin light brown with orange/yellow posterior margin. Anal fin yellow/brown with 0–2 small yellow spots in posterior margin. Pectoral fin clear. Pelvic fin orange/yellow with white leading edge.

—Nkhungu population (Fig. 8E). Males with yellow flank and 7–10 black bars; center of many flank scales blue; belly yellow/gray-blue. Interorbital gray/yellow with 1 pale blue interorbital bar; opercle brown/yellow with dark orange opercle spot; throat orange. Dorsal fin blue with black submarginal band, a blue/green margin, and rust-orange lappets. Caudal fin with blue rays, black membranes, and orange distal margin. Anal fin black with 2–7 yellow ocelli in posterior margin and white/blue lappets. Pectoral fin with gray rays and clear membranes. Pelvic fin black with white leading edge.

Females light brown/beige; scales outlined in blue; white belly. Head brown with white throat. Dorsal fin light brown with orange/white lappets; light spots in membranes. Caudal fin with brown rays and clear membranes with distal yellow margin. Anal fin proximally white and distally yellow. Pectoral fin clear. Pelvic fin with clear rays and yellow membranes; white leading edge.

Distribution. *Metriaclima nigrodorsalis* is known from N'kolongwe, Thundu, Nkhungu, Chiloelo, and Charlie's Bay, Lake Malaŵi, Mozambique.

Etymology. The name *nigrodorsalis*, from Latin, means black dorsal, alluding to the black submarginal band in the dorsal of males and some females.

Discussion

Metriaclima zebra is arguably the most iconic cichlid from Lake Malaŵi even though it was described from a single type of unknown origin. Following the recent advances in recognizing a multitude of species and forms phenotypically similar to the holotype, it became of critical concern to identify the type population, and to verify that the holotype of *M. zebra* is indeed conspecific with the species we assumed it was. Two of the five populations we collected at Likoma Island are within one kilometer distance from the St. Peter's Cathedral, which was built on the site of the British Mission that was active in the late 19th century when the holotype of *M. zebra* was collected by one of the missionaries. *Metriaclima zebra* inhabits the rocky habitat solely and it is thus more probable that the holotype was caught on hook and line from a nearby rocky habitat than that it was brought in by seine fishermen. Our PCA analysis (Fig. 3) shows that the holotype falls within the population from Madimba, but increasingly differs from populations further away. The analyses of more than 20 different populations of *M. zebra* from all parts of the lake have shown that a relatively wide variation exists in shape and color pattern, so the finding by Stauffer *et al.* (1997) that the nine *M. zebra* populations from across the lake are morphologically different is not surprising. There was no noticeable difference in coloration among the five populations from Likoma Island but morphological differences became apparent for those collected further away from the St. Peter's Cathedral on the island.

Although we embrace the evolutionary species concept (Simpson 1951, Wiley 1978), we have used morphological traits and color patterns to delimit species. When we have been able to observe sympatric forms that assortiatively mate, we concluded that the populations had achieved independent evolutionary pathways and regarded them as distinct species. One of the new species, *Metriaclima tarakiki*, was found to exhibit a polymorphic color pattern, expressed as the so-called orange-blotch (OB) pattern (mainly in females but rarely also in males), but such individuals are not in the process of speciation as they do not mate assortatively. The OB pattern is linked to sex determination genes and is thought to give the individual a better camouflage coloration and thus an enhanced chance of survival (Ser *et al.* 2010). When allopatric populations of seemingly closely related taxa (occupying the same niche at a neighboring locality) exhibited differentiation in color pattern we initially marked these as putative different species and when we were able to demonstrate differences in morphometrics we have described these as separate species. In view of the repeated rising and falling of the lake level (e.g. Lyons *et al.* 2011) with concomitant intermingling of rock-dwelling species (falling level) and founding of new species (rising level) it is not unlikely to assume that the nearest relatives of a rock-dwelling mbuna are found in neighboring rocky habitats where like species occupy similar habitats, even when the species in question originated from a hybridization of two different species. The rock-dwelling mbuna of Lake Malawi are extremely stenotopic and have never been found in the open waters of the lake in which case they could found a new population/species at a far away locality. Those species or populations that inhabit areas along steep rocky shores just move up and down the shore along with the fluctuating water level and only give rise to new species when novel habitat is formed, discontinuous from that of the mother population. Koblmüller *et al.* (2011) found that populations of *Tropheus moorii* in Lake Tanganyika, which are analogous to the mbuna in Lake Malawi, along a steep rocky shore showed barely gene flow between populations less than 5 km apart for more than 100,000 years.

Our strategy in determining whether a population represents a different evolutionary lineage is to examine neighboring populations of similar species. In essence, we have used morphometric differences between neighboring populations to determine whether sufficient morphological differences existed that coincided with observed differences in color patterns in order to indicate heterospecificity. One of the morphs we expected to be different from *M. zebra* was referred to as "Blue Blaze Zebra" (Konings 2007) and is distinguished by its male color pattern. The males lack interorbital bars and appear to have a blue blaze on the head. This particular form appears to have a wide, but discontinuous distribution in the northeastern part of the lake and is known to inhabit Lundo Island, Londo Bay, the northern part of Chizumulu Island, and the mainland coast between Kirondo and Manda (Fig. 1). This form is not sympatric with *M. zebra*, either barred or non-barred. The morphometric and meristic data of this form from Makonde and Manda, Tanzania was compared with more typical *M. zebra* from neighboring populations, i.e. Pombo Rocks, Thumbi Point, and Sanga Rocks, Tanzania. A multivariate analysis of this comparison suggests that the "blue blaze" form is probably conspecific with *M. zebra* as no significant differences could be discerned. The plot of the first principal component of the meristic data versus the sheared second principal component of the morphometric data (Fig. 9) clearly illustrates that the two groups overlap. The morphometric data of these groups were not significantly different ($P>0.05$, MANOVA). This finding is supported by mate choice experiments by Knight and Turner (2004) that concluded that *M. zebra* from Nkhata Bay and the "blue blaze" form from Chizumulu Island did not exhibit any marked degree of assortative mating.

Males of another *M. zebra*-like form at Lumessi, Mozambique, exhibit a color pattern—including a distinctive yellow breast—that is reminiscent of male *M. fainzilberi* or *M. xanstomachus*. A morphological comparison of this population with more typical *M. zebra* from neighboring populations, Nkhungu, N'kolongwe, Tumbi Point (all three in Mozambique), and Gome (Malaŵi), suggests that also this form is likely conspecific with *M. zebra* (Fig. 10). There was major overlap in the minimum polygon clusters formed by plotting the first principal component of the meristic data against the second sheared principal component of the morphometric data. We failed to find any significant (P>0.05, MANOVA) differences in the minimum polygon clusters of these forms and we therefore regard the yellow-breasted form at Lumessi as conspecific with *M. zebra*.

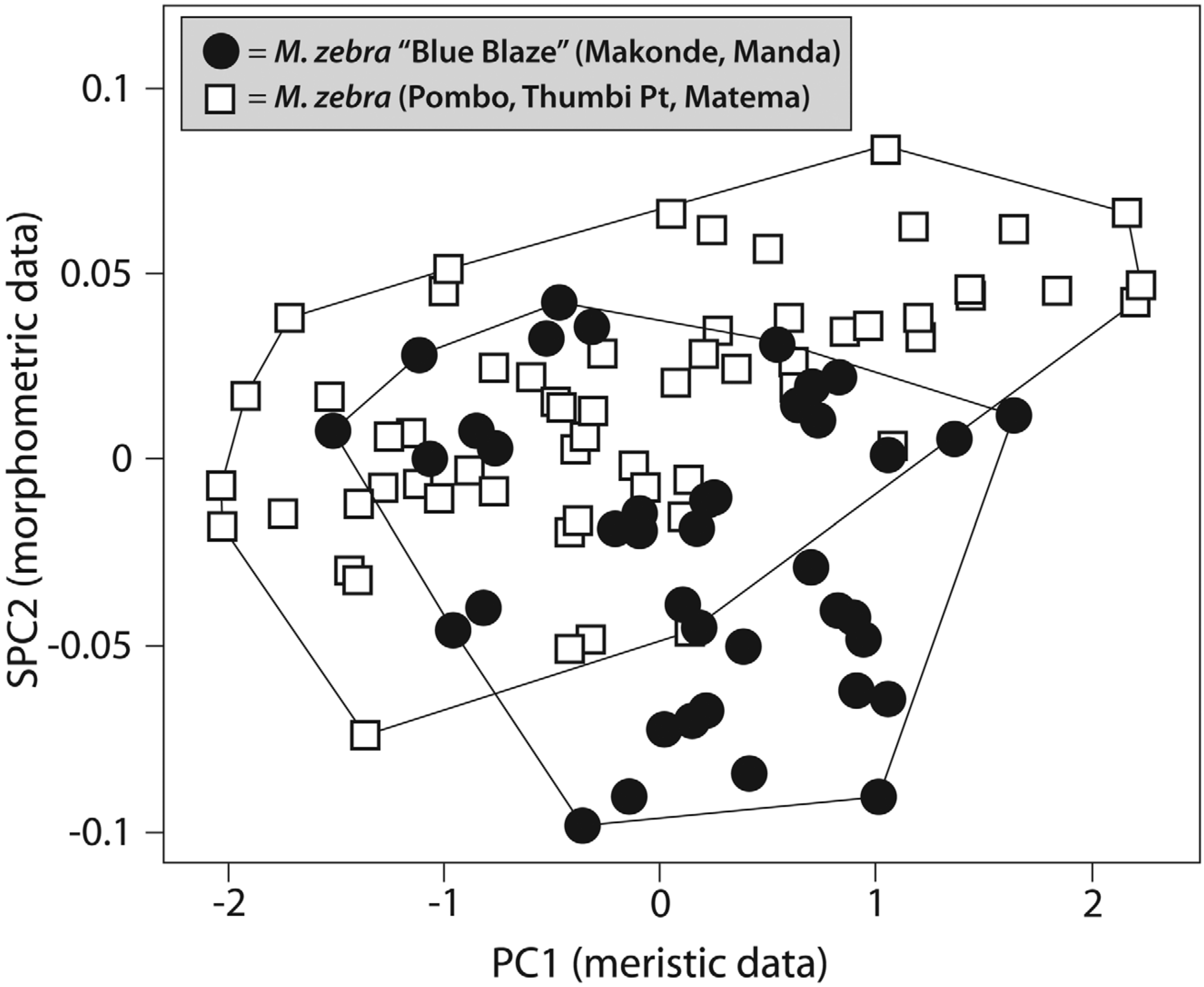

FIGURE 9. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Metriaclima zebra* "Blue Blaze" from Makonde (n=20) and from Manda (n=20), and of *Metriaclima zebra* with a classic color pattern from Pombo Rocks (n=20), Thumbi Point (n=20), and Matema (n=20); all localities in Tanzania.

Metriaclima pambazuko shares the red/orange dorsal fin (Londo Bay population) with *M. emmiltos* and *M. pyrsonotos*, but can be distinguished from these two species on other characters of the color pattern. The distribution of *M. pambazuko* is separated from the other two species by large distances and deep water, across which mbuna will not travel (*M. emmiltos* and *M. pyrsonotos* are from the western shores of Lake Malaŵi while *M. pambazuko* is found on the eastern shores). We therefore have no doubt regarding the heterospecificity of these species. In contrast, some populations of *M. fainzilberi* share a similar color pattern and *M. pambazuko* could also be regarded as a geographical variant of *M. zebra*. *M. fainzilberi*, however, occurs sympatrically with *M. pambazuko* throughout its range and in Londo Bay *M. pambazuko* is also sympatric with *M. zebra* while it is sympatric with *M. midomo* at Lundo Island. Intermediates between it and the other three *Metriaclima* have not been found.

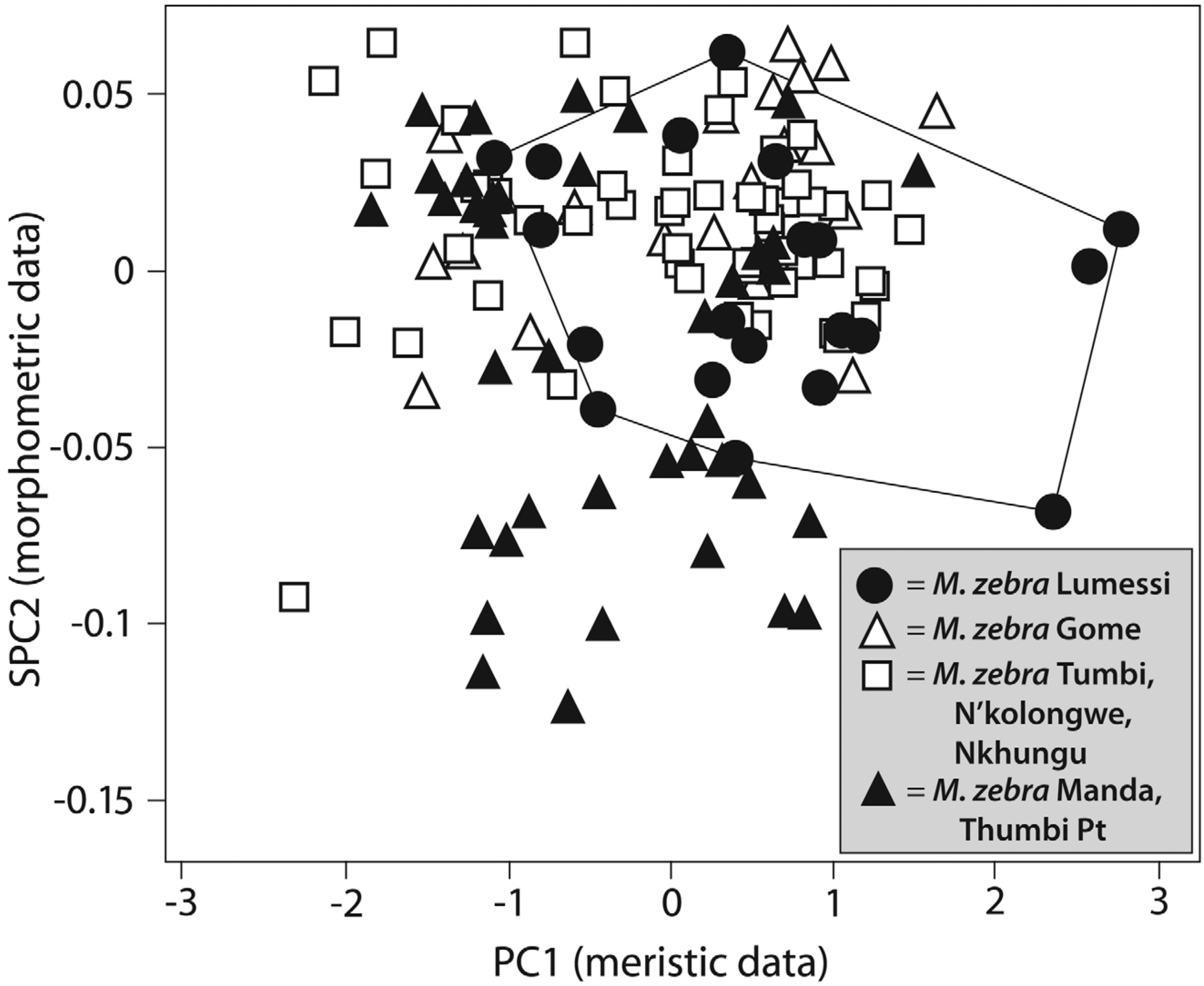

FIGURE 10. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Metriaclima zebra* "Lumessi" from Lumessi, Mozambique (n=20) and of *Metriaclima zebra* with a classic color pattern from Gome, Malawi (n=20), Tumbi Point (n=20), N'kolongwe (n=20) and Nkhungu Point (n=20) in Mozambique, and from Manda (n=20) and Thumbi Point (n=20) in Tanzania.

Metriaclima lundoense is a member of the informal *flavifemina* group and the geographically nearest member of that group is *M. phaeos* which occurs between Undu Point, Tanzania, and Cobwé, Mozambique. In addition to the differences in color pattern, in particular that of the females, the heterospecificity of *M. lundoense*, *M. phaeos*, and *M. flavifemina* is further supported by a multivariate analysis of the morphometric and meristic data of these species. The minimum polygon cluster of *M. lundoense* does not overlap with those of *M. phaeos* (type material from Cobwé, Mozambique) and *M. flavifemina* (type material from Maleri Island, Malaŵi) (Fig. 11). The first principal component (PC1), which includes size, accounts for 76% of the variation and the second principal component for 40% of the remaining variation. The first principal component of the meristic data accounts for 23% of the total variation.

We originally suspected that *M. midomo* would be a geographical variant of *M. zebra* ("Blue Blaze Zebra"), as a more typical *M. zebra* was not found at Lundo Island. This island has the distinction of harboring five different *Metriaclima* species, i.e. *M. fainzilberi*, the three newly described forms *M. lundoense*, *M. pambazuko*, and *M. midomo*, and the as yet undescribed form referred to as *M.* sp. 'msobo heteropictus' (Konings 2007). In order to determine if *M. midomo* at Lundo Island represented a "thick-lipped" population of *M. zebra*, a multivariate analysis of morphometric and meristic data from neighboring populations of *M. zebra* (from five localities along the Tanzanian shore and Chiwindi in Mozambique) was conducted. The results support the heterospecificity of these two species. The plot of the first principal component of the meristic data versus the sheared second principal component of the morphometric data (Fig. 12) strongly suggests the heterospecificity of *M. midomo* because the minimum polygon of *M. midomo* and that of the six populations of *M. zebra* do not overlap. Size accounted for 87% of the variation and the second principal component for 20% of the remaining variation. The first principal component of the meristic data accounts for 24% of the total variation. The fact that *M. midomo* was only encountered at the two islands further enforced our decision to regard it as a distinct species because it is very unlikely that there is any measurable gene flow from (mainland) populations of *M. zebra* at present. Both this species and *M. midomo* are strictly rock-dwelling haplochromines.

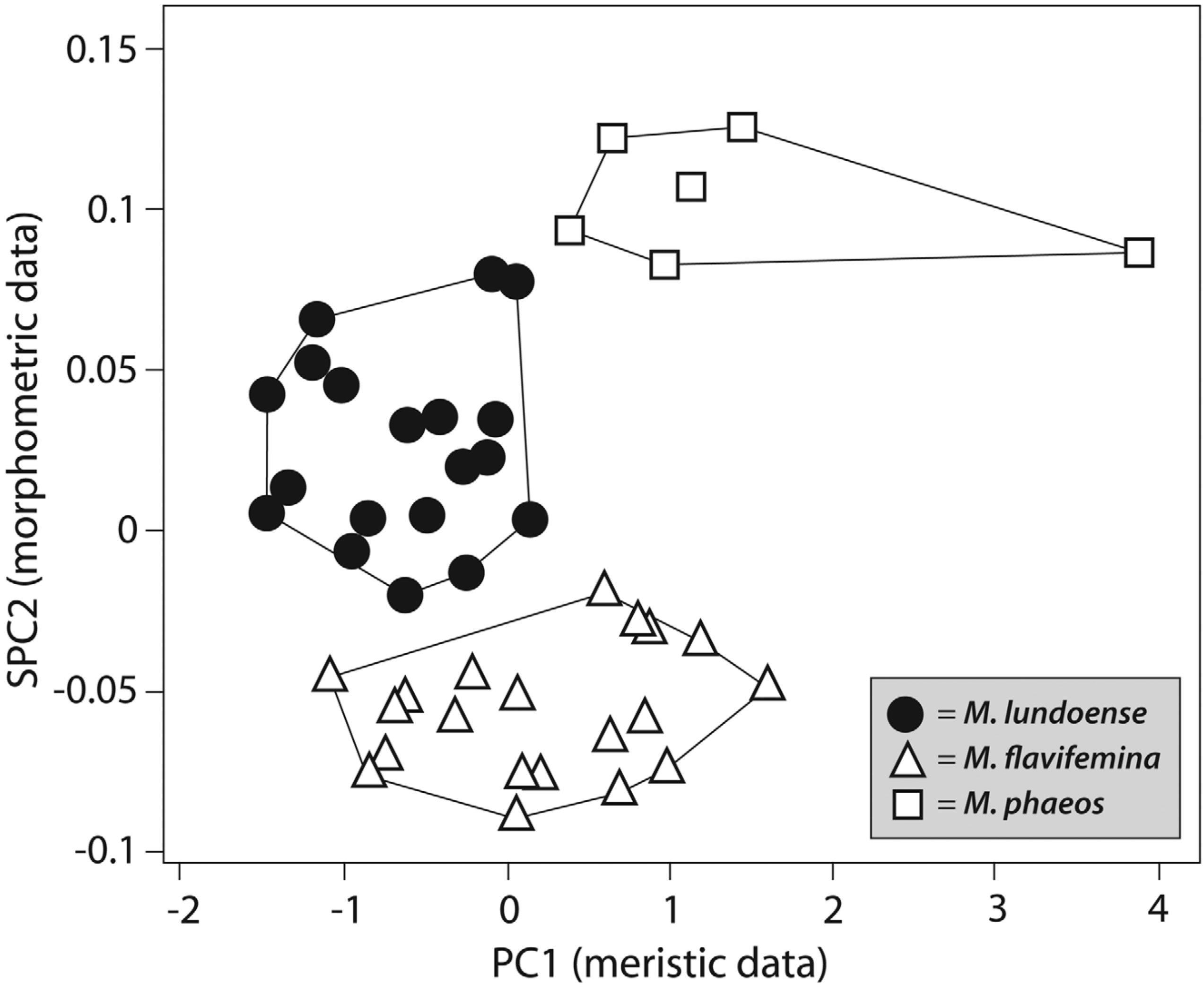

FIGURE 11. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Metriaclima lundoense* from Lundo Island, Tanzania (n=20), *Metriaclima flavifemina* from Maleri Island, Malawi (n=20), and *Metriaclima phaeos* from Cobwé, Mozambique (n=6).

Metriaclima tarakiki most closely resembles *M. zebra* but has a more slender body than *M. zebra*. It is sympatric with *M. fainzilberi* throughout its range and is thus not a geographic variant of that species. Because typical *M. zebra* are not present at either Ngkuyo Island or Higga Reef, we compared *M. tarakiki* to neighboring (mainland) populations of more typical *M. zebra* (from Chiwindi, Mozambique, and Thumbi Point, Tanzania). Results of a multivariate analysis of morphometric and meristic data support our hypothesis that *M. tarakiki* and *M. zebra* are not conspecific. The plot of the first principal component of the meristic data versus the sheared second principal component of the morphometric data (Fig. 13) shows that the minimum polygon of *M. tarakiki* and *M. zebra* do not overlap. The holotype of *M. zebra* falls within the minimum polygon clusters of the two populations of *M. zebra*. Size accounts for 92% and the second principal component for 43% of the remaining variation. The first principal component of the meristic data accounted for 26% of the total variation. *Metriaclima tarakiki* occurs within 15 km of Lundo Island, which is inhabited by other *M. zebra*-like species—*M. midomo*, *M. pambazuko*, and

M. lundoense. A plot of the comparison of these species using principal component analysis (not shown) revealed distinct clustering of *M. tarakiki*, which suggests that it is not a geographical variant of any of these other three species.

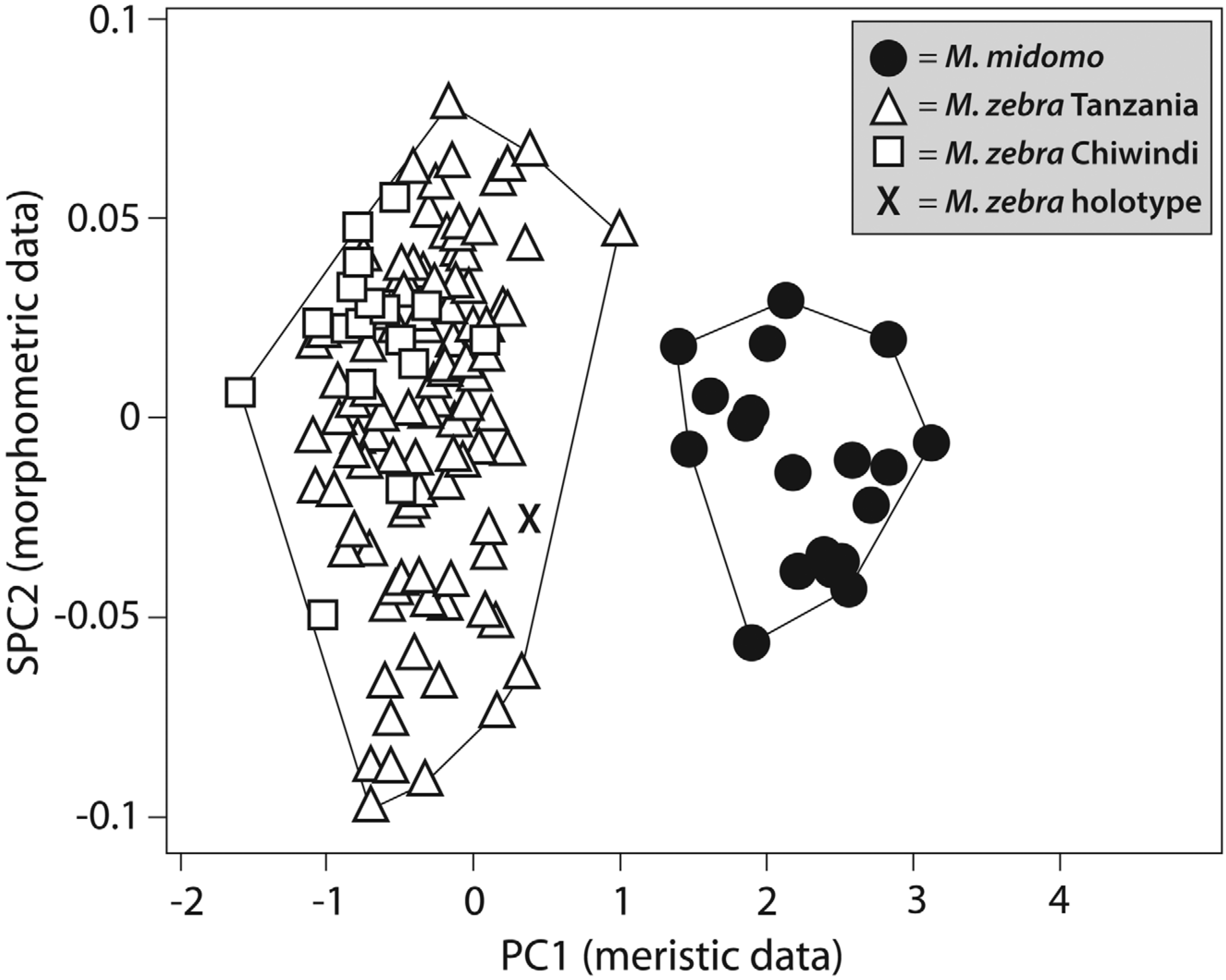

FIGURE 12. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Metriaclima midomo* from Lundo Island, Tanzania (n=19) and of *Metriaclima zebra* from five localities in Tanzania (Matema (n=20), Makonde (n=20), Manda (n=20), Pombo Rocks (n=20), and Thumbi Point (n=20)) and the holotype.

At first we suspected that the color variations found in *M. nigrodorsalis* represented several species, but we failed to find any morphological support for such a scenario. The results of the multivariate analysis of the morphometric and meristic data show that the five populations of *M. nigrodorsalis* included in this investigation are morphologically indistinguishable and that therefore the populations with different male breeding colors represent geographical variants of a single species. The males of the five populations have variable coloration and one could classify them as four different species as was perceived by Konings (2007). As with all mbuna the color pattern of the specimen photographed or taken for color description is an individual pattern and we have tried to indicate in each color description to give the range or extend of a particular color character based on the specimens collected and combined with existing underwater photographs. In contrast to *M. midomo* and *M. tarakiki*, which are pure rock-dwelling species and likely to be strict stenotopic (they also occur around an island), *M. nigrodorsalis* inhabits the intermediate zones at deeper levels along the mainland shore. We have no DNA analyses to prove our point but we believe that it is much more likely that there is more gene flow between the five sampled populations of *M. nigrodorsalis* than there is between *M. tarakiki* and *M. zebra*. If future DNA analyses suggest that we are actually dealing with separate species, we will have to accept that fact and find a way to describe these morphs, but with the data available we found it justified to regard these populations representatives of a single species. We have not sampled populations in between the five reported localities, but we expect males with a breeding coloration intermediate between those of the collected sites neighboring such an assumed population. We found little use in assigning the five populations to three or four different species as there would be no certain way to distinguish preserved specimens.

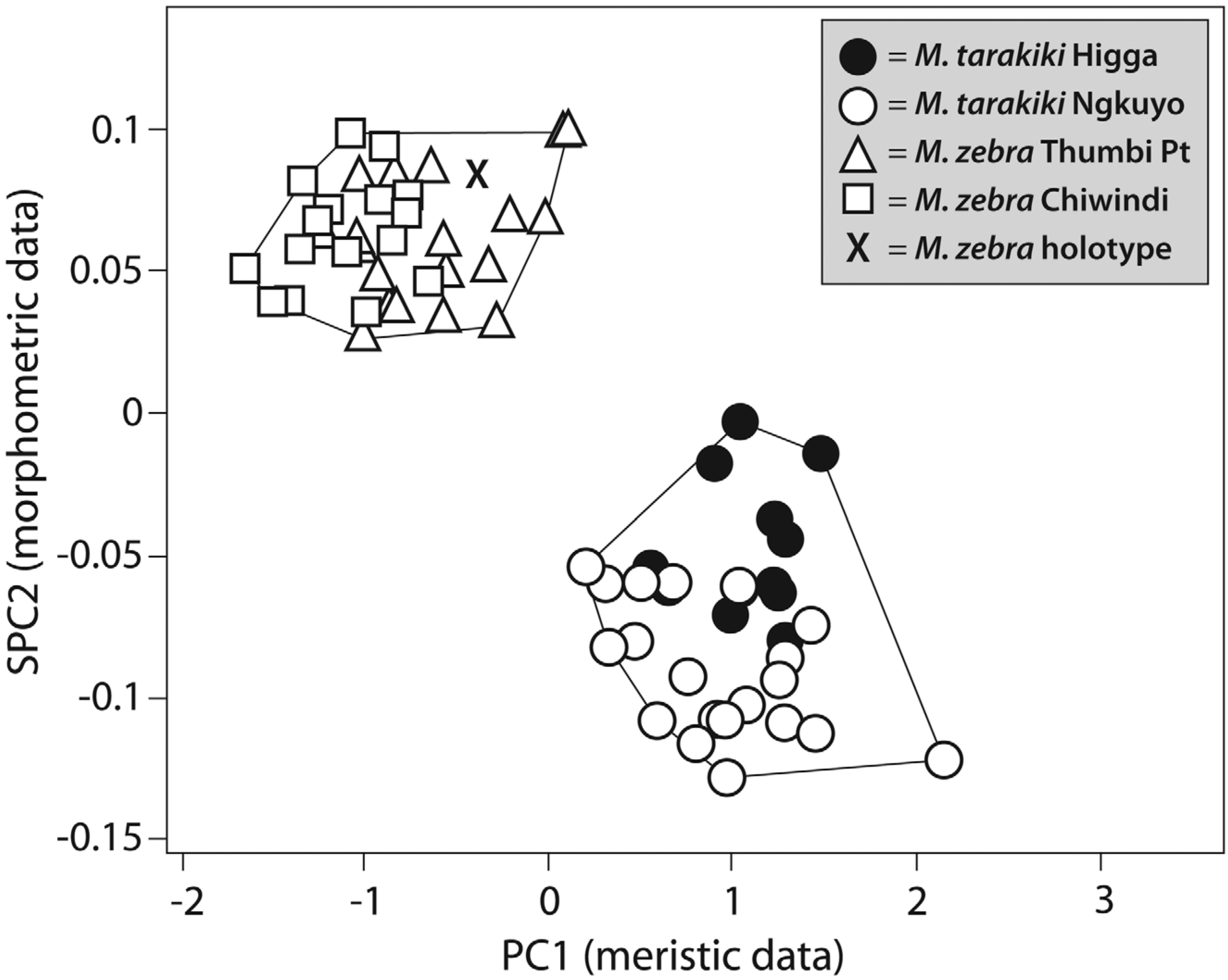

FIGURE 13. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Metriaclima tarakiki* from Higga Reef, Tanzania (n=11) and from Ngkuyo Island (n=20), and of *Metriaclima zebra* from Thumbi Point, Tanzania (n=20), from Chiwindi, Mozambique (n=20), and the holotype.

The only other members of the genus *Metriaclima* possessing a dark submarginal band in the dorsal fin are *M. phaeos*, *M. lundoense*, and some populations of *M. flavifemina* and *M. fainzilberi*. The yellow anal fins of the females and juveniles of *M. nigrodorsalis*, a trait not found in *M. fainzilberi*, supports the heterospecificity of these two species.

In order to examine the heterospecificity of *Metriaclima nigrodorsalis* from the geographically nearest members of the *flavifemina* group (*M. phaeos* to the north and *M. flavifemina* to the south) two multivariate analyses of the morphometric and meristic data were completed. The plot of the first principal component of the meristic data versus the sheared second principal component of the morphometric data demonstrates that the minimum polygon of *M. nigrodorsalis* is distinct from that of *M. phaeos* (Fig. 14). Size accounted for 86% and the second principal component for 27% of the remaining variation. The first principal component of the meristic data accounted for 15% of the total variation. *Metriaclima nigrodorsalis* and *M. flavifemina* are also morphologically distinct based on the results of the second multivariate analysis. The plot of the first principal component of the meristic data versus the sheared second principal component of the morphometric data (Fig. 15) clearly demonstrates that the minimum polygon of the most southerly distributed *M. nigrodorsalis* (Charlie's Bay and Chiloelo, Mozambique) and *M. flavifemina* from Maleri Island, Malaŵi, do not overlap. Size accounts for 80% and the second principal component for 41% of the remaining variation. The first principal component of the meristic data accounts for 23% of the total variation. These analyses and the fact that we failed to find any morphological distinction among the various populations of *M. nigrodorsalis* let us conclude that this species consists of at least four distinct variants separated into geographically different populations that may, genetically seen, not have not been isolated effectively enough to have evolved into morphologically distinguishable species.

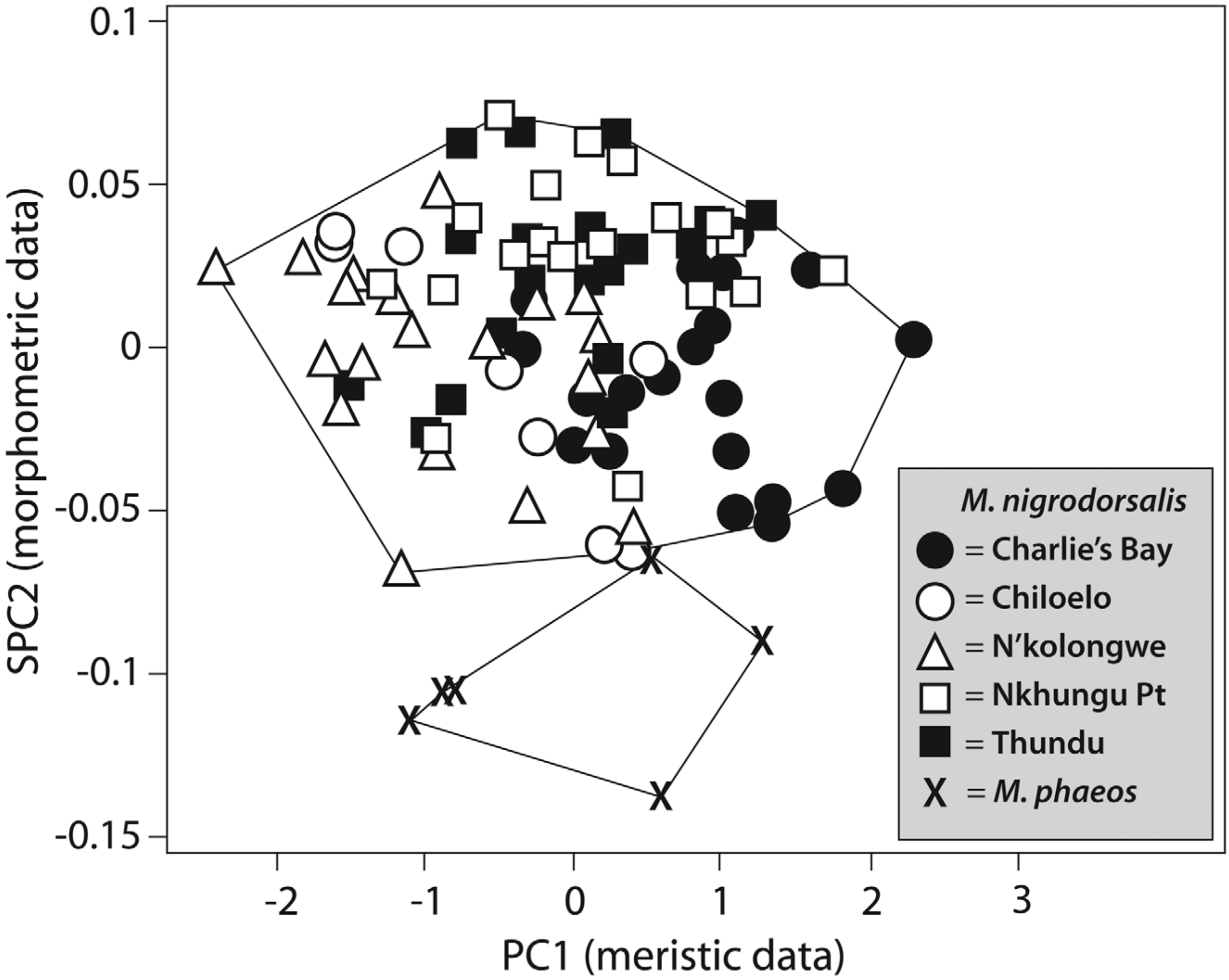

FIGURE 14. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Metriaclima nigrodorsalis* from Charlie's Bay (n=20), from Chiloelo (n=8), from N'kolongwe (n=20), from Nkhungu Point (n=20), and from Thundu (n=20) and *Metriaclima phaeos* from Cobwé (n=6); all localities in Mozambique.

Our study resulted in the probable establishment of the type locality of *M. zebra*, and its conspecificity with numerous populations around the lake. We add a further five species to the genus in which we now recognize a total of 31 species. It should be noted that several nominal species, once included in *Metriaclima* are no longer recognized in this genus. *Metriaclima melabranchion* was considered to be conspecific with *M. zebra* and therefore a junior synonym (Ciccotto *et al.* 2011). In Stauffer *et al.* (1997) *Pseudotropheus heteropictus* Staeck 1980 was included in *Metriaclima* on the assumption that it represented the species found at Thumbi West Island, later described as *M. flavifemina*, but is now again (Konings & Stauffer 2006) referred to as *Pseudotropheus heteropictus*. We concur with Konings (2007) who argued that *M. sandaracinos* and *M. thapsinogen* should be regarded as junior synonyms of *M. pyrsonotos* and also with his removal of *livingstonii* from *Metriaclima* because he found that the vomer of a specimen of *Pseudotropheus livingstonii* formed an angle too steep (62°) to include in

Metriaclima (vomer-parasphenoid angle range of 35–50°). Also the observed feeding behavior of *P. livingstonii* was notably different from that of *Metriaclima* species. Konings (2007) believed that *Pseudotropheus elegans* was a junior synonym of *Pseudotropheus livingstonii*, but later rediscovered (Konings 2010) *P. elegans* near Chilumba, at its type locality, and re-established the taxon. Stauffer & Konings (unpubl. manuscript) found that *P. elegans* does not possess a swollen rostral tip on the steeply downward bent vomer and underwater observations showed a feeding behavior different from that of *Metriaclima* species. It therefore remains in the genus *Pseudotropheus.*

Hereafter we present an artificial key to the formally described species of *Metriaclima*, which is based mainly on color patterns. Note that OB or O morphic specimens without collection locality cannot be reliably identified. The following polymorphic species have been encountered with such a pattern: *M. callainos*, *M. estherae*, *M. fainzilberi, M. mbenjii, M. pyrsonotos, M. tarakiki, M. xanstomachus,* and *M. zebra*.

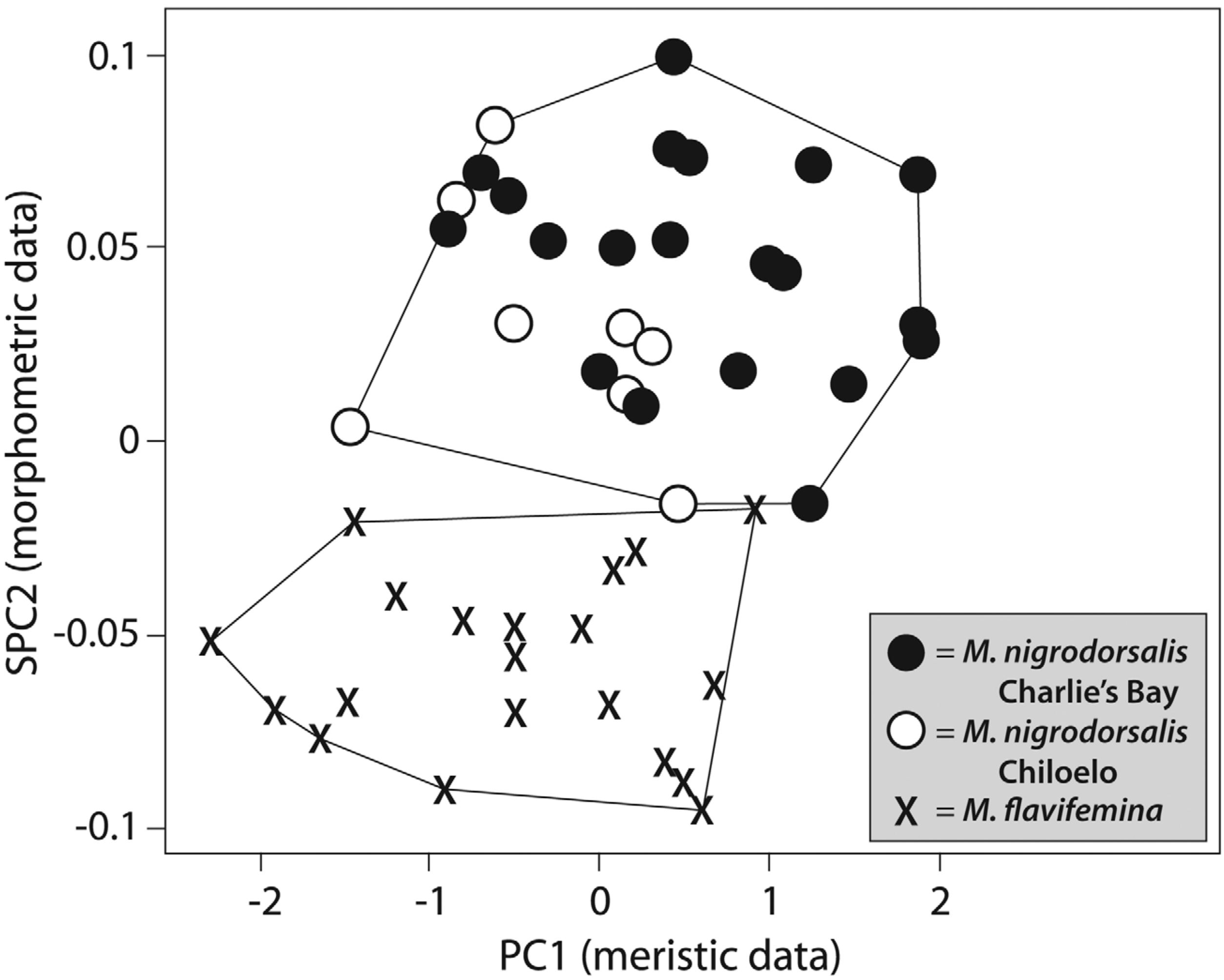

FIGURE 15. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Metriaclima nigrodorsalis* from Charlie's Bay (n=20) and from Chiloelo (n=8) in Mozambique, and *Metriaclima flavifemina* from Maleri Island in Malawi (n=20).

Key to the formally described species of *Metriaclima*

1	Females beige to yellow with yellow pigment in anal fin	2
-	Females brown, dark gray or blue without yellow anal fin	15
2	Males with black markings in dorsal fin	3
-	Males without black markings in dorsal fin	5
3	Males with yellow pigment on cheek and breast	4
-	Males without yellow pigment on cheek and breast	*M. phaeos*

4	Cheek depth less than 25% body depth (20.3–24.8%BD)	*M. flavifemina*
-	Cheek depth more than 25% body depth (25.3–32.0% BD)	*M. nigrodorsalis*
5	Six or fewer bars (distinct or faint) below dorsal fin	6
-	Seven or more bars (distinct or faint) below dorsal fin	7
6	Lower jaw length 28.4–33.5 %HL (mean 31.2)	*M. aurora*
-	Lower jaw length 34.6–36.7 %HL (mean 35.4)	*M. xanthos* (part)
7	Males with distinct vertical bars	8
-	Males without distinct vertical bars	11
8	Males with entirely black pelvic fin	*M. sciasma*
-	Males with clear pelvic fin or dark band in pelvic fin	9
9	Males with black submarginal band in anal fin	10
-	Males without black pigment in anal fin	*M. hajomaylandi*
10	Males with yellow dorsal fin	*M. xanthos* (part)
-	Males with white/blue dorsal fin	*M. mossambicum* (part)
11	Males with yellow occipital region	*M. barlowi*
-	Males with blue occipital region	12
12	Males with distinct interorbital bar	*M. benetos*
-	Males without distinct interorbital bar	13
13	Males with yellow dorsal fin	*M. mossambicum* (part)
-	Males with white/blue dorsal fin	14
14	Fourteen–nineteen, mode 16 of teeth in outer row of lower left jaw	*M. glaucos*
-	Fifteen–twenty five, mode 22 of teeth in outer row of lower left jaw	*M. chrysomallos*
15	Females light blue or white	16
-	Females brown to blue-gray	18
16	Females with distinct vertical bars	*M. lombardoi*
-	Females without distinct vertical bars	17
17	Lower jaw length 29–34%HL	*M. nkhunguense*
-	Lower jaw length 35–43%HL	*M. callainos*
18	Males without distinct vertical bars	19
-	Males with distinct vertical bars	23
19	Males with orange to red pigment in dorsal fin	20
-	Males with blue dorsal fin	21
20	Males with yellow pectoral fin	*M. mbenjii*
-	Males with clear pectoral fin	*M. greshakei*
21	Males with yellow gular region	*M. xanstomachus*
-	Males with white gular region	22
22	Females light brown	*M. zebra* (part)
-	Females dark gray-blue	*M. estherae*
23	Five or fewer bars below dorsal fin	24
-	Six or more bars below dorsal fin	25
24	Teeth in outer jaw of left lower jaw 8–11	*M. lanisticola*
-	Teeth in outer jaw of left lower jaw 12–17	*M. purum*
25	Males with orange to red pigment in dorsal fin	26
-	Males with blue dorsal fin	28
26	Anal fin same orange color as dorsal fin	*M. cyneusmarginatum* (part)
-	Anal fin blue	27
27	Black submarginal band in anal fin	28
-	No black band in anal	29
28	Distance between snout and pelvic-fin origin more than 35 %SL	*M. pambazuko*
-	Distance between snout and pelvic-fin origin less than 33 %SL	*M. emmiltos*
29	Base of pectoral fin in males yellow	*M. fainzilberi* (part)
-	Base of pectoral in males white to blue	*M. pyrsonotos*
30	Anal fin black and black streaks in tail fin	31
-	Anal fin blue and no black streaks in tail	31
31	Occipital region light blue without dark bars or spots	*M. pulpican*
-	Occipital region blue with dark bar	*M. lundoense*
32	Base of pectoral fin in males yellow	*M. fainzilberi* (part)
-	Base of pectoral in males white to blue	33
33	Males without black submarginal band in dorsal fin	34
-	Males with black submarginal band in dorsal fin	36
34	Males without extension of lateral bars onto dorsal fin	35
-	Males with extension of lateral bars onto dorsal fin	37
35	Fewer than 6 rows of teeth in lower jaw	*M. zebra* (part)
-	More than 6 rows of teeth in lower jaw	*M. midomo*

36	Males with black pigment in anal fin	*M. zebra* (part)
-	Males without black pigment in anal fin	*M. cyneusmarginatum* (part)
37	Five to 8 tooth rows in lower jaw	*M. tarakiki*
-	Three to 4 tooth rows in lower jaw	*M. zebra* (part)

Other material examined

Metriaclima zebra, PSU 10575, 20, (63.0–79.8 mm SL), 10° 39.720' S, 34° 38.380' E, Pombo Rocks, Lake Malaŵi, Tanzania, A. F. Konings & J. R. Stauffer Jr., 24 Jan. 2004.

Metriaclima zebra, PSU 10577, 20, (61.8–84.6 mm SL), 11° 01.702' S, 34° 36.700' E, Thumbi Point, Lake Malaŵi, Tanzania, A. F. Konings & J. R. Stauffer Jr., 27 Jan. 2004.

Metriaclima zebra, PSU 10580, 17, (59.4–69.7 mm SL), 11° 35.007' S, 34° 57.882' E, Chiwindi, Lake Malaŵi, Mozambique, A. F. Konings & J. R. Stauffer Jr., 30 Jan. 2004.

Metriaclima zebra, PSU 10589, 20, (57.8–75.7 mm SL), 9°30.456' S, 34° 03.148' E, Sanga Rocks, Lake Malaŵi, Tanzania, A. F. Konings & J. R. Stauffer Jr., 5 Feb. 2005.

Metriaclima zebra, PSU 10593, 16, (56.7–86.6 mm SL), 12° 47.671' S, 34° 47.159' E, N'kolongwe, Lake Malaŵi, Mozambique, A. F. Konings & J. R. Stauffer Jr., 16 Feb. 2002.

Metriaclima zebra, PSU 10598, 16, (55.0–81.7 mm SL), 13° 30.744' S, E 34° 52.021' E., Gome, Lake Malaŵi, Malaŵi, A. F. Konings & J. R. Stauffer Jr., 12 Feb. 2002.

Metriaclima zebra, PSU 10585, 20, (62.1–72.3 mm SL), S9° 56.882' S, 34° 27.297' E, Makonde, Lake Malaŵi, Tanzania, A. F. Konings & J. R. Stauffer Jr., 24 Feb. 2005.

Metriaclima zebra, PSU 10592, 20, (62.5–86.9 mm SL), 12° 20.297' S, 34° 41.853' E, Tumbi Point, Lake Malaŵi, Mozambique, A. F. Konings & J. R. Stauffer Jr., 17 Feb. 2002.

Metriaclima zebra, PSU 10601, 20, (68.6–85.3 mm SL), 12° 58.801' S, 34° 45.807' E, Nkhungu Point, Lake Malaŵi, Mozambique, A. F. Konings & J. R. Stauffer Jr., 15 Feb. 2002.

Metriaclima zebra, PSU 10612, 20, (65.3–82.7 mm SL), 10° 27.617' S, 34° 34.357' E, Manda, Lake Malaŵi, Tanzania, A. F. Konings & J. R. Stauffer Jr., 12 Feb. 2004.

Metriaclima zebra, PSU 10597, 20, (63.6–86.7 mm SL), 13° 08.196' S, 34° 47.844' E, Lumessi, Lake Malaŵi, Mozambique, A. F. Konings & J. R. Stauffer Jr., 12 Feb. 2002.

Metriaclima zebra, PSU 10602, 10, (62.6–89.7 mm SL), 12° 02.947' S, 34° 36.930' E, Mkanila Bay, Chizumulu Island, Lake Malaŵi, Malaŵi, A. F. Konings & J. R. Stauffer Jr., 20 Feb. 2002.

Metriaclima flavifemina, PSU 3729, 1, (78.0 mm SL), 13° 53.910' S, 34° 38.020' E, Maleri Island, Lake Malaŵi, Malaŵi, J.R. Stauffer & A. F. Konings, 2 Feb. 2004.

Metriaclima flavifemina, PSU 3729, 14; AMNH 237672, 2; UMBC 10, 3; (68.5–80.6 mm SL), 13° 53.910' S, 34° 38.020' E, Maleri Island, Lake Malaŵi, Malaŵi, J.R. Stauffer & A. F. Konings, 2 Feb. 2004.

Metriaclima phaeos, PSU 3054, 1, (85.1 mm SL), 13° 53.910' S, 34° 38.020' E, Cobwé, Lake Malaŵi, Mozambique, S.M. Grant, 1 Mar. 1996.

Metriaclima phaeos, PSU 3055, 5, (68.3–86.5 mm SL), 13° 53.910' S, 34° 38.020' E, Cobwé, Lake Malaŵi, Mozambique, S.M. Grant, 1 Mar. 1996.

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