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Revised diagnosis of *Metriaclima* with description of a new species (Teleostei: Cichlidae) from Lake Malaŵi National Park, Africa

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The diagnosis of *Metriaclima* is expanded to include several feeding behavioral characteristics. Species of *Metriaclima* feed at almost perpendicular angles to the substrate and are able to align the teeth of both upper and lower jaws in the same plane by abducting the jaws to a 180°-angle opening. While closing the mouth, the teeth comb through the algae anchored to the substrate and collect loose material. The bites to the substrate follow in rapid succession. We have further expanded the diagnosis of *Metriaclima zebra* to include a population without distinct vertical bars. Finally, we describe a new species, *M. flavifemina*, which inhabits the rock-sand interface in the southern part of the lake.

Introduction

The small, rock-dwelling haplochromine cichlid fishes in Lake Malaŵi, Africa, are commonly referred to as mbuna. The genus *Pseudotropheus* – one of the dozen genera currently recognized within the mbuna – originally included a widely diverse group of cichlids and served as a catch-all genus for newly-discovered species. Several complexes have been recognized within the genus (Ribbink et al., 1983) and some of them have been treated as distinct genera, e.g., *Tropheops* (Trewavas, 1984) and *Metriaclima* (Stauffer et al., 1997). The genus *Metriaclima* was diagnosed to accommodate the *Pseudotropheus zebra* complex. The main characters that delimit members of *Metriaclima* from other complexes in *Pseudotropheus* are a moderately-sloped ethmo-vomerine block with a swollen rostral tip. Morphological characteristics of the feeding apparatus reflect the manner in which these fishes browse from the substrate and one of the purposes of this paper is to include characters of feeding behavior in the diagnosis of *Metriaclima*.

When Stauffer et al. (1997) described *Metriaclima*, the following species, hitherto in *Pseudotropheus*, were included: *M. zebra* (Boulenger), *M. heteropictus* (Staeck), *M. callainos* (Stauffer & Hert), *M. xanstomachus* (Stauffer & Boltz), *M. greshakei* (Meyer & Foerster), *M. aurora* (Burgess), *M. barlowi* (McKaye & Stauffer), *M. elegans* (Trewavas), *M. estherae* (Konings), *M. hajomaylandi* (Meyer & Schartl), *M. lombardoi* (Burgess), *M. lanisticola* (Burgess), *M. livingstonii* (Boulenger), and

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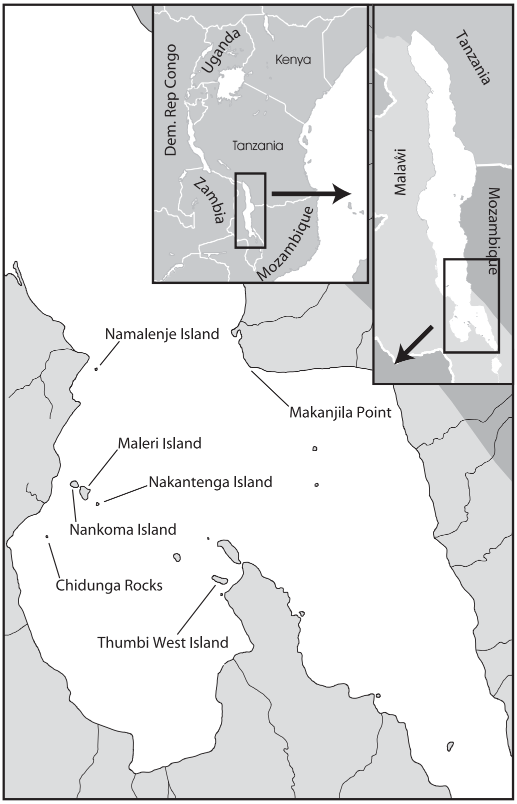

Fig. 1. Map of Lake Malaŵi with localities mentioned in the text.

M. pursus (Stauffer). In the same publication, these authors also described 10 more species in the new genus: *M. melabranchion*, *M. chrysomallos*, *M. phaeos*, *M. cyneusmarginatus*, *M. benetos*, *M. pyrsonotos*, *M. sandaracinos*, *M. emmiltos*, *M. mbenjii*, and *M. thapsinogen*. Several subgroups are recognized within *Metriaclima*: 1. a so-called BB Zebra group (blue-black barred mbuna allied with *M. zebra*; see Stauffer et al., 1997); 2. an Aurora group (allied with *M. aurora*); 3. a Black Dorsal group allied with an undescribed form called *Pseudotropheus* 'zebra black dorsal' by Ribbink et al. (1983) and which is described herein.

We recognize populations of the Black Dorsal group at Nakantenga, Maleri, and Thumb West islands and at Chidunga Rocks. The population from Thumbi West Island had been confused repeatedly in scientific and popular literature with *P. heteropictus* Staeck. Staeck (1980) states that *P. heteropictus* was collected at Thumbi West Island, but its likely origin, Chizumulu Island, had been withheld by its collector (P. Davies et al.) for commercial reasons (P. Davies, pers. comm.). Ribbink et al. (1983) and Stauffer et al. (1997) used the name *P. heteropictus* for a hitherto undescribed species of *Metriaclima* found at this island that phenotypically resembles *P. heteropictus*.

In a continuing effort to better characterize the taxon *M. zebra*, the purposes of this paper are to 1) describe the populations of the Black Dorsal group from Nakantenga, Maleri, and Thumbi West islands and from Chidunga Rocks (Fig. 1); 2) compare these forms with type material of *P. heteropictus*; 3) compare blue-black barred individuals from Namalenje Island to a neighboring population, at Maleri Island, that consists of light-blue individuals lacking black bars; and 4) compare the Namalenje and Maleri island populations to *M. pyrsonotos*, a blue-black barred form with a red dorsal fin from neighboring Nakantenga Island.

Methods

Fishes were collected by the authors in southern Lake Malaŵi (Fig. 1) by chasing them into a monofilament net while SCUBA diving. Fishes were anesthetized with clove oil, preserved in 10 % formalin, and placed in 70 % ethanol for permanent storage. All counts and measurements were made on the left side of the fish, with the exception of gill-raker counts. Counts and measurement follow Barel et al. (1977) and Stauffer (1991; 1994) with the following exceptions. Head depth was measured from the hyoid symphysis to the top of the head (jaws not extended) at a 90° angle to the horizontal body axis (horizontal line drawn through the lower part of lateral line). Body depth was measured from the dorsal-fin origin to the ventral outline of the fish at a 90° angle to the horizontal body axis. The pre-orbital depth was measured as the length of the intersection of the lachrymal bone with a line continuing the radius of the orbit and parallel to the snout profile, dissecting the lachrymal bone (Eccles & Trewavas, 1989). Institutional abbreviations follow Leviton et al. (1985), except UMBC, University of Malaŵi, Bunda College.

Pigmentation pattern was recorded in the field, in territorial and non-territorial males, females, and juveniles. The different patterns are variable in all species examined and in the descriptions such variation is recorded by placing a slash between the two colors between which the specific pattern varies, i.e. blue/white is used to designate that the color ranges from blue to white and includes intermediate shades in certain individuals. The angle of the ethmo-vomerine block was assessed by measuring the angle between the horizontally-aligned parasphenoid and a line bisecting the vomer (in lateral view) in two equal halves.

Morphometric data were analyzed using sheared principal component analysis (SPCA), with the covariance matrix factored (Humphries et al., 1981; Bookstein et al., 1985). Meristic data were analyzed with principal component analysis (PCA), with the correlation matrix factored. Differences among species were illustrated by plotting the sheared second principal components of the morphometric data against the first principal components of the meristic data (Stauffer & Hert, 1992).

Metriaclima Stauffer, Bowers, Kellogg & McKaye

Type species. The type species of *Metriaclima* is *M. zebra* (Boulenger, 1899) and the holotype of this species comes from an unknown locality within Lake Malaŵi. As currently used, the name *M. zebra* includes a large number of populations of blue-black barred mbuna distributed all over Lake Malaŵi that include the holotype but which have not yet been resolved convincingly at the species level. Even though Stauffer et al. (1997) found that in a PCA plot the holotype is distinct from all other forms investigated, they decided to retain the name *M. zebra* for all these populations because of a possibly extensive intraspecific variability, a lack of samples identifiable with the holotype, and because of its wide usage in scientific and popular literature.

Diagnosis. A genus comprised of rock-dwelling cichlids endemic to Lake Malaŵi. The presence of many small scales in the nape region and the reduction of the left ovary are characters present also in other rock-dwelling genera in Lake Malaŵi. The following three morphological characters are taken from Stauffer et al. (1997). 1. The presence of bicuspid teeth in the anterior portion of the outer row of both upper and lower jaws. 2. A moderately-sloped ethmo-vomerine block with a swollen rostral tip. 3. The lower jaw at 45° angle to a line from the tip of the snout to the hypural plate. Additional morphological characters that define *Metriaclima* are as follows: 4. The lower jaw is often slightly longer and thicker than the upper. 5. A large part of the upper dental arcade is normally exposed when the mouth is closed. 6. The tips of the teeth in the premaxilla and dentary are in a V-shaped line with the anteriormost in upper and lower jaw furthest apart. 7. The placement of the bicuspid teeth in the outer row along the side of the jaws does not follow the contour of the jaw bone. The lateral teeth are rotated so that the plane of their two-pronged tips runs parallel with those in the anterior part of the jaw.

Metiaclima is further diagnosed by the manner it feeds from algae. It feeds at a perpendicular angle to the substrate (Konings, 1995a; Stauffer & Posner, 2006) and is able to align the teeth of both upper and lower jaws in the same plane by abducting its jaws to a near 180°-angle opening. The jaws are then pressed against the substrate and closed. While closing the mouth, the teeth rake through the algae anchored to the substrate and collect loose material (Fryer, 1959). Numerous bites to the substrate follow in rapid succession. During the process nothing is actually torn from the substrate; only diatoms and loose algal strands are harvested.

In this respect, *Metriaclima* distinguishes itself from the species in *Pseudotropheus*, *Tropheops*, and *Melanochromis* because these are not able to neither open their mouths to a 180° angle nor do these rake the loose algae from the substrate. *Tropheops* feed from the algae by shearing the strands from the substrate. *Cyathochromis obliquidens* feeds in a manner very similar to that of *Metriaclima*, albeit from plant fronds; it is, however, distinguished because its specialized teeth consist of slender shafts and compressed, spoon-like crowns with an obliquely rounded edge and with a minute lateral cusp. Also, members of the genus *Petrotilapia* feed in a manner similar to those of *Metriaclima*, but they are distinguished by the possession of tricuspid teeth in the outer tooth rows.

The possession of bicuspid teeth distinguishes *Metriaclima* from many of the other mbuna genera (i.e., *Cyathochromis*, *Cynotilapia*, *Genyochromis*, *Gephyrochromis*, *Iodotropheus*, *Labeotropheus*, *Labidochromis*, *Petrotilapia*, and part of *Melanochromis*) except *Pseudotropheus*, *Tropheops*, and some *Melanochromis*. The ethmo-vomerine block

Fig. 2. Cranium of: **a,** *Metriaclima zebra*, male, approx. 95 mm SL; Malaŵi: Likoma Island: Maingano; angle ethmo-vomerine block is 34° with parasphenoid; **b,** *Tropheops tropheops*, male, approx. 90 mm SL; Malaŵi: Zimbawe Rock; angle ethmo-vomerine block is 85° with parasphenoid.

in *Metriaclima* is moderately-sloped and forms an angle of 31-48° with the parasphenoid (n = 23 species) (Fig. 2a). *Tropheops* has a steeply-sloped ethmo-vomerine block (71-96° with parasphenoid; n = 13 species) (Fig. 2b) while the vomer angle in those forms of *Melanochromis* characterized by bicuspid teeth ranges between 72-75° (n = 3 species). Species of *Melanochromis*, *Tropheops* and *Pseudotropheus* lack a swollen rostral tip of the ethmo-vomer.

In *Tropheops*, the lower jaw is much shorter than the upper and not thickened; only a small section of the dental arcades are exposed when the mouth is closed, and the tips of the tightly-packed teeth in upper and lower jaws are in a more or less straight line. In *Pseudotropheus* and in the bicuspid *Melanochromis*, the upper and lower jaws have about equal lengths and the tips of the tightly-packed teeth in premaxilla and dentary form a more or less straight line. The tip of the palatines are wider apart in *Metriaclima* than in *Tropheops* and *Pseudotropheus* allowing for a further anterior push of the maxilla when extending the premaxilla. The width of the vomer, which restricts the smallest distance between the palatines, is narrower in *Tropheops* (20-29 % of width of ethmoid; n = 17) than in *Metriaclima* (29-37 %; n = 30). In *Pseudotropheus* the width of the vomer overlaps with those of the previous two genera: 27-34 % (n = 13).

Metriaclima flavifemina, new species

(Figs. 3-5)

Pseudotropheus zebra 'black dorsal': Ribbink et al., 1983: 162.

Metriaclima sp. "black dorsal": Konings, 2001: 154.

Pseudotropheus heteropictus (non Staeck, 1980): Ribbink et al., 1983: 161.

Pseudotropheus sp. "black dorsal heteropictus": Konings, 1995a: 146.

Metriaclima heteropictus (non Staeck, 1980): Stauffer et al., 1997: 196.

Metriaclima sp. "black dorsal heteropictus": Konings, 2001: 154.

Holotype. PSU 3729, 78 mm SL; Malaŵi: Lake Malaŵi: Maleri Island, 13°53.910'S 34°38.020'E; J. R. Stauffer & A. F. Konings, 2 Feb 2004.

Paratypes. PSU 3730, 14; AMNH 237672, 2; UMBC 10, 3; 68.5-80.6 mm SL; data as for holotype. – PSU 3731, 18; AMNH 237673, 2; 63.6-83.0; Malaŵi: Lake Malaŵi: Nakantenga Island, 13°55.121'S 34°38.648'E; J. R. Stauffer & A. F. Konings, 2 Feb 2004. – PSU 3732, 16; AMNH 237674, 2; UMBC 11, 2; 61.9-83.0; Malaŵi: Lake Malaŵi: Thumbi West Island, 14°01.528'S 34°49.388'E, J. R. Stauffer & A. F. Konings, 6 Feb 2004. – PSU 4201, 18; AMNH 237675, 2; 58.6-80.1 mm SL; Malaŵi: Lake Malaŵi: Chidunga Rocks, 13°57.774'S 34°33.584'E; A. F. Konings, 29 Oct 2005. – PSU 4200, 1, 85.2 mm SL; Malaŵi: Lake Malaŵi: Namalenje Island,

Fig. 3. *Metriaclima flavifemina*, holotype, PSU 3729, 78 mm SL; Malaŵi: Lake Malaŵi: Maleri Island.

Fig. 4. *Metriaclima flavifemina*, male in habitat at Maleri Island, Malaŵi; approx. 80 mm SL; not preserved.

13°43.755'S 34°38.419'E, M. G. Geerts & A.F. Konings, 14 Feb 2005.

Diagnosis. Juveniles and females *M. flavifemina* are light blue-beige to all yellow with a bright yellow anal fin, features that distinguish them from other *Metriaclima* (anal fin translucent, gray, or brown) except *M. phaeos*, *M. barlowi*, and *M. hajomaylandi*. Males have a black anal fin and black membranes in the caudal that distinguish them from all other *Metriaclima* (anal fin blue or yellow; caudal with yellow or blue membranes), except *M. phaeos*. In coloration, both males and females resemble those of *M. phaeos*; however, *M. flavifemina* has a shorter snout (27.7-36.6 % HL vs. 37.9-44.7) and shallower cheeks (18.8-28.8 % HL vs. 26.3-31.7). Females of *M. flavifemina* of the Thumbi West and Nakantenga populations resemble those of *M. hajomaylandi*, but can be distinguished by the narrow yellow margin in the gray caudal fin vs. entirely yellow caudal in female *M. hajomaylandi*. Females of *M. flavifemina* can be distinguished from those of *M. barlowi* by a longer caudal peduncle (10.8-16.7 % SL vs. 9.0-12.0) and a shallower body (32.9-38.8 % SL vs. 35.3-40.7).

Description. Morphometric and meristic data in Table 1. Head decurved; dorsal snout profile straight to slightly concave in larger individuals; gape inclination of mouth about 20° to horizontal; jaws isognathous. Teeth on dentary in three to four rows, on premaxilla in three to five rows; outer row teeth bicuspid and procumbent; inner rows teeth tricuspid, erect to recumbent. Part of upper dental arcade normally exposed when mouth is closed. Tips of teeth in premaxilla and dentary in a V-shaped line with anteriormost in upper and lower jaw furthest apart and not touching when

Table 1. Morphometric and meristic values of *Metriaclima flavifemina* from Maleri, Nakantenga, Thumbi West, and Namalenje islands, and from Chidunga Rocks, Malaŵi. H, holotype.

	H	all mean	Maleri n=20 range	Nakantenga n=20 range	Chidunga n=20 range	Thumbi W n=18 range	Namalenje n=1
Standard length, mm	80.6	74.4	68.5-80.6	63.6-83.0	58.6-80.1	61.9-83.0	85.2
Head length, mm	24.4	23.0	20.9-25.4	20.2-25.2	18.6-25.4	18.5-25.5	26.2
Percent standard length							
Head length	30.3	31.0	29.7-32.4	29.7-32.5	29.2-32.1	29.0-31.9	30.8
Body depth	37.0	34.1	33.8-37.0	32.9-38.8	31.7-36.6	29.8-34.1	36.9
Snout to dorsal	33.9	34.3	33.0-36.7	32.9-36.0	33.8-36.9	29.9-36.2	35.3
Snout to pelvic	39.8	38.9	37.9-40.8	35.0-41.5	35.1-40.7	36.1-41.6	39.7
Dorsal-fin base length	61.5	62.3	59.3-64.6	61.6-66.2	60.7-64.1	58.0-65.6	63.7
Anterior dorsal to anterior anal	56.2	54.4	53.3-56.9	54.5-57.8	51.0-57.1	47.1-53.8	56.3
Anterior dorsal to posterior anal	64.4	65.1	63.8-67.7	64.6-68.4	62.5-67.8	57.9-66.9	66.2
Posterior dorsal to anterior anal	30.0	31.5	30.0-34.7	29.3-33.7	31.5-33.4	27.8-31.5	34.1
Posterior dorsal to posterior anal	15.7	15.4	14.8-17.1	14.2-16.8	14.9-17.4	13.2-16.5	66.2
Posterior dorsal to ventral caudal	17.4	17.4	16.1-18.5	16.2-18.7	16.5-19.3	16.1-17.7	17.4
Posterior anal to dorsal caudal	19.7	19.0	18.2-20.4	18.0-20.8	17.6-20.9	17.0-19.7	18.3
Anterior dorsal to pelvic-fin origin	37.7	36.6	35.0-40.4	35.3-41.6	33.1-39.7	30.1-36.1	40.1
Posterior dorsal to pelvic-fin origin	58.6	59.1	55.6-60.9	57.6-62.5	57.2-63.2	52.3-60.3	59.9
Caudal peduncle length	13.5	13.9	11.8-15.0	10.8-16.2	12.2-15.3	12.6-16.7	14.4
Least caudal peduncle depth	11.6	12.5	11.6-13.4	12.0-13.9	11.7-13.7	10.5-12.7	13.8
Percent head length							
Snout length	32.0	32.1	28.0-36.1	27.7-33.8	29.6-35.1	28.8-36.6	36.5
Postorbital head length	37.7	38.1	36.2-40.0	36.7-39.7	34.8-40.9	36.0-42.4	39.6
Horizontal eye diameter	33.3	33.5	31.0-36.7	30.7-35.1	31.9-37.6	30.1-36.7	33.1
Vertical eye diameter	31.9	33.6	31.7-37.6	30.5-34.9	31.4-37.5	30.5-36.7	32.6
Head depth	95.3	95.5	88.3-108.7	87.5-107.0	85.8-105.2	86.2-98.7	100.2
Preorbital depth	21.2	20.0	15.0-22.1	17.5-22.9	15.2-22.5	18.5-23.4	21.8
Cheek depth	24.1	23.7	18.8-26.1	20.6-25.6	21.6-28.8	19.3-27.9	26.4
Lower jaw length	35.5	34.8	27.3-37.0	29.4-34.5	32.1-43.8	30.8-38.0	38.2
Meristics		mode	range	range	range	range	
Dorsal fin spines	19	18	17-19	17-19	17-19	17-19	18
Dorsal fin rays	8	9	8-10	8-10	8-10	8-9	9
Anal fin spines	3	3	3	3	3	3-4	3
Anal fin rays	8	8	8	7-9	7-8	6-8	8
Pectoral fin rays	13	13	13-14	13-14	12-14	12-14	5
Pelvic fin rays	5	5	5	5	3-5	5	13
Lateral line scales	33	32	31-34	31-33	31-33	30-33	32
Pored scales post lateral line	2	2	1-3	1-2	0-2	1-2	2
Scale row cheek	5	4	4-5	4-5	3-4	4-5	4
Gillrakers 1st ceratobranchial	10	11	10-13	9-12	10-13	10-12	12
Gillrakers 1st epibranchial	3	3	3-4	2-3	3	3-4	3
Teeth outer left lower jaw	12	12	10-13	10-13	10-13	11-12	12
Teeth row upper jaw	3	3	3-4	3-4	3-5	3-4	4
Teeth rows lower jaw	3	3	3	3	4	3	3

mouth is closed. Angle of ethmo-vomerine block with parasphenoid of three individuals 31-41°.

Coloration. Breeding males: head pale blue with black interorbital and two light-blue interorbital bands; cheek and chin rusty-red in males from Maleri (Fig. 4) and Chidunga, but blue in males from Nakantenga, Namalenje, and Thumbi West islands (Fig. 5a). Body light-blue with six or seven conspicuous black bars anterior to vent and three faint bars posterior to vent; belly rusty-brown anteriorly and black posteriorly. Dorsal fin pale blue with prominent submarginal black band, but black band lacking in some males of Thumbi West population; all males with black membranes in rayed portion of dorsal fin and bars from body extend into dorsal fin, merging with submarginal band when present; lappets white; some males with small yellow-orange spots on distal margin. Caudal fin pale blue with black margins and black membranes; narrow yellow/orange distal margin. Anal fin black with narrow white margin anteriorly, with 1-9 yellow ocelli. Pelvic fin black with white or white/yellow leading margin. Pectoral fin clear to gray.

Females (Maleri Island (Fig. 5b) and Chidunga populations): head yellow or pale yellow. Body yellow to beige/yellow. Dorsal fin light yellow with orange/yellow lappets; orange/yellow spots on distal margin. Caudal fin yellow with tiny blue highlights on membranes. Anal fin bright yellow to orange/yellow with narrow hyaline band proximally; no ocelli present. Pelvic fin yellow with white leading margin. Pectoral fin with fine yellow pigment.

Females (Thumbi West and Nakantenga populations): Head gray/beige with two pale yellow/blue interorbital bars; green/blue highlights on postorbital region and green/blue to gray opercular spot. Body light blue/beige with faint gray bars. Dorsal fin light blue/beige with gray submarginal band and gray membranes in trailing portion; lappets white/yellow proximally and orange/yellow distally; orange/yellow spots in rayed portion. Caudal fin gray with narrow upper and lower border yellow with white margin; trailing border yellow; tiny blue highlights on membranes. Anal fin bright yellow to orange/yellow with hyaline band proximally; 1-2 small yellow/orange spots on trailing edge. Pelvic fin yellow with dark gray submarginal band and white leading margin. Pectoral fin hyaline.

Distribution and field observations. *Metriaclima flavifemina* occurs at all three Maleri Islands (Maleri, Nakantenga, Nankoma islands), at Thumbi West Island, at Chidunga Rocks, and at Namalenje Island (Fig. 1), where only a single male was collected and the species' behavior was not observed under water. *Metriaclima flavifemina* lives in the intermediate zones around the islands at a depth varying between 5 and 40 m and is most common at a depth of about 15 m. At Chidunga Rocks, it was most common near the bottom of the reef at a depth of about 6 m. The male at Namalenje Island was collected at a depth of 6 m, the maximum depth of the rocky habitat at the island. Males are territorial and chase mainly conspecific males from their territories. A territory normally consists of a space between the rocks, often with a sandy bottom. Males at the bottom of the reef usually burrow from beneath a rock to create a spawning cave. Females are often solitary or sometimes occur in small groups, rarely numbering more than three individuals. *Metriaclima flavifemina* feeds from the sediment-rich aufwuchs on the rocks from which it rakes diatoms and loose algal strands.

Geographical variation. Males at Maleri and Nankoma islands and at Chidunga Rocks have a rusty-red to orange patch on cheek and chin while such is absent in males of other populations. Females at Maleri and Nankoma islands and at Chidunga Rocks have a yellow head and body, while that in those of the other populations is gray/beige. Males at Thumbi West Island have variable dorsal fin coloration where some males lack a black stripe in the spinous part of the dorsal while others, like males in all other populations, do have a black band running throughout the length of the dorsal fin. Such polychromatism has not been found in the other populations. *Metriaclima flavifemina* of the Thumbi West population have on average a shallower body than those of the other populations (29.8-34.1 % SL vs. 32.9-38.8) and those of Chidunga Rocks have on average a longer lower jaw than those of other populations (32.1-43.8 % HL vs. 27.3-38.2).

Etymology. The specific epithet refers to the yellow color of females and derives from the Latin 'flavus' (yellow) and 'femina' (female); a noun in apposition.

Fig. 5. **a,** *Metriaclima flavifemina*, male in habitat at Thumbi West Island, Malaŵi; approx. 75 mm SL; not preserved; **b,** *M. flavifemina*, female at Maleri Island, Malaŵi; approx. 70 mm SL; not preserved.

Remarks. The population of *M. flavifemina* at Thumbi West Island was initially thought, on grounds of differences in color pattern in male and female, not to be conspecific with those at the Maleri islands. The minimum polygon clusters formed by plotting the PC1 of the meristic data against the SPC2 of the morphometric data for the Thumbi West population compared to the two populations of Maleri and Nakantenga islands (Fig. 6) were significantly different ($P < 0.05$, MANOVA). However, when the population of Chidunga Rocks, which resembles that of the Maleri islands in male and female coloration, was similarly analyzed (Fig. 6) it appeared again distinguishable from the other populations. The principle component analysis is a useful tool in distinguishing morphologically distinct populations; we believe, however, that it should not be taken as the sole decisive factor in determining whether allopatric populations are heterospecific. When on the other hand two ecologically similar populations from neighboring locations are morphologically congruent, a PCA offers a potent suggestion that they are conspecific. Our

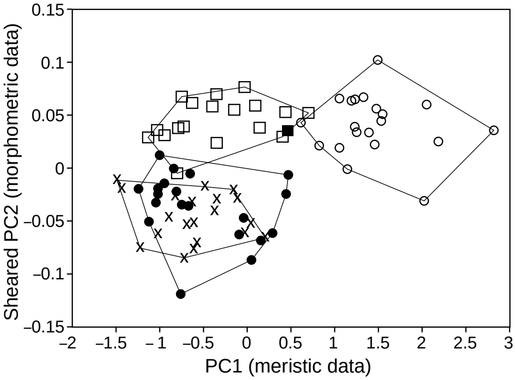

Fig. 6. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Metriaclima flavifemina* from Nakantenga Island (**x**), Maleri Island (●), Chidunga Rocks (○), Thumbi West Island (□), and from Namalenje Island (■).

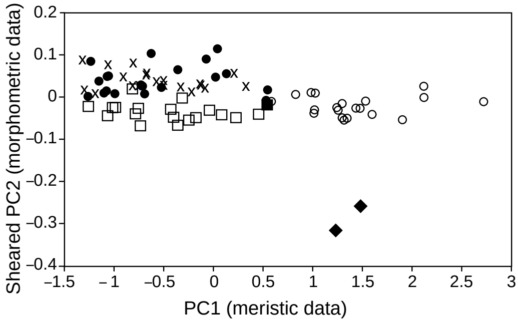

Fig. 7. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Metriaclima flavifemina* (●, Maleri; **x**, Nakantenga; □, Thumbi West; ○, Chidunga; ■, Namalenje) and from *Pseudotropheus heteropictus*, paratypes (n = 2) (◆).

finding that some populations of *M. flavifemina* are morphologically distinguishable was not reflected in other characteristics of the various populations. In behavior, habitat preference, as well as in coloration the species *M. flavifemina* could not be segregated into sub-groups that would correspond to the morphological differences revealed in our analyses. We therefore consider that all these populations are conspecific.

A comparison of our analyses of all populations of *M. flavifemina* with two paratypes of *Pseudotropheus heteropictus* (SMF 15179, SMF 15180), the species with which they were repeatedly confused, indicates that the latter species is not conspecific with the new taxon (Fig. 7). The angle of the ethmo-vomerine block with the parasphenoid in two specimens of *P. heteropictus* from Chizumulu Island (PSU 4214, 47 mm SL; PSU 4215; 58 mm SL) showed 68 and 58° respectively.

Metriaclima zebra (Boulenger)

Pseudotropheus 'zebra blue': Ribbink et al., 1983: 161.
Metriaclima sp. "zebra blue": Konings, 2001: 54.

Material examined. PSU 3734, 19; 57.3-81.7 mm SL; Malaŵi: Lake Malaŵi: Namalenje Island, 13°43.755'S 34°38.419'E; J. R. Stauffer & A. F. Konings, 14 Feb 2004. – PSU 3735, 20; 55.9-76.8; Malaŵi, Lake Malaŵi: Maleri Island, 13°53.910'S 34°38.020'E; J. R. Stauffer & A. F. Konings, 2 Feb 2004.

Coloration. Breeding males at Maleri Island: head light-blue; cheek gray/blue with yellow highlights; ventral border of cheek yellow; gular region blue/white. Body bright blue with 5-7 faint gray/black bars anterior to caudal peduncle; caudal peduncle blue/gray; belly and breast gray/blue. Dorsal fin pale blue. Caudal fin with pale gray rays, membranes blue with trailing yellow/orange edge. Anal fin blue/gray, with 1-5 orange/yellow ocelli. Pelvic fin with white leading margin; membranes black anteriorly, clear posteriorly. Pectoral fin with gray rays and clear membranes.

Breeding males at Namalenje Island: head black with two light-blue interorbital bands; gular region blue/black. Body light-blue with 6-8 black bars anterior to caudal peduncle; caudal peduncle dark blue/gray; belly and breast blue/black. Dorsal fin pale blue. Caudal fin with gray rays, membranes blue with narrow yellow/orange edge. Anal fin blue/gray, with 1-5 orange/yellow ocelli; sometimes vertical bar extending onto membranes between first 3 spines. Pelvic fin black with white leading margin. Pectoral fin with gray rays and clear membranes.

Females at Maleri Island: head light brown with gray gular region. Body light brown/gray. Dorsal, caudal, and anal fins light brown/gray; small yellow spots on trailing edge of anal fin. Pelvic fin black with white leading margin. Pectoral fin with gray rays and clear membranes.

Females at Namalenje Island: head dark brown/black with brown gular region. Body dark brown/black with bright-blue highlights. Dorsal, caudal, and anal fins dark brown/black; small yellow spots on trailing edge of anal fin. Pelvic fin black with white leading margin. Pectoral fin with brown rays and clear membranes.

Remarks. Morphometric and meristic data of both populations in Table 2. *Metriaclima zebra* at Maleri Island (Fig. 9a) was initially thought not to be conspecific with the "classic" blue-black barred *M. zebra* found elsewhere (Ribbink et al.,

Table 2. Morphometric and meristic values of *Metriaclima zebra* from Maleri and Namalenje islands, and of *Metriaclima pyrsonotos* from Nakantenga Island, Malaŵi.

	M. zebra Maleri n=20		*M. zebra* Namalenje n=20		*M. pyrsonotos* Nakantenga n=18	
	mean	range	mean	range	mean	range
Standard length, mm	67.7	55.9-76.8	73.0	57.3-81.7	66.3	56.9-76.6
Head length, mm	21.1	17.2-23.8	23.5	18.7-26.7	20.8	18.2-23.6
Percent standard length						
Head length	31.1	29.1-33.0	32.2	31.0-33.3	31.4	30.5-32.6
Body depth	34.5	33.2-38.0	36.2	34.0-38.2		
Snout to dorsal	33.4	29.8-35.3	33.9	31.4-35.6	34.6	32.0-37.1
Snout to pelvic	37.2	35.6-39.0	39.2	37.0-42.7	37.5	35.3-39.8
Dorsal-fin base length	62.1	58.7-65.6	63.1	59.6-66.2	62.6	60.8-66.0
Anterior dorsal to anterior anal	52.9	50.9-54.7	53.2	50.7-55.0	53.9	51.9-55.9
Anterior dorsal to posterior anal	65.6	63.1-68.0	66.1	63.2-68.6	66.2	64.6-68.4
Posterior dorsal to anterior anal	32.8	30.2-35.0	33.4	30.2-35.1	32.8	30.6-35.3
Posterior dorsal to posterior anal	16.4	14.9-17.6	16.1	14.8-17.9	17.0	16.0-18.8
Posterior dorsal to ventral caudal	18.2	16.6-19.8	18.3	16.4-20.5	18.6	17.2-21.5
Posterior anal to dorsal caudal	20.3	18.7-22.2	19.9	17.5-22.2	21.4	20.2-22.3
Anterior dorsal to pelvic-fin origin	36.9	35.1-39.0	38.5	35.9-40.9	37.8	35.3-41.5
Posterior dorsal to pelvic-fin origin	59.4	57.5-61.7	58.4	56.6-60.5	58.5	56.0-60.7
Caudal peduncle length	15.5	13.3-18.4	15.1	13.1-17.3	14.6	13.0-16.4
Least caudal peduncle depth	12.8	12.1-14.1	13.1	11.6-14.3	13.1	12.2-14.3
Percent head length						
Snout length	32.0	27.6-36.9	32.0	29.1-34.6	32.1	29.7-34.2
Postorbital head length	39.5	37.3-42.8	38.6	35.8-41.8	39.5	37.0-40.8
Horizontal eye diameter	32.1	30.3-34.3	32.1	29.4-34.4	32.9	31.1-35.3
Vertical eye diameter	32.6	29.8-37.4	32.3	28.1-35.0	33.0	31.8-35.3
Head depth	96.8	87.3-103.5	97.8	89.5-109.3	105.7	97.0-115.4
Preorbital depth	20.9	18.3-23.6	21.9	19.4-24.3	20.1	18-1-21.6
Cheek depth	25.0	21.4-27.7	27.4	22.6-32.0	27.9	23.1-31.7
Lower jaw length	38.2	30.2-43.2	37.8	34.4-40.0	39.6	37.9-42.5
Meristics	mode	range	mode	range	mode	range
Dorsal fin spines	17	16-18	17	16-18	17	16-18
Dorsal fin rays	9	8-10	9	8-10	9	8-10
Anal fin spines	3	3	3	3-4	3	3
Anal fin rays	8	8	8	7-9	7	6-8
Pectoral fin rays	13	13-14	13	13-14	13	12-14
Pelvic fin rays	5	5	5	5	5	5
Lateral line scales	31	29-32	31	30-32	31	30-32
Pored scales post lateral line	2	1-2	2	0-3	2	0-2
Scale row cheek	5	4-6	5	4-6	4	3-5
Gillrakers 1st ceratobranchial	11	10-13	11	10-13	12	10-14
Gillrakers 1st epibranchial	3	2-3	3	2-3	3	2-3
Teeth outer left lower jaw	9	8-11	11	10-12	7	4-10
Teeth row upper jaw	3	3	3	3-4	2	2-3
Teeth rows lower jaw	3	3	3	3-4	3	2-3

1983), but in our morphometric analysis with a neighboring population (Namalenje Island; Fig. 9b) the two populations clearly overlap. The minimum polygon clusters formed by plotting the PC1 of the meristic data against the SPC2 of the morphometric data for the two populations (Fig. 8) were not significantly different (P > 0.05, MANOVA). Based on these data, a new diagnosis of *M. zebra* should now include the form that lacks the distinct black bars of the holotype.

Male *M. zebra* are distinguished from those of other species of *Metriaclima* by a light-blue ground coloration with or without distinct black vertical bars, a light-blue anal fin, and a light blue dorsal fin, lacking a submarginal band. Barred male *M. zebra* are distinguished from those of *M. fainzilberi* by a black throat and a blue-black pectoral fin base (vs. yellow/orange). The Maleri population of non-barred male *M. zebra* is distinguished from *M. callainos* by a deeper body (33.2-38.0 % SL vs. 28.8-33.5), a shallower preorbital (18.3-23.6 % HL vs. 20.1-25.0), and fewer teeth in the left outer row of the dentary (mode 9, range 8-11 vs. mode 14, range 11-17). The non-barred *M. zebra* further resembles *M. benetos* and *M. estherae* but can be distinguished by a deeper body expressed, in the case of *M. benetos*, by the distance between the dorsal fin origin and the origin of the pelvic fin (35.1-39.0 % SL vs. 30.3-35.6) and expressed, in the case of *M. estherae*, by the ratio body depth/standard length (Konings, 1995b: ratio 2.5 in SL vs. 2.8). The non-barred *M. zebra* of Maleri Island is distinguished from the sympatric *M. xanstomachus* by a longer snout-to-pelvic distance (35.6-39.0 % SL vs. 29.0-32.1) and by a higher number of dorsal-fin rays (mode 9, range 8-10 vs. mode 8, range 7-8) and anal fin rays (mode 8, range 8 vs. mode 7, range 6-7) and from *M. chrysomallos* by a larger snout-to-pelvic length (35.6-39.0 % SL vs. 23.2-33.9). Male *M. zebra* of Maleri Island lacks the yellow throat that characterizes the sympatric *M. xanstomachus*; based on coloration alone females of these two species cannot be reliably distinguished at the island.

Female *M. zebra* have a gray/blue to blue/brown ground color and lack yellow pigment in unpaired fins; thus they are distinguished from most other members of *Metriaclima* except *M. cyneusmarginatus*. Females of latter species lack ocelli in the anal fin which distinguishes them from those of *M. zebra*. They further have a shorter snout-to-pelvic length than *M. zebra* (18.6-31.3 vs. 35.6-42.7 % of SL in *M. zebra*).

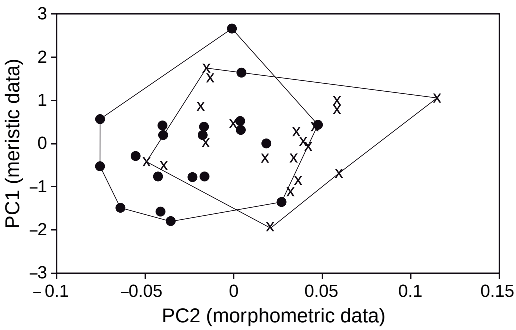

Fig. 8. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Metriaclima zebra* from Namalenje Island ('BB' form; ●) and from Maleri Island ('blue' form; **x**).

Metriaclima pyrsonotos Stauffer, Bowers, Kellogg & McKaye

Material examined. PSU 3062, holotype; PSU 3063, 8; USNM 341926, 4; ANSP 176200, 3; MFU 7, 4; 56.9-76.6 mm SL; Malaŵi: Lake Malaŵi: Nakantenga Island, 13°55.121'S 34°38.648'E; Stauffer, Mar 1991.

Remarks. Morphometric and meristic data in Table 2. *Metriaclima pyrsonotos* (Fig. 10) had been regarded as a possible geographical variant of *M. zebra* by Konings (2001: 50) and we therefore chose to compare it with the non-barred *M. zebra* from Maleri Island and the blue-black barred *M. zebra* from Namalenje Island. The minimum polygon clusters formed by plotting the PC1 of the meristic data against the SPC2 of the morphometric data for the three populations (Fig. 11) were significantly different (P < 0.05, MANOVA). Variables that had the highest loading on the second principal components of the morphometric data were caudal peduncle length (0.62), cheek depth (−0.62), and head depth (−0.20); while those with the highest loadings on the principal components of the meristic data were anal fin rays (0.85), rows of cheek scales (0.69), and tooth rows on the upper jaw (0.70).

Konings (2001) questioned the validity of *M. pyrsonotos* (Stauffer et al., 1997) because the main characteristic differentiating it from *M. zebra* was the possession of a red dorsal fin in territorial males. His hesitation was based on a population of *M.* zebra present around the shallow reefs off Makanjila Point (13°43.995'S 34°52.065'E) where part of the male population displayed a red dorsal, while that of others was light-blue or

Fig. 9. **a,** *Metriaclima zebra*, male in habitat at Maleri Island, Malaŵi; approx. 75 mm SL; not preserved; **b,** *Metriaclima zebra* at Namalenje Island, Malaŵi; approx. 80 mm SL; not preserved.

a mixture of both. Smith et al. (2003), however, established that this particular population represented, genetically, a natural hybrid between *M. zebra* and *M. thapsinogen*. Our principal component analysis of *M. zebra* at the Maleri and Namalenje islands and the ecologically equivalent *M. pyrsonotos* at neighboring Nakantenga Island (Fig. 10) supports the hypothesis that *M. zebra* and *M. pyrsonotos* are two separate taxa. The distinct difference in coloration between *M. pyrsonotos* and both forms of *M. zebra* concurs with marked differences in morphometrics and we therefore conclude that these forms are heterospecific. This is further corroborated by the presence of a small, introduced population of *M. pyrsonotos* at Maleri Island (Ribbink et al., 1983: 162), which,

Fig. 10. *Metriaclima pyrsonotos*, male in habitat at Nakantenga Island, Malaŵi; approx. 75 mm SL; not preserved.

over two decades, has maintained its status (AK; unpub. obs.) within the large population of *M. zebra* without visible hybridization and / or introgression.

Discussion

Apart from *M. flavifemina* we know of no other members of the *Pseudotropheus zebra* complex *sensu* Ribbink et al. (1983) that inhabit the Lake Malaŵi National Park and that are still formally undescribed. *Metriaclima*, however, is diagnosed mainly by the angle and structure of the ethmovomerine block, not by overall morphological similarity with *M. zebra*. Some members of the *Pseudotropheus elongatus* complex (Ribbink et al., 1983) share the angle and structure of the ethmovomerine block of *Metriaclima* and probably belong to this genus, while the structure and angle of the ethmo-vomer of others places them in *Tropheops* (Stauffer & Konings, in prep.) None of these forms have been formally described.

The principal component analysis of the blue-black barred *M. zebra* at Namalenje Island and the non-barred blue form at Maleri Island (Fig. 8) suggests that *M. zebra* has a variable melanin pattern that includes populations that lack the "classic" barred patterning. Several of such populations are known to occur around the lake where they are usually encountered in sediment-rich, shallow rocky habitats; these are Membe Island near Chizumulu, Malawi; Cobwè, Mozambique; Jalo Reef near Nkhotakota, Malawi; Undu Reef, Tanzania. The populations around Chizumulu Island contain intermediates (geographically as well as in patterning) between completely non-barred individuals and those exhibiting bars, suggesting that they are all members of the same species.

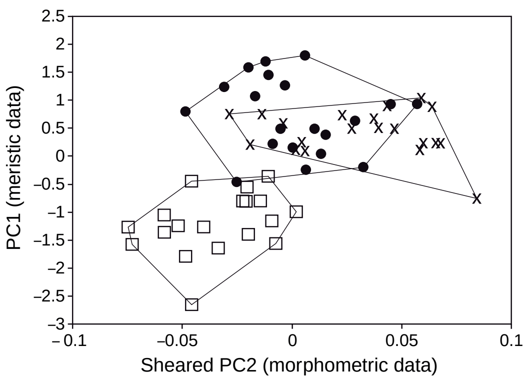

Fig. 11. Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (PC2) of *Metriaclima pyrsonotos* from Nakantenga Island (□) and *Metriaclima zebra* from Maleri (**X**) and Namalenje (●) islands.

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