

A revision of the blue-black *Pseudotropheus zebra* (Teleostei: Cichlidae) complex from Lake Malaŵi, Africa, with a description of a new genus and ten new species

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ABSTRACT — A new genus, *Metriaclima*, is described for members of the *Pseudotropheus zebra* complex from Lake Malaŵi. The presence of bicuspid teeth in the anterior portion of the outer row of both the upper and lower jaws distinguishes *Metriaclima* from many of the previously described genera of rock-dwelling cichlids that inhabit Lake Malaŵi, including *Cyathochromis*, *Cynotilapia*, *Gephyrochromis*, *Labidochromis*, and *Petrotilapia*. The absence of two horizontal stripes along its flanks, distinguishes it from *Melanochromis*. The isognathous jaws of *Metriaclima* delimits it from *Genyochromis*, which is characterized by having the lower jaw extend in front of the upper jaw. The mouth of *Metriaclima* is terminal, while that of *Labeotropheus* is inferior. Within the genus *Pseudotropheus* as it is now recognized, species of *Metriaclima* are unique because they have a moderately sloped ethmo-vomerine block and a swollen rostral tip. Ten previously undescribed species that have a slight variation from the characteristic blue/black barring are described. The new species are recognized primarily by their distinctive adult coloring in conjunction with the discontinuity of morphological differences throughout their range.

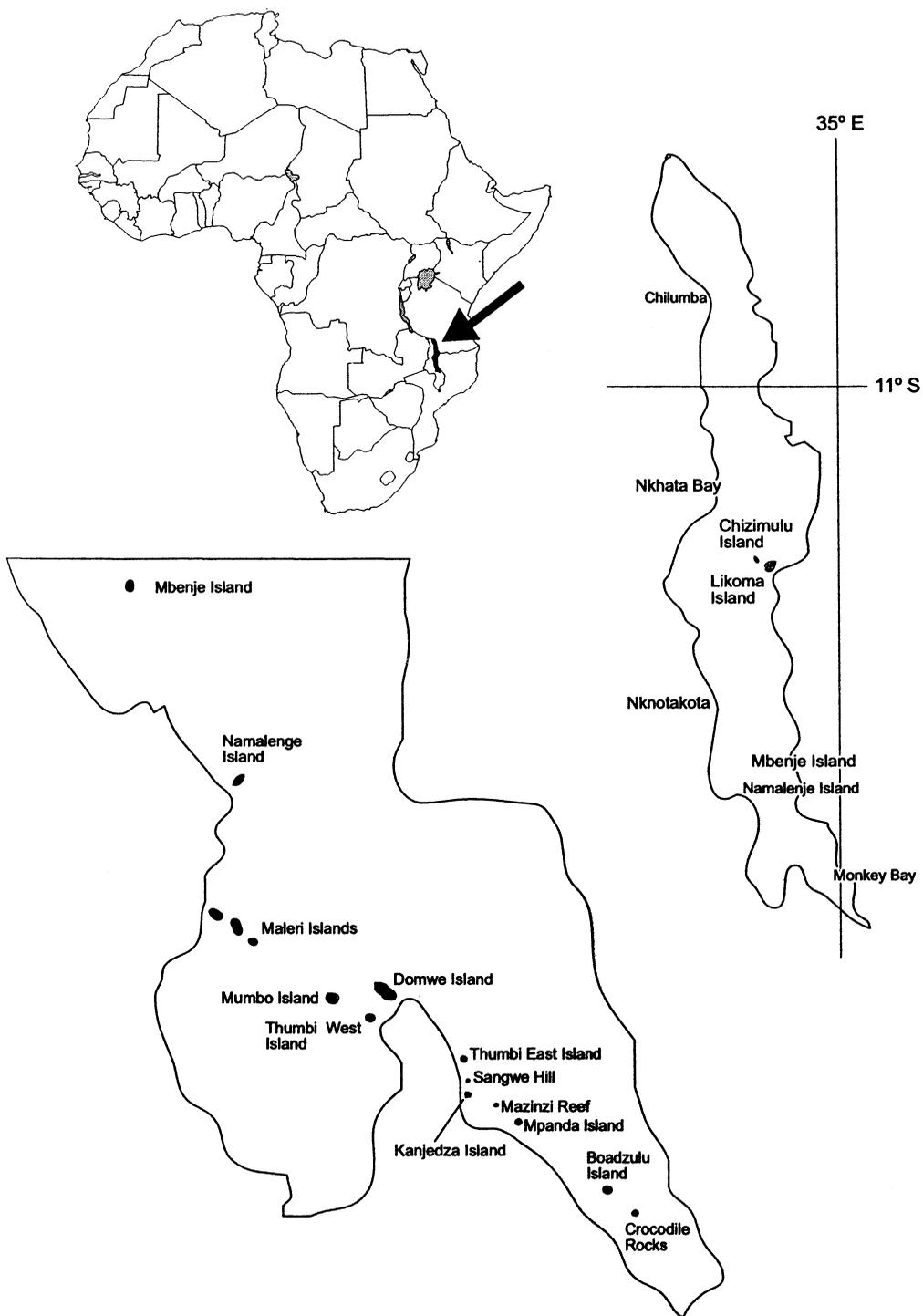
GENERA ET SPECIES NOVAE: *Metriaclima*, *M. melabranchion*, *M. chrysolallos*, *M. phaeos*, *M. cyneusmarginatus*, *M. benetos*, *M. pyronotos*, *M. sandaracinos*, *M. emmiltos*, *M. mbenjii*, *M. thapsinogen*.

INTRODUCTION

In the lakes of East Africa, fishes of the family Cichlidae have undergone an extraordinarily rapid and extensive radiation. Within Lake Malaŵi there are over 450 described species of fish, and there may be as many as 1500 species which inhabit the lake, all of which have arisen in the last 2 million years (Bowers et al. 1994). The cichlids within Lake Malaŵi are represented by two major groups, which are regarded as tribes by some investigators: the tilapiines, of which there are from five to seven species and the haplochromines, of which there are some 450 described species (Konings 1990). Within the haplochromines, two major and several minor lineages exist; the major lineages being the rock-dwelling cichlids, commonly called *mbuna*, and the pelagic and sand-dwelling cichlids, although recent molecular evidence suggests splitting the second major lineage into several minor ones (Moran et al. 1994).

Trewavas (1935) recognized the nine genera of *mbuna* (*Cyathochromis*, *Cynotilapia*, *Genyochromis*, *Gephyrochromis*, *Labeotropheus*, *Labidochromis*, *Melanochromis*, *Petrotilapia*, and *Pseudotropheus*) to be more closely related to each other than to other

genera within the lake. Oliver & Loiselle (1972) later added *Iodotropheus* to this group. The majority of the species within this group are all strongly lithophilous and form complex communities throughout the lake along the rocky shorelines and rocky islands. Endemism within this group is high, and many species are restricted to a single, isolated rock group (Fryer and Iles 1972, Ribbink et al. 1983, Stauffer 1988). Although the *mbuna* cannot be distinguished from other genera of cichlids on the basis of synapomorphies, they can be recognized by a suite of characters, some of which may be shared by other deep-water and sand-dwelling haplochromine taxa. These characters include large number of small scales in the nape and chest region, an abrupt transition from large flank scales to small chest scales, reduction of the left ovary, coloration, and habitat preferences (Fryer 1959). The possession of true ocelli has also been suggested to be a distinguishing characteristic of *mbuna* (Oliver 1984). Recently, Moran et al. (1994) identified three additional genera, *Aulonocara*, *Alticorpus*, and *Lethrinops*, which although lacking many of *mbuna* characters, shared an affinity with the *mbuna* on the basis of RFLP analysis of mtDNA.



MAP. Locations of sites mentioned in the text.

Of the aforementioned mbuna genera, *Pseudotropheus* is the most diverse and certainly polyphyletic. The type species of the genus is *Pseudotropheus williamsi* (Gunther), and species complexes recognized within the genus include the: *P. williamsi* complex, *Pseudotropheus tropheops* Regan complex, *Pseudotropheus elongatus* Fryer complex, *Pseudotropheus aggressive* complex, and the *Pseudotropheus zebra* (Boulenger) complex. Additionally, there is a miscellaneous group within *Pseudotropheus* that shows no clear affinity with any of the other complexes and is itself certainly polyphyletic (Ribbink et al. 1983). Finally, the placement of *Pseudotropheus fainzilberi* Staeck in *Pseudotropheus* is problematic. Although its body coloration superficially resembles *P. zebra*, it differs, because of its peculiar mouth shape and teeth position, which more closely resembles that of *Petrotilapia* species (Staeck 1976, fig. 12, p. 489).

Currently, the *P. zebra* complex consists of 13 described species including: *P. zebra*, *P. elegans* Trewavas, *P. livingstonii* (Boulenger), *P. heteropictus* Staeck, *P. lombardoi* Burgess, *P. aurora* Burgess, *P. lanisticola* Burgess, *P. greshakei* Meyer and Foerster, *P. barlowi* McKaye and Stauffer, *P. xanstomachus* Stauffer and Boltz, *P. pursus* Stauffer, *P. callainos* Stauffer and Hert, *P. hajomaylandi* Meyer and Schartl, and *P. estherae* Konings. In addition, there are some 20 species that are currently recognized by aquarists for which there are no formal descriptions (Ribbink et al. 1983, Konings 1990). As with the majority of the mbuna, most of these species live over a rocky substrate; however, there are several forms in this complex represented by *P. elegans*, *P. livingstonii*, *P. lanisticola*, and *P. pursus*, that have invaded the sand habitat and are associated with snail shells either as juveniles, adults, or both life stages. The purpose of this paper is to describe a new genus for members of the *P. zebra* complex and to describe ten new species that have the characteristic blue/black (BB) barring found in *P. zebra*. Future papers will describe the sand-dwelling forms and the forms of this complex that do not conform to the BB color pattern.

METHODS AND MATERIALS

Adult fishes were collected throughout Lake Malaŵi by chasing them into a monofilament net (7 m x 1 m x 1.5 cm) while SCUBA diving. External counts and measurements follow Barel et al. (1977) and Stauffer (1991). The number of scales in the lateral-line series do not include scales in the overlapping portion of the lower lateral line; pored scales located posterior to the hypural plate were recorded separately. Standard length (SL) is

used throughout. Except for gill raker meristics, all counts and measurements were made on the left side of the fish. Morphometric values are expressed as percent SL or percent head length (HL).

Differences in body shape were analyzed using sheared principal component analysis (SPCA) of the morphometric data (Humphries et al. 1981, Bookstein et al. 1985). Pectoral-fin length and pelvic-fin length were not included in the analysis, because these measurements are dependent on the reproductive stage of the fish. Meristic data were analyzed using principal component analysis (PCA). The correlation matrix was factored in all principal component analyses of meristic data, while the covariance matrix was factored in the calculation of all sheared principal components of the morphometric data. This analysis ordines factors independently of a main linear ordination (Reyment et al. 1984). Differences among species were illustrated by plotting either the sheared second or third principal components of the morphometric data against the first principal components (labeled as factor score) of the meristic data (Stauffer and Hert 1992). If the mean multivariate scores of the clusters were significantly different along one axis, independent of the other axis, a Duncan's multiple range test ($p < 0.05$) was used to determine which clusters differed from each other. If, in fact, the clusters were not significantly different along one axis independent of the others, then a MANOVA, in conjunction with a Hotelling-Lawley trace, was used to determine whether the mean multivariate scores of clusters formed by the minimum polygons of the PCA scores were significantly different ($p < 0.05$).

TAXONOMIC ANALYSES

[NOTE: Tables 1-11, containing morphometric and meristic values for type and referred material, are grouped at the end of this paper.]

Metriaclima Stauffer, Bowers, Kellogg and McKaye, n. gen.

Type Species.—*Metriaclima zebra* Boulenger.

Diagnosis.—This genus comprises a series of rock-dwelling species endemic to Lake Malaŵi, Africa. The presence of many small scales in the nape region and the reduction of the left ovary aligns this genus to the other rock-dwelling genera in Lake Malaŵi. The presence of bicuspid teeth in the anterior portion of the outer row of both the upper and lower jaws distinguishes *Metriaclima* from many of the previously described genera of mbuna. *Cyathochromis* is distinguished because its

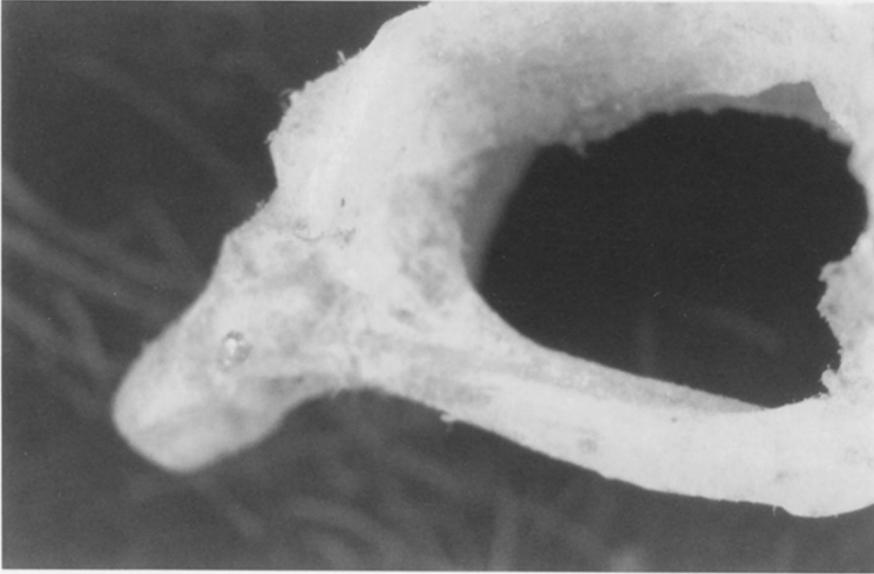


Fig. 1. Skull of *Metriaclima zebra*.

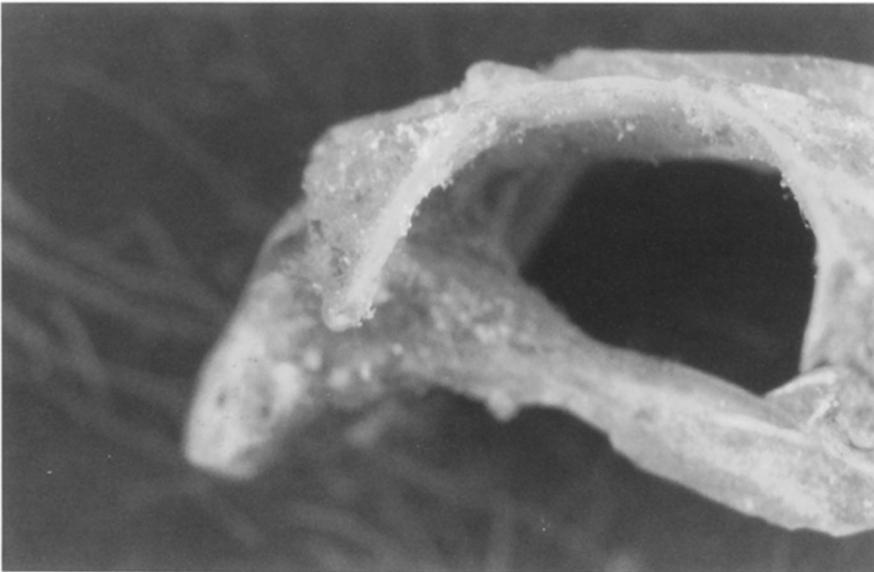


Fig. 2. Skull of *Pseudotropheus elongatus*.

teeth consist of slender shafts with compressed crowns. *Cynotilapia*, *Gephyrochromis*, and *Labidochromis* all have unicuspid teeth in the anterior portion of the outer rows of both the upper and lower jaws. *Petrotilapia* possesses tricuspid teeth in the outer rows of both the lower and upper jaws and is further distinguished by visibility of the teeth when the jaws are closed. The isognathous jaws of *Metriaclima* distinguishes it from *Genyochromis*, which is characterized by having the lower jaw extending in front of the upper jaw.

The mouth of *Metriaclima* is terminal, while that of *Labeotropheus* is inferior. The absence of two horizontal stripes along its flanks, delimits *Metriaclima* from *Melanochromis* (Bowers and Stauffer 1997). Within the genus *Pseudotropheus* as it is now recognized, those species being placed in *Metriaclima* are unique because they have a moderately sloped ethmo-vomerine block and a swollen rostral tip (Fig. 1), compared to *P. elongatus* (Fig. 2) and *P. tropheops* (Fig. 3) complexes. *Pseudotropheus williamsi* complex differs in that when the

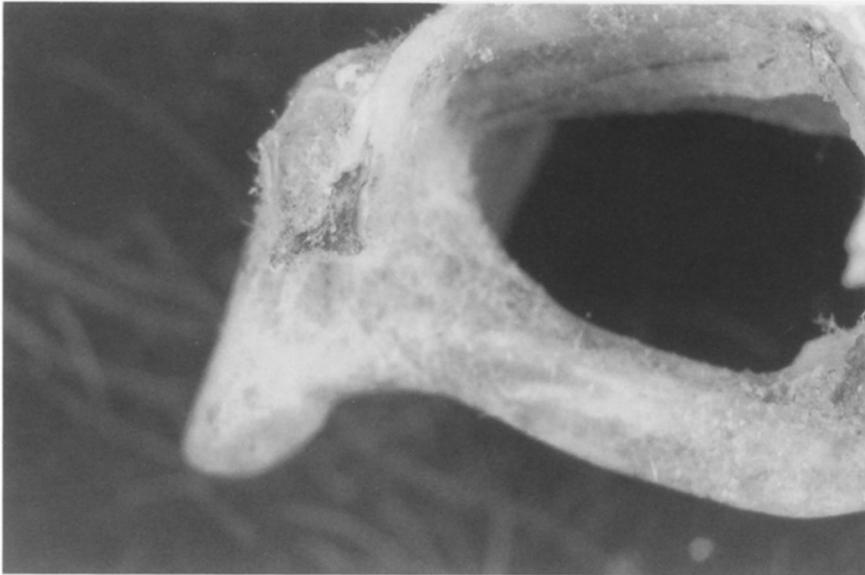


Fig. 3. Skull of *Pseudotropheus tropheops*.

mouth is closed the lower jaw is parallel to a line from the tip of the snout to the hypural plate (Fig. 4), while the lower jaw of *Metriaclima* species is angled approximately 45° relative to this line (Fig. 5). Meyer and Foerster (1984) suggested that certain members of this group be included in the subgenus *Maylandia*; however, although *Maylandia* was proposed as a subgenus no description or diagnosis accompanied this suggestion. Therefore, *Maylandia*, in effect, is a nomen nudum and thus is an invalid name.

Etymology.—*Metriaclima*, from the Greek, meaning moderately sloped to indicate the moderately sloped head of members of this genus.

Metriaclima zebra Boulenger

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The absence of any interrupted pigment in the pale blue dorsal fin in combination with black bars on a blue ground color distinguish this form from all other members of the genus.

Description.—Jaws isognathous; teeth on jaws in 2-5 rows; majority of teeth in outer rows bicuspid, with a few posterior unicuspid teeth; those in inner rows tricuspid; 4-14 teeth in outer rows of the left lower jaw. Dorsal fin with 16-19 spines and 7-10 rays. Pectoral fins (P_1) with 12-15 rays; anal fin with 3 spines except in some specimens from Mazinzi Reef and Mitande Rocks, which had 4; anal fin with 6-8 rays. Lower pharyngeal bone

triangular in outline. Scales along side ctenoid; 29-33 lateral-line scales. First gill arch with 9-14 rakers on the ceratobranchial, 1-3 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 1).

Breeding males have a blue ground coloration laterally with 6-8 black vertical bars, very faint or no bars on posterior one-third. Although extremely rare, a few males in some populations (e.g. Songwe Hill) exhibit a blue/black or orange/black blotched coloration. Belly anterior to the pelvic fins (P_2) black fading to light blue posteriorly; head dark blue to black with a single light interorbital bar; gular dark gray in most populations, but yellow in some northern populations. Dorsal fin uniformly blue gray in most populations, with tips of posterior rays orange in some populations and a continuous black horizontal stripe in some northern populations; caudal fin blue/gray; anal fin blue gray with 1-5 yellow ocelli; in some populations the proximal two-thirds of the anal fin is black, while the distal one-third is light gray; P_2 light blue leading edge, spine and first two rays black, posterior rays clear; P_1 clear. Females generally with brown cast and 1-4 faint ocelli on anal fin. The females alternatively may be dull blue or exhibit an orange/black blotched coloration. This blotched coloration is observed more frequently in females than males and appears to be completely absent in some populations.

Distribution.—*Metriaclima zebra* is widely distributed throughout the lake. Differences in meristics and morphometrics among populations

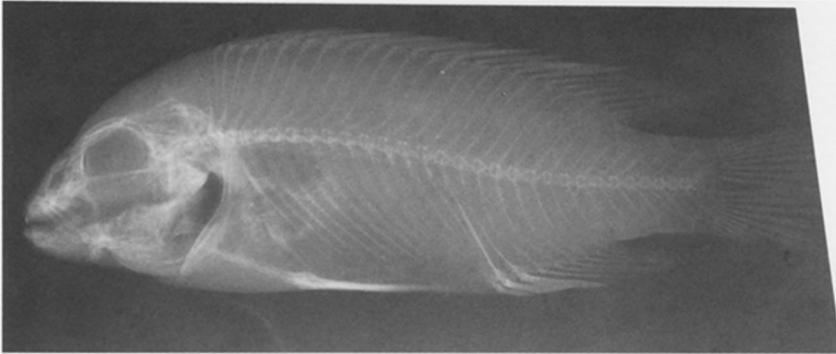


Fig. 4. X-ray of *Pseudotropheus williamsi*.

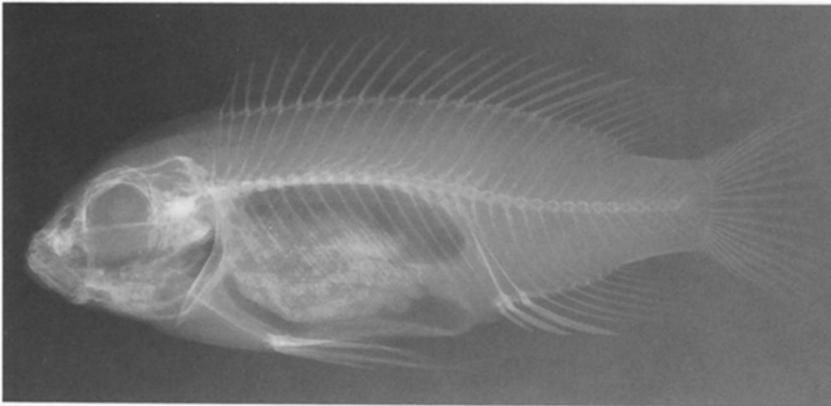


Fig. 5. X-ray of *Metriaclima zebra*.

can be attributed to clinal variation, as there is a great deal of overlap in the minimum polygon clusters that are formed when the first principal components of the meristic data are plotted against the sheared second principal components of the morphometric data (Figs. 6a, 6b, & 6c). Thus, these populations are considered to be conspecific, even though McKaye et al. (1984) reported allelic frequency differences of the same magnitude as observed between sympatric heterospecific populations of *Metriaclima*.

Discussion.—The type locality of *Metriaclima zebra* is Lake Nyassa and the original description was based on a single specimen (BMNH 91.12.17.7) cataloged into the Natural History Museum (London). The HOLOTYPE of *M. zebra* has a longer snout length (40 % HL vs. 30.7 - 39.3 %

HL), a greater distance between the anterior insertion of the dorsal fin and the anterior insertion of the anal fin (57.9 % HL vs. 47.0 - 57.3 % HL), and more teeth rows on the lower jaw (5 vs. 2-4) when compared to all other populations of *M. zebra* (Table 1). The lack of a more specific type locality precluded collecting topotypes. Because there is no overlap when the first principal components of the meristic data are plotted against the sheared second principal components of the morphometric data (Fig. 6c) with *M. zebra* and any of the populations of *M. zebra*, we were first tempted to restrict the name *M. zebra* to the single specimen housed in the Natural History Museum (London) and propose a new name for the other populations. Ultimately, we chose to preserve the name *M. zebra*, because of its wide usage in both

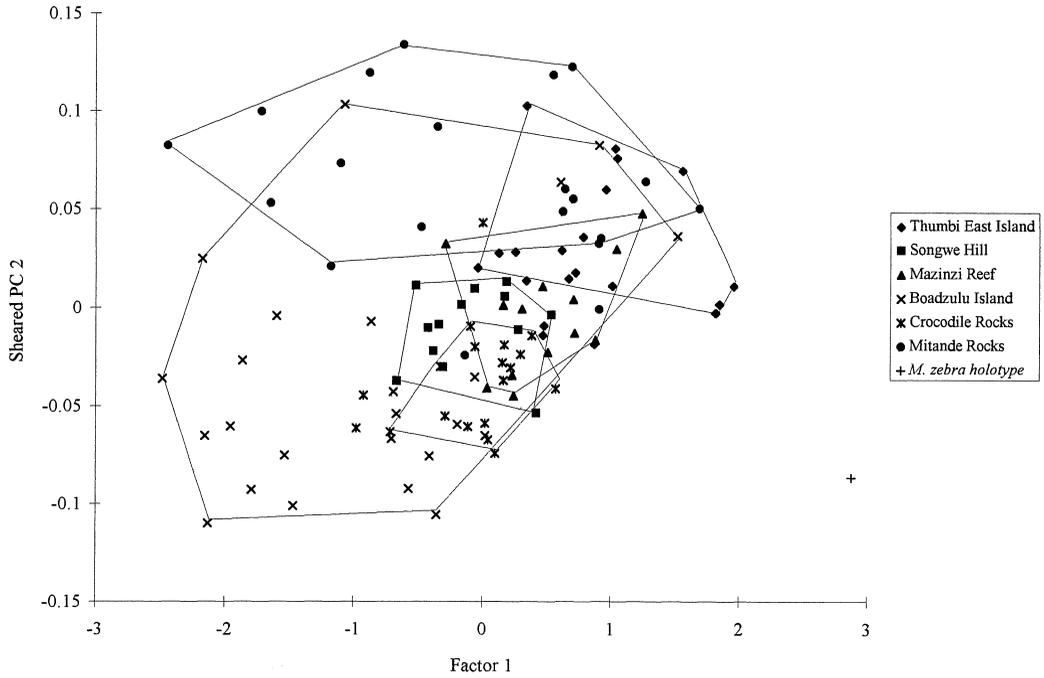


Fig. 6a. Plot of the sheared second principal components (morphometric data) and the first factor score (meristic data) for *Metriaclima zebra* populations from the southern end of Lake Malaŵi.

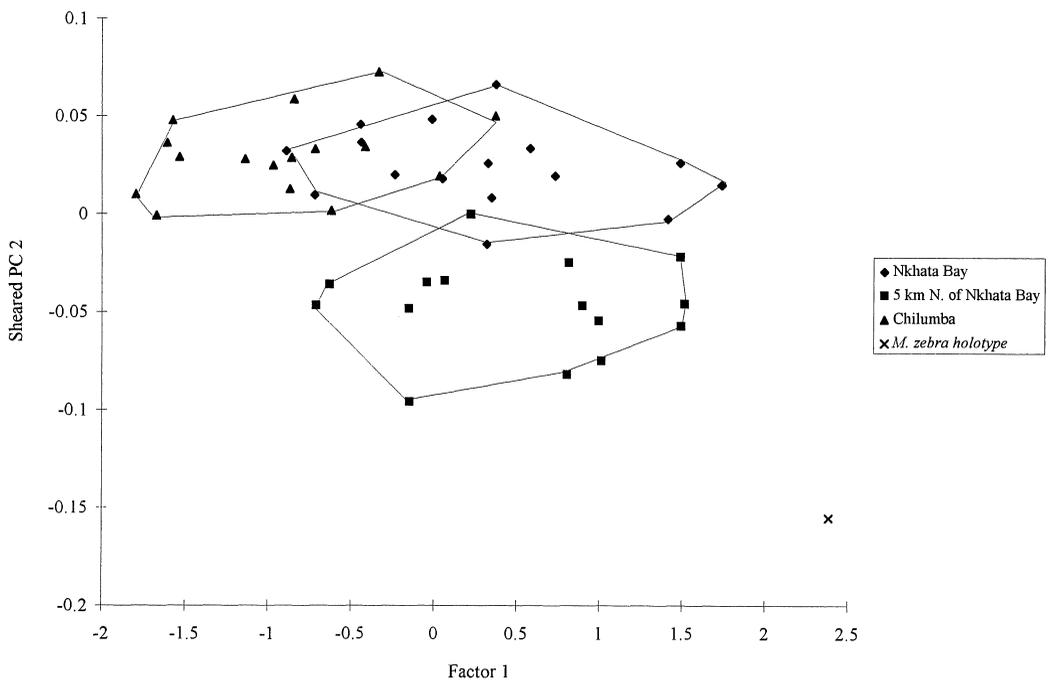


Fig. 6b. Plot of the sheared second principal components (morphometric data) and the first factor score (meristic data) for *Metriaclima zebra* populations from the northern end of Lake Malaŵi.

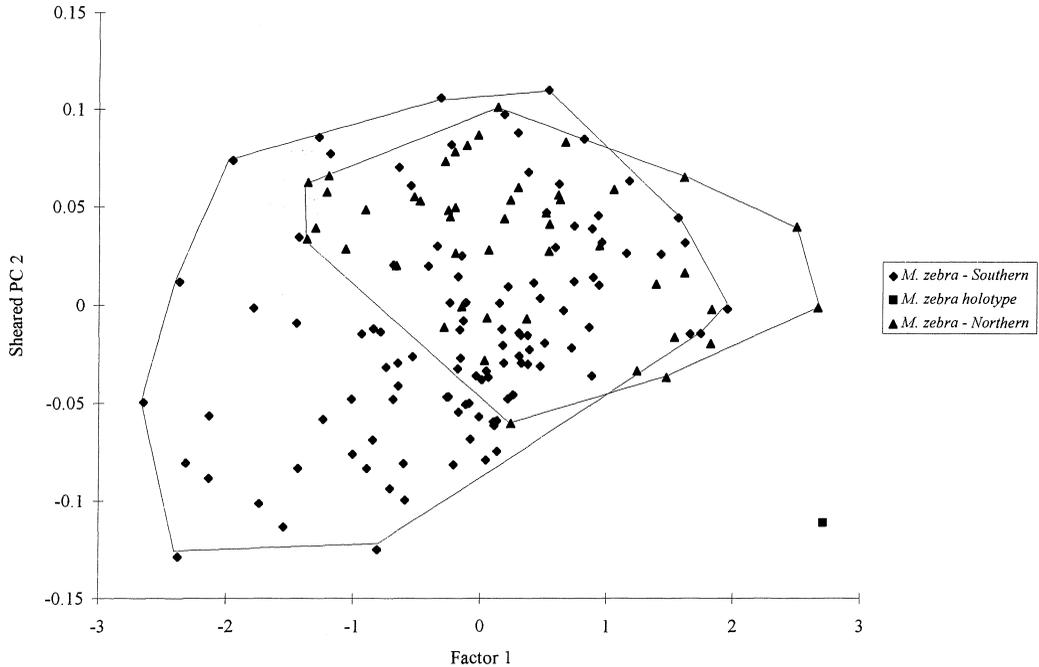


Fig. 6c. Plot of the sheared second principal components (morphometric data) and the first factor score (meristic data) for *Metriaclima zebra* populations from the northern and southern end of Lake Malaŵi.

the scientific and popular literature and regard the holotype as being atypical.

Etymology.—The name *zebra*, from the Greek, meaning black-barred to note the black bars on the lateral side.

Specimens Examined.—BMNH 91.12.17.7, Lake Malaŵi; PSU 3036, PSU 3037, 3; USNM 341908, 3; ANSP 176182, 3; MFU (Malaŵi Fisheries Unit) 11, 3; (63.7 - 88.4 mm), Mazinzi Reef, Lake Malaŵi, Malaŵi Africa, 7-10 m, March, 1991. PSU 3038, 10; USNM 341909, 3; ANSP 176183, 3; MFU 12, 3; (56.1 - 91.9 mm), Crocodile Rocks, Lake Malaŵi, Malaŵi, Africa, 2-10 m, May, 1991. PSU 3039, 9; USNM 341910, 5; ANSP 176184, 5; MFU 13, 5; (61.2 - 89.6 mm), Boadzulu Island, Lake Malaŵi, Malaŵi, Africa, 1-10 m, January, 1991. PSU 3040, 8; USNM 341911, 4; ANSP 176185, 4; MFU 14, 4; (55.5 - 80.0 mm), Thumbi East Island, 3-7 m, February, 1991. PSU 3041, 6; USNM 341912, 2; ANSP 176186, 3; MFU 15, 2; (56.2 - 80.0 mm), Songwe Hill, Lake Malaŵi, Malaŵi, Africa, 3-5 m, January, 1991. PSU 3042, 8; USNM 341913, 4; ANSP 176187, 4; MFU 16, 4; (57.7 - 90.6 mm), Mitande Rocks (Thumbi West Island), Lake Malaŵi, Malaŵi, Africa; 3-5 m, January, 1991. PSU 3043, 7; USNM 341914, 3; ANSP 176188, 3; MFU 17, 3; (57.0 - 84.2 mm), Nkhata Bay, Lake Malaŵi, Malaŵi, Africa, 2-4 m, May, 1991. PSU 3044, 6; USNM 341915, 3; ANSP 176189, 3; MFU 18, 3; (60.2 - 83.6 mm), 5 km north of Nkhata Bay, Lake Malaŵi, Malaŵi, Africa, 2-6 m, June, 1991. PSU 3045, 7; USNM 341916, 3; ANSP 176190, 3; MFU 19, 3; (61.2 - 84.6 mm), Chitande Rocks, Lake Malaŵi, Malaŵi, Africa, 2-6m, July, 1991.

Metriaclima heteropictus (Staeck)

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The high number of teeth rows on the upper jaw (6) and the lower jaw (5-6) distinguishes this form from all other member of the genus.

Description.—Jaws isognathous; teeth on jaws in 5-6 rows; majority of teeth in outer rows bicuspid, with a few unicuspid teeth; those in inner rows tricuspid; 14-16 teeth in outer row of left lower jaw. Dorsal fin with 18 spines and 9-10 rays. Pectoral fin with 13 rays; anal fin with 3 spines and 9-10 rays. Scales along side ctenoid with 32 lateral-line scales. First gill arch with 12 rakers on the ceratobranchial and 2 on the epibranchial, and 1 between the epibranchial and ceratobranchial (Table 2).

Distribution.—Staeck (1980) lists the type locality as Thumbi West Island, Lake Malaŵi; however, no forms which resemble the paratypes have ever been collected at this locality. The name, *Metriaclima heteropictus*, has historically been applied to a large species from Thumbi West Island (Konings 1995); thus, the locality of this form is currently unknown.

Material Examined.—SMF (Natur-Museum und Forschungs-Institut Senckenberg) 15179, SMF 15180, PARATYPES.

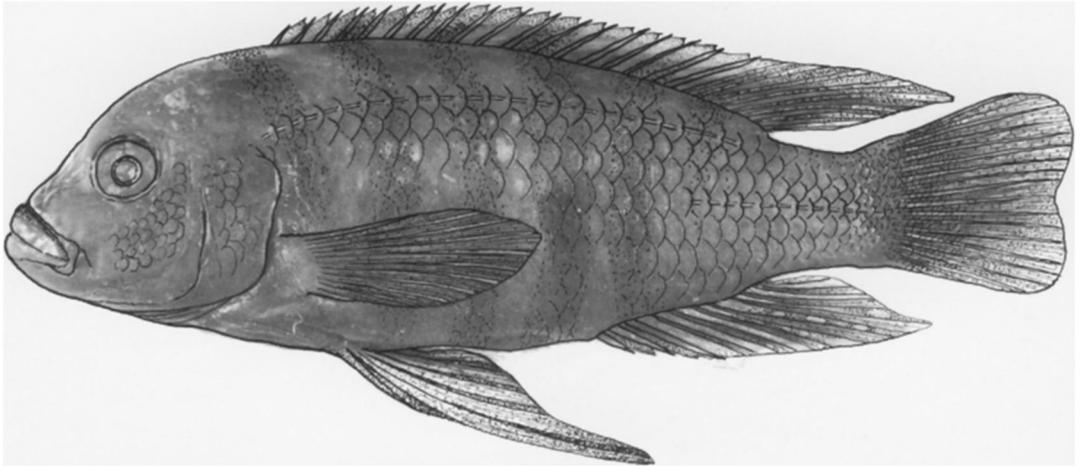


Fig. 7. *Metriaclima melabbranchion*, HOLOTYPE, PSU 3049, adult male, 84.8 mm SL.

Metriaclima melabbranchion Stauffer, Bowers, Kellogg and McKaye, n. sp. (Fig. 7)

Pseudotropheus zebra, Ribbink et al. 1983:158 (in part); Konings (1990) (in part).

HOLOTYPE.—PSU 3049, adult male, 85.7 mm, Mumbo Island, Lake Malaŵi, Malaŵi, Africa, 1-5 m, May, 1991 (Figs. 7 & 8).

PARATYPES.—PSU 3050, 10; USNM 341921, 3; ANSP 176191, 3; MFU 24, 3; (76.8 - 91.5 mm), data as for holotype. PSU 3051, 11; USNM 341922, 3; ANSP 176192, 3; MFU 25, 3; (78.2 - 105.4 mm); Zimbabwe Rocks, Lake Malaŵi, Africa, 1-3 m, May, 1991; PSU 3046, 11; USNM 341917, 3; ASNP 176193, 3; MFU 20, 3; (64.2 - 81.5 mm); Mitande Rocks, Cape MaClear, Lake Malaŵi, Malaŵi, Africa; 11-17 m; March, 1988. PSU 3047, 11; USNM 341918, 3; ASNP 176194, 3; MFU 21, 3; (55.3 - 88.6 mm); Domwe Island, Cape MaClear, Lake Malaŵi, Malaŵi, Africa; 1-3 m, May, 1991. PSU 3048, 11; USNM 341919, 3; ASNP 176195, 3; MFU 22, 3; (64.3 - 86.6 mm); Namalenge Island, Lake Malaŵi, Malaŵi, Africa, 3-9 m, July, 1991.

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The extension of the lateral vertical bars into the dorsal fin discriminates *M. melabbranchion* from *M. zebra*.

Description.—Jaws isognathous (Fig. 7); teeth on jaws in 2-5 rows; majority of teeth in outer rows bicuspid, with a few posterior unicuspid teeth; those in inner rows tricuspid; 9 teeth in outer row of left lower jaw of holotype, 3-12 in paratypes. Dorsal fin with 18 spines in the holotype and 16-19 in paratypes; dorsal-fin rays 8 in holotype and 8-10 in paratypes. Pectoral fin with 12 rays in

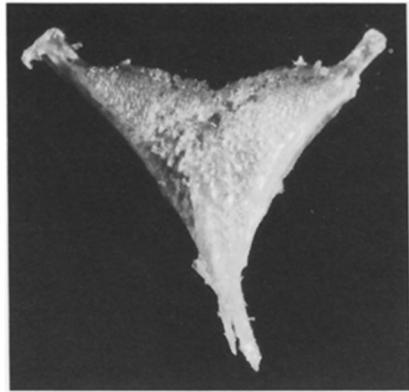


Fig. 8. Lower pharyngeal bone of the holotype of *Metriaclima melabbranchion*, PSU 3049.

holotype and 12-14 in paratypes; anal fin with 3 spines, 8 rays in holotype and 7-9 in paratypes. Lower pharyngeal bone triangular in outline (Fig. 8). Scales along side ctenoid; holotype with 32 lateral-line scales and 31-34 in paratypes. First gill arch with 11-14 rakers on the ceratobranchial, 2-5 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 3).

Breeding males have a dark blue ground coloration laterally with 6-10 vertical bars; breast with a reddish cast on some specimens and tends to be more pronounced in the population from Zimbabwe Rocks; head dark blue to black with 1-2 blue interorbital bars, gular blue/black. Dorsal fin blue with black vertical bars from side extending into dorsal fin; some individuals have orange spots in the posterior three membranes. Caudal fin with black rays and blue/gray membranes; anal fin gray/black with 3-5 yellow ocelli; P_2 black with

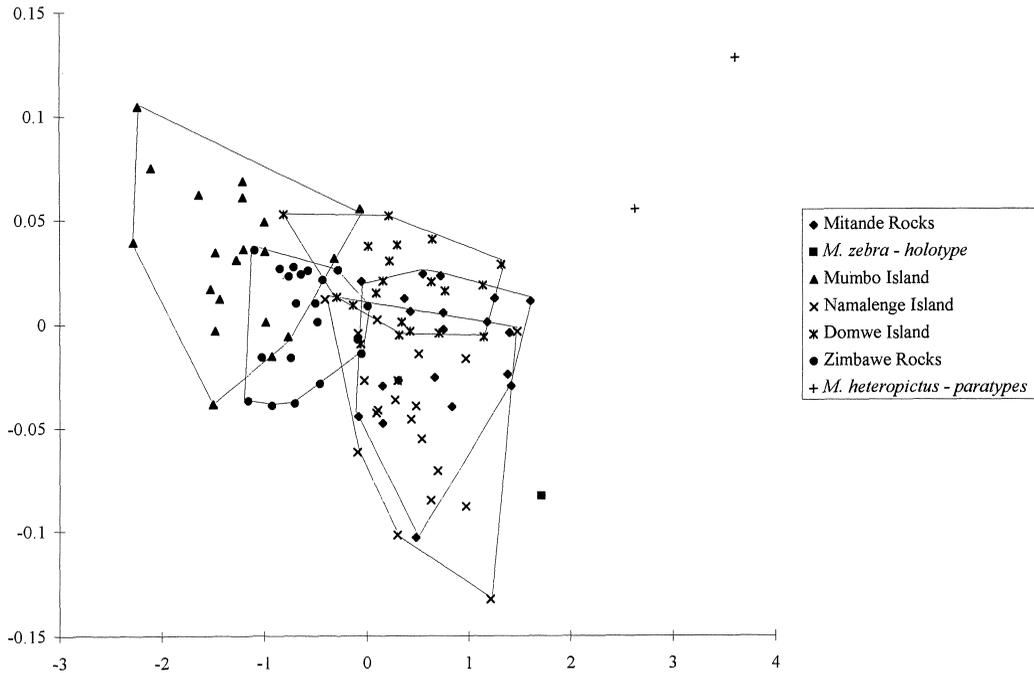


Fig. 9. Plot of the sheared second principal components (morphometric data) and the first factor score (meristic data) for *Metriaclima melabranchion* populations and *Metriaclima heteropictus* PARATYPES.

white leading edge; P_1 clear. Females brown/green laterally with blue/green highlights and 5-7 vertical bars; head dorsally dark brown with 1-2 green interorbital bars; gular blue/white with scattered micromelanophores; cheek and opercular light blue. Dorsal fin blue/gray to brown; caudal fin brown with yellow tips in some individuals; anal fin gray to brown with 0-4 yellow ocelli; P_2 blue/white leading edge, first two rays and membranes black with posterior ones clear; P_1 clear.

Distribution.—*Metriaclima melabranchion* occurs at Mitande Rocks (Thumbi West Island), Domwe Island, Mumbo Island, Zimbabwe Rocks, and Namalenge Island. The minimum polygon clusters formed when the first principal components of the meristic data are plotted against the sheared second principal components of the morphometric data for the populations of *M. melabranchion* appear to form a clinal grade (Fig. 9). The fact that *M. melabranchion* is sympatric with *M. zebra* at Mitande Rocks supports the conclusion that these two taxa are heterospecific.

Etymology.—The name *melabranchion* from the Greek, meaning black fin to note the extension of the lateral black bars onto the dorsal fin.

Metriaclima chrysomallos Stauffer, Bowers, Kellogg and McKaye, n. sp. (Fig. 10)

HOLOTYPE.—PSU 3052, adult male, 84.8 mm, Mumbo Island, Lake Malaŵi, Malaŵi, Africa, 1-5 m, May, 1991 (Figs. 10 & 11).

PARATYPES.—PSU 3053, 7; USNM 34192, 4; ANSP 176196, 4; MFU 23, 4; (61.0 - 89.6 mm); data as for holotype.

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The continuation of the vertical bars on the side of fish into the dorsal fin separates this species from *M. zebra*. The gold highlights on the light blue ground coloration distinguishes this species from *M. melabranchion*.

Description.—Jaws isognathous (Fig. 10); teeth on jaws in 2-3 rows; majority of teeth in outer rows bicuspid, with a few posterior unicuspid teeth; those in inner rows tricuspid; 13 teeth in outer row of left lower jaw of holotype, 6-13 in paratypes. Dorsal fin with 17 spines in the holotype and 17-18 in paratypes; dorsal-fin rays 9 in holotype and 8-10 in paratypes. Pectoral fin with 13 rays; anal fin with 3 spines and 6-8 rays. Lower pharyngeal bone triangular in outline (Fig. 11). Scales along side ctenoid; holotype with 32 lateral

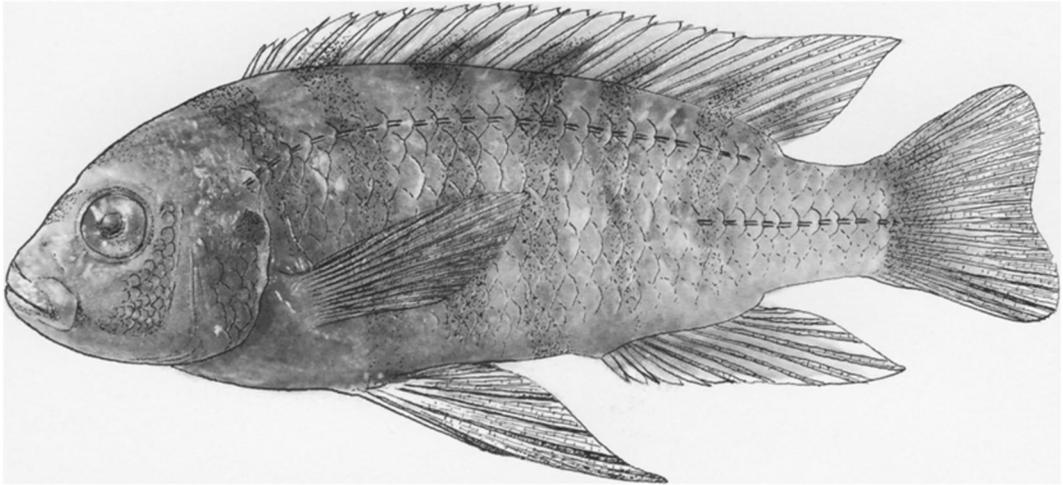


Fig. 10. *Metriaclima chrysomallos*, HOLOTYPE, PSU 3052, adult male, 85.7 mm SL.

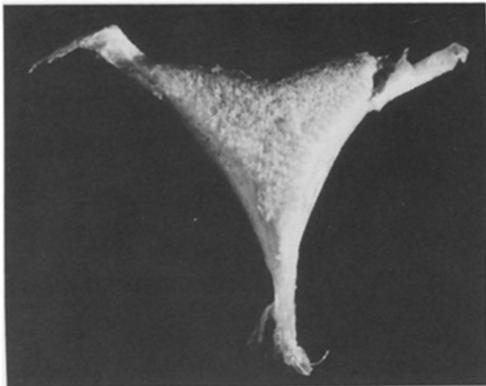


Fig. 11. Lower pharyngeal bone of the type specimen of *Metriaclima chrysomallos*, PSU 3052.

scales and 31-33 in paratypes. First gill arch with 11-14 rakers on ceratobranchial, 2-3 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 4).

Breeding males have a light blue ground coloration laterally with gold highlights and 6 gray vertical bars; ventral portion fades to pale blue/green; head gray with 2 blue interorbital bars, green opercle, blue cheek, and gray gular. Dorsal fin pale blue with vertical bars extending into it; posterior 4 membranes are rust/orange distally. Caudal fin light blue/green; anal fin blue with 3-5 yellow ocelli; P₂ with light blue leading edge, spine and first 2 membranes black, remainder clear; P₁ clear. Females have a pale green/beige ground coloration with gold highlights and 6 gray vertical bars; head gray with 2 blue interorbital bars, green opercle and cheek, and white gular.

Distribution.—*Metriaclima chrysomallos* is endemic to Mumbo Island.

Etymology.—The name *chrysomallos*, from the Greek, meaning gold-fleeced to note the gold highlights on the lateral side in both sexes.

Metriaclima phaeos Stauffer, Bowers, Kellogg and McKaye, n. sp. (Fig. 12)

HOLOTYPE.—PSU 3054, adult male, 85.1 mm, Cobue, Lake Malaŵi, Mozambique, Africa, 1-5 March, 1996 (Figs. 12 & 13).

PARATYPES.—PSU 3055, 5; USNM 341923, 1; ANSP 176197, 1; MFU 26, 1; (68.3 - 86.5 mm), data as for holotype.

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. *Metriaclima phaeos* superficially resembles *M. zebra*, but the dusky submarginal band in the dorsal fin of *M. phaeos* distinguishes it from all other BB members of the genus. The minimum polygons formed by plotting the first principal components of the meristic data against the sheared second principal components of the morphometric data (Fig. 14) illustrate that the minimum polygons formed by *M. phaeos* do not overlap with those formed by any of the populations of *M. zebra*.

Description.—Jaw isognathous (Fig. 12); teeth on jaws in 3-4 rows; majority of teeth in outer rows bicuspid, with a few posterior unicuspid teeth; those in inner rows tricuspid; 12 teeth in outer row of left lower jaw of holotype, 11-13 in paratypes. Dorsal fin with 17 spines in the holotype and 17-18 in paratypes; dorsal-fin rays 9. Pectoral

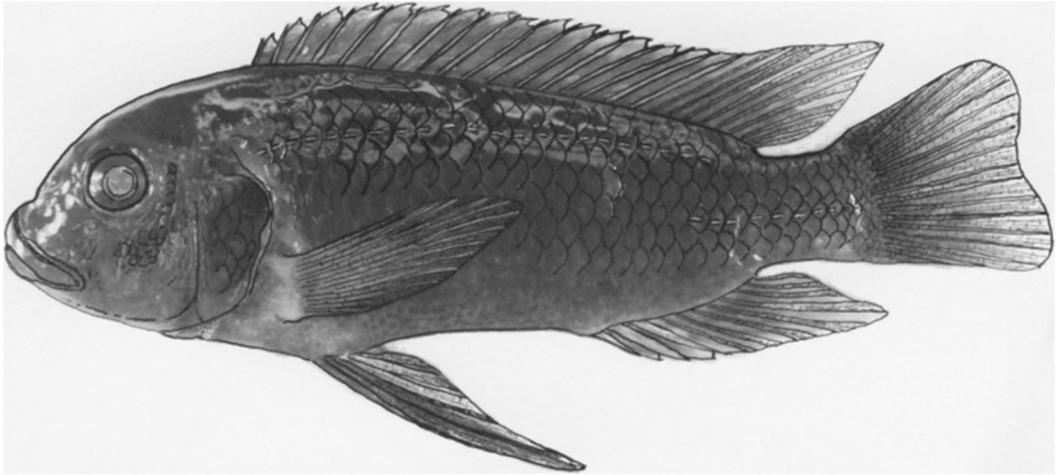


Fig. 12. *Metriaclima phaeos*, HOLOTYPE, PSU 3054, adult male, 85.1 mm SL.

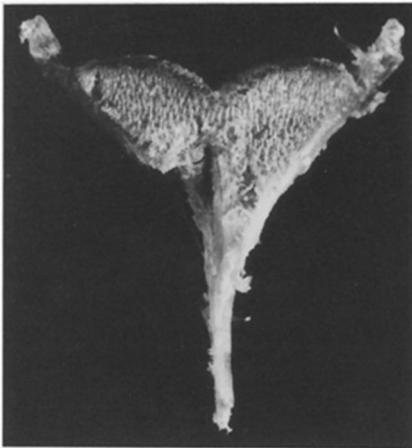


Fig. 13. Lower pharyngeal bone of the type specimen of *Metriaclima phaeos*, PSU 3054.

fin with 14 rays in holotype and 14-15 in paratypes; anal fin with 3-4 spines and 8 rays. Lower pharyngeal bone triangular in outline (Fig. 13). Scales along side ctenoid; holotype with 31 lateral-line scales and 31-32 in paratypes. First gill arch with 11-13 rakers on the ceratobranchial, 2-4 on the epibranchial, and 1 between the epibranchial and ceratobranchial (Table 5).

Breeding males dark blue ground coloration laterally with 6-8 vertical bars; belly white; head dark blue with iridescent blue interorbital bar; gular gray/white; dorsal fin light blue proximally, becoming lighter distally; thin dusky submarginal band and white lappets; rayed portion of the dorsal fin is yellow/white in distal one-third; caudal fin deep blue proximally, light blue distally

with trailing yellow edge; anal fin light blue/purple becoming dusky then white in posterior distal portion with 3 yellow ocelli; P_2 blue/white leading edge with distinct, bold submarginal black band, remainder hyaline; P_2 clear. Females dark blue/gray with 6-8 dark gray bars; ventral one-fifth of flank yellow/brown; head dark brown with faint blue/brown interorbital bar; cheek and operculum yellow/brown; dorsal fin yellow/brown highlights on a light blue ground; very faint thin dusky submarginal band with white lappets and yellow/brown tips of serial elements; rayed portion with yellow/brown spots; caudal fin with faint light blue membranes and yellow/brown rays; anal fin blue/gray with transparent edge and 3 faint yellow/brown ocelli; P_2 with white leading edge and black submarginal band with yellow/brown membranes; P_1 clear.

Distribution.—*Metriaclima phaeos* was collected only at Cobue, Mozambique, but may have a more extensive distribution along the Mozambique coastline.

Etymology.—The name *phaeos*, from the Greek, meaning dusk to note the dusky submarginal band present in the dorsal fin of both sexes.

***Metriaclima cyneusmarginatus* Stauffer, Bowers, Kellogg and McKaye, n. sp. (Fig. 15)**

HOLOTYPE.—PSU 3056, adult male, 73.9 mm, Nkhota khota, Lake Malaŵi, Malaŵi, Africa, 1-3 m, February, 1995 (Figs. 15 & 16).

PARATYPES.—PSU 3057, 11; USNM 341924, 3; ANSP 176198, 3; MFU 27, 3; (51.9 - 80.4 mm), data as for holotype.

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathus jaws, and the presence of bicuspid teeth in the

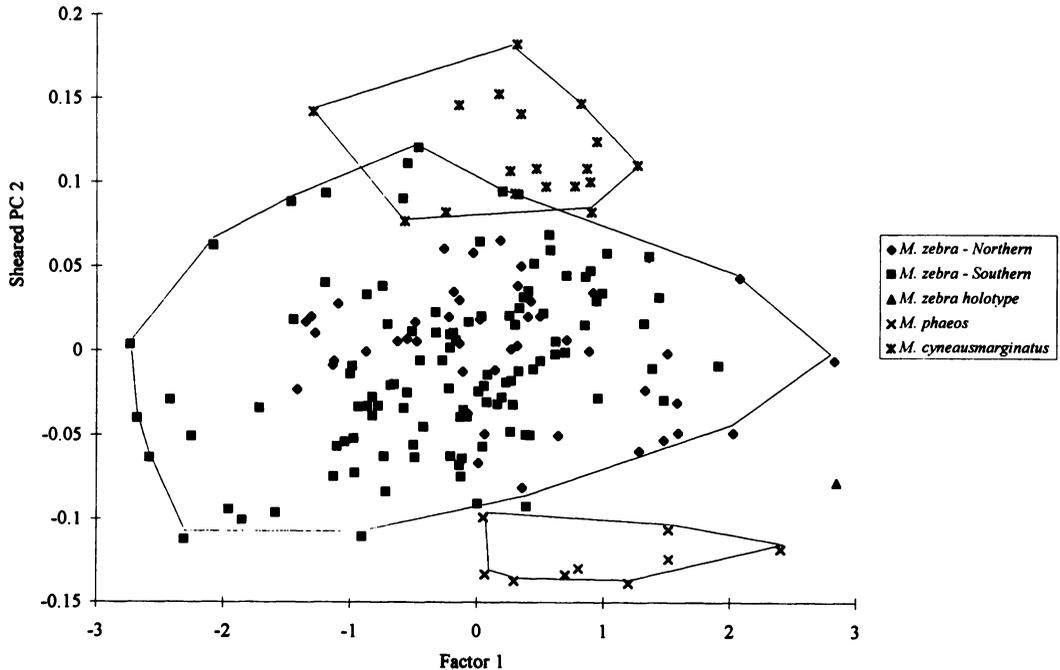


Fig. 14. Plot of the sheared second principal components (morphometric data) and the first factor score (meristic data) for *Metriaclima zebra* populations from the northern and southern end of Lake Malaŵi, as well as, *Metriaclima phaeos* and *Metriaclima cyneusmarginatus*.

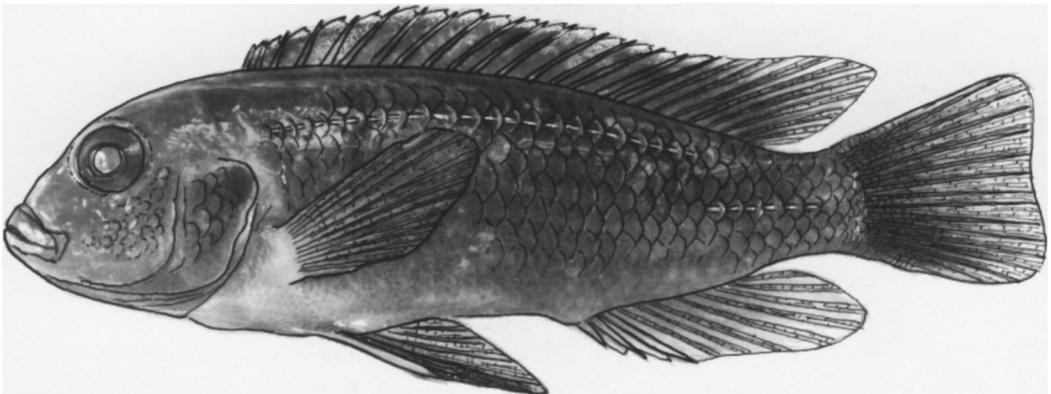


Fig. 15. *Metriaclima cyneusmarginatus*, HOLOTYPE, PSU 3056, adult male, 73.9 mm SL.

outer rows of the jaws place this species in *Metriaclima*. The blue marginal band and brown lappets distinguishes it from other members of *Metriaclima*. The minimum polygons formed by plotting the first principal components of the meristic data against the sheared second principal components of the morphometric data (Fig. 14) illustrate that the minimum polygon formed by *M. cyneusmarginatus* is significantly different with those formed by *M. phaeos*.

Description.—Jaws isognathous (Fig 15); teeth on jaws in 2-3 rows; majority of teeth in outer rows bicuspid, with a few posterior unicuspid teeth; those in inner rows tricuspid; 12 teeth in outer row of left lower jaw of holotype, 8-12 in paratypes. Dorsal fin with 17 spines in holotype, 17-18 in paratypes; dorsal-fin rays 9 in holotype, 8-10 in paratypes. Pectoral fin with 13 rays in holotype, 11-15 in paratypes; anal fin with 3 spines; anal-fin rays 8 in holotype, 7-8 in paratypes. Lower phar-



Fig. 16. Lower pharyngeal bone of the type specimen of *Metriaclima cyneusmarginatus*, PSU 3056.

pharyngeal bone triangular in outline (Fig. 16). Scales along side ctenoid; holotype with 32 lateral-line scales and 31-33 in paratypes. First gill arch with 10-12 rakers on the ceratobranchial, 2-3 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 6).

Breeding males have a blue ground coloration laterally with 5-6 gray vertical bars and a white belly. Dorsal fin blue/gray with a blue marginal band and brown lappets; caudal-fin rays gray, membranes blue, with brown tips; anal fin blue with 2 yellow ocelli; P_2 with light blue leading edge, spine and first 2 membranes black, posterior rays and membranes clear; P_1 clear. Females similarly colored but not as intense and they lack ocelli on the anal fin.

Distribution.—*Metriaclima cyneusmarginatus* was collected only at Nkhota khota.

Etymology.—The name *cyneusmarginatus*, from the Greek, meaning blue margin to note the blue marginal band in the dorsal fin.

***Metriaclima benetos* Stauffer, Bowers, Kellogg and McKaye, n. sp. (Fig. 17)**

Pseudotropheus zebra 'mazinzi', Ribbink et al. 1983: 160;

Pseudotropheus zebra Konings 1990: 442 (in part).

HOLOTYPE.—PSU 3058, adult male, 81.4 mm, Mazinzi Reef, Lake Malaŵi, Malaŵi, Africa, 10-15 m, January, 1991 (Figs. 17 & 18).

PARATYPES.—PSU 3059, 9; USNM 349125, 3; ANSP 176199, 3; MFU 28, 3; (59.7 - 81.4 mm), data as for holotype.

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The pale blue ground color with the absence of distinct black vertical bars distinguishes *M. benetos* (Fig. 19a) from all other members of this genus, with the exception of *Metriaclima callainos* (Fig. 19b). *Metriaclima benetos* females are brown with green highlights, while *M. callainos* females are either light blue or white (Fig. 19c). In general, *M. benetos* have fewer dorsal-fin spines (mode - 17) than *M. callainos* (mode - 18) (Table 7). The first principal components of the meristic data were plotted against the sheared second principal components of the morphometric data. There was no overlap in the minimum polygon clusters formed by *M. benetos* with that formed by *M. callainos* (Fig. 20). Variables that had the highest loadings on the sheared second principal compo-

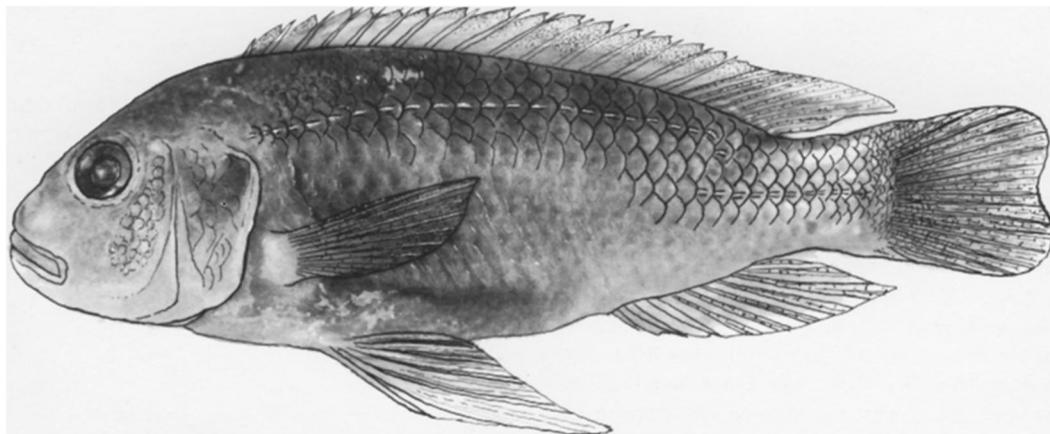


Fig. 17. *Metriaclima benetos*, HOLOTYPE, PSU 3058, adult male, 81.4 mm SL.

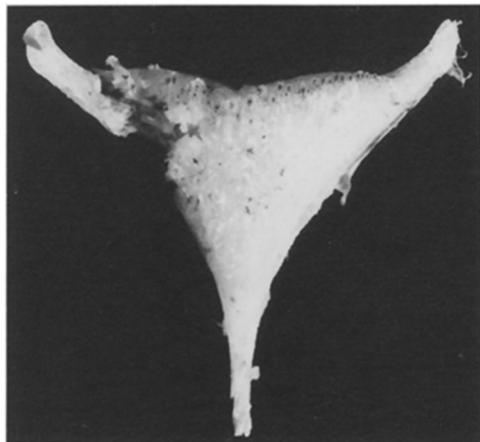


Fig. 18. Lower pharyngeal bone of the type specimen of *Metriaclima benetos*, PSU 3058.

nents were horizontal eye diameter (-0.439), caudal peduncle length (0.409), and preorbital depth (0.313); while those with the highest loadings on the principal components of the meristic data were number of dorsal spines (0.227), number of P_1 rays (0.215), and number of teeth on the left side of the lower jaw (0.216).

Description.—Jaws isognathous (Fig. 17); teeth on jaws in 3-4 rows; majority of teeth in outer rows bicuspid, with a few posterior unicuspid teeth; those in inner rows tricuspid; 9 teeth in outer row of left lower jaw of holotype, 9-13 in paratypes. Dorsal fin with 16 spines in holotype and 16-18 in paratypes; dorsal-fin rays 9 in holotype, 8-10 in paratypes. Pectoral fin with 13 rays in holotype and 12-14 in paratypes; anal fin with 3 spines; anal fin with 7 rays in holotype and 6-8 in paratypes. Lower pharyngeal bone triangular in outline (Fig. 18). Scales along side ctenoid; holotype with 29 lateral-line scales and 29-32 in paratypes. First gill arch with 9-12 on the ceratobranchial, 3-4 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 7).

Breeding males have a light blue ground coloration laterally that is darker dorsally and fades to white ventrally. For the most part, no vertical bars are visible, but on occasion, faint bars are noticeable immediately after preservation. Head blue/gray, cheek light blue, white gular. Some larger males in the wild have yellow gulars. Although rarely seen in wild specimens, alpha males held in aquaria will sometimes develop a bright yellow gular. Dorsal fin proximally blue gray with green highlights and white marginal band; caudal fin proximally blue/gray with white membranes with a yellow cast on distal two-thirds; anal fin with white membrane with yellow cast be-



Fig. 19a. *Metriaclima benetos* from Mazinzi Reef.



Fig. 19b. *Metriaclima callainos* male from Mitande Rocks.



Fig. 19c. *Metriaclima callainos* female, white morph, from Mitande Rocks.

tween spine and first ray, remainder of the membranes light blue with 2 yellow ocelli; P_2 with yellow rays and light transparent blue membranes; P_1 yellow rays and clear membranes. Females have a brown ground coloration with green and blue highlights and 6-8 faint vertical bars; head brown with blue highlights below eye and on cheek, gular white with blue cast. Dorsal fin uniformly orange/brown; caudal fin orange/brown; anal fin transparent brown with no ocelli; P_2 brown with black leading edge; P_1 clear.

Distribution.—*Metriaclima benetos* is endemic to Mazinzi Reef in the southeastern arm of Lake Malaŵi.

Etymology.—The name *benetos*, from the Greek, meaning blue to note the light blue ground coloration of breeding males.

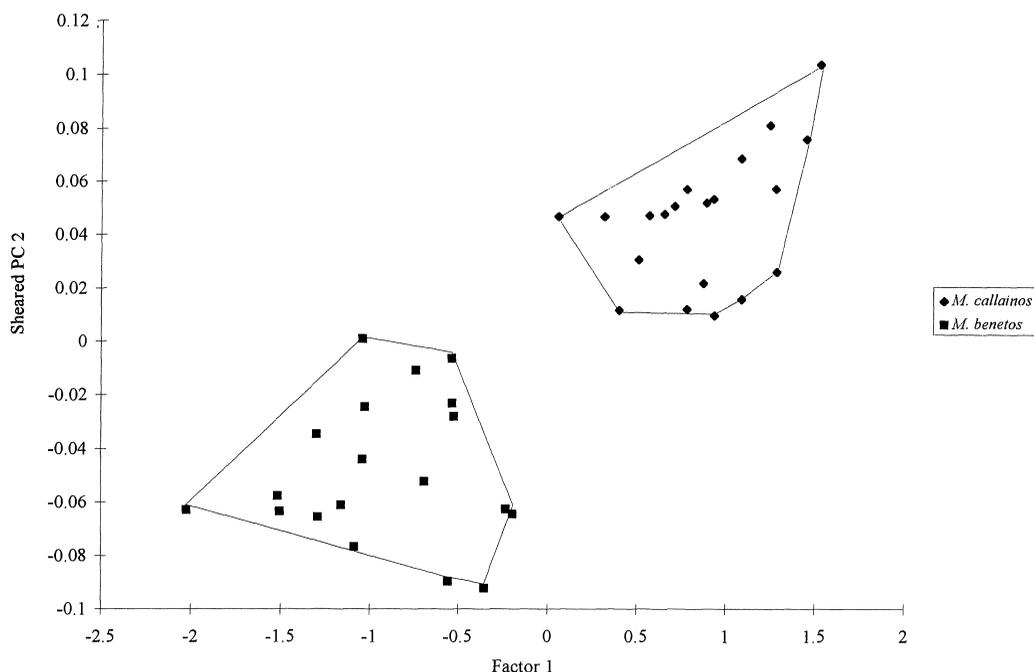


Fig. 20. Plot of the sheared second principal components (morphometric data) and the first factor score (meristic data) for *Metriaclima benetos* and *Metriaclima callainos*.

Metriaclima callainos (Stauffer and Hert)

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The pale blue ground color with the absence of distinct black vertical bars distinguishes *M. callainos* (Fig. 19b) from all other members of this genus, with the exception of *M. benetos* (Fig. 19a). *M. callainos* females are either light blue or white (Fig. 19c), while *Metriaclima benetos* females are brown with green highlights. In general, *M. callainos* have a greater number of dorsal-fin spines (mode - 18) than *M. benetos* (mode - 17) (Table 7). The first principal components of the meristic data were plotted against the sheared second principal components of the morphometric data for *M. benetos* and *M. callainos*. There was no overlap in the minimum polygon formed by *M. benetos* with that formed by *M. callainos* (Fig. 20). Variables that had the highest loadings on the sheared second principal components were horizontal eye diameter (-0.439), caudal peduncle length (0.409), and pre-orbital depth (0.313); while those with the highest loadings on the principal components of the meristic data were number of dorsal spines (0.227), number of P_1 rays (0.215), and number of teeth on the left side of the lower jaw (0.216).

Description.—Jaws isognathous (Stauffer and

Hert 1992); teeth on jaws in 3-4 rows; majority of teeth in outer rows bicuspid, with a few posterior unicuspid teeth; those in inner rows tricuspid; 13-17 teeth in outer row of left lower jaw. Dorsal fin with 17-18 spines and 8-9 rays. Lower pharyngeal bone triangular in outline (Stauffer and Hert 1992). Scales along side ctenoid with 30-32 lateral-line scales. First gill arch with 11-12 rakers on the ceratobranchial, 1-3 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 7).

Breeding males have a light blue ground coloration with green highlights on dorsal one-third; head light blue with green highlights dorsally, with white gular and black opercular spot. Occasionally, males will be either white or blue/white blotched. Dorsal fin light blue; caudal fin light blue; anal fin white proximally, light blue distally, with 1-3 yellow ocelli; P_2 with black rays and clear membranes; P_1 clear with white leading edge. A few females are similarly colored, but not as intense and lack ocelli; some females white overall (Fig. 19c; Stauffer and Hert 1992), and an occasional blue/white blotched female is observed (Schroder 1980).

Distribution.—*Metriaclima callainos* is indigenous to the Nkhata Bay area, but has been introduced to Likoma, Namalenje, and Thumbi West islands (Ribbink et al. 1983; Stauffer and Hert 1992). In

Nkhata Bay, *M. callainos* is sympatric with *M. zebra*. Schroder (1980) concluded that these two forms were heterospecific, because he observed assortative mating. The introduced population at

Thumbi West Island has diverged morphologically from the Nkhata Bay population, and specimens have been observed that may be hybrids between the *M. zebra* and the introduced population of *M.*

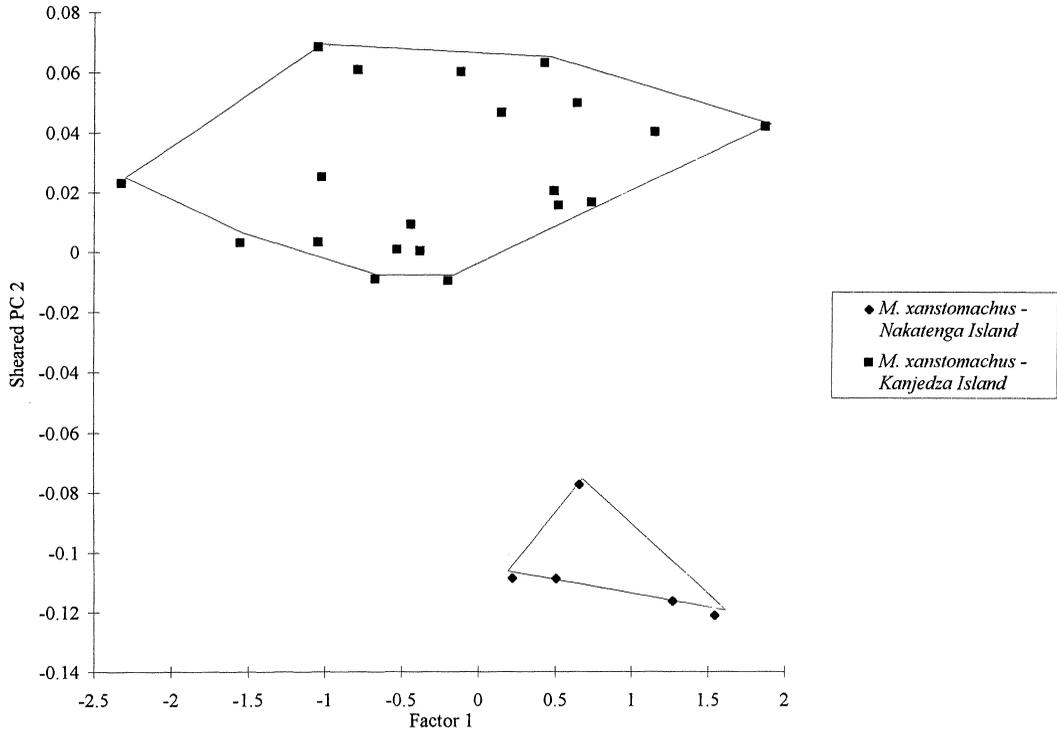


Fig. 21. Plot of the sheared second principal components (morphometric data) and the first factor score (meristic data) for *Metriaclima xanstomachus*.

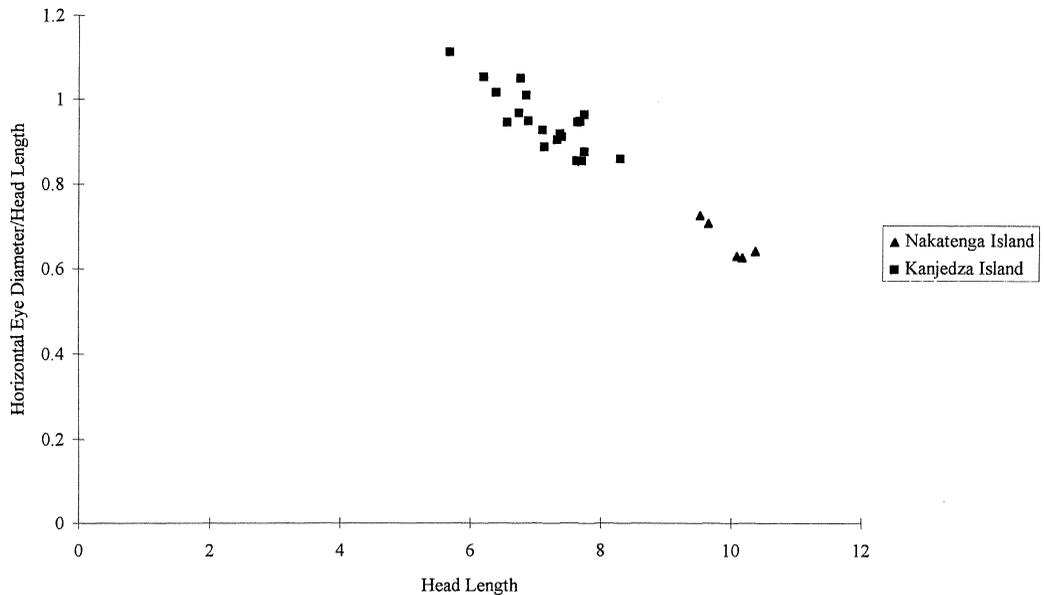


Fig. 22. Plot of the horizontal eye diameter/head length ratio versus head length for two allopatric populations of *Metriaclima xanstomachus*, indicating allometric growth.

callainos (Stauffer and Hert 1992). There is an undescribed species in which all males and females are white at Ruarwe, which we consider to be heterospecific and will be described in a subsequent paper.

Material Examined.—PSU 2542.1, PSU 2542.2, MFU 2, USNM 322426; Nkhata Bay, Lake Malaŵi, Malaŵi, Africa, 3-4 m, May, 1988.

Metriaclima xanstomachus (Stauffer and Boltz)

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The light blue body coloration with 6 vertical bars coupled with a bright yellow gular and blue dorsal fin delimits *M. xanstomachus* from all other known *Metriaclima* species.

Description.—Jaws isognathous (Stauffer and Boltz 1989: 9); teeth on jaws in 3-5 rows; majority of teeth in outer rows bicuspid, with a few posterior or unicuspid teeth; those in inner rows tricuspid; 9-11 teeth in outer row of left lower jaw. Dorsal fin with 16-18 spines and 8-10 rays. Pectoral fin with 12-14 rays; anal fin with 3 spines and 7-8 rays. Lower pharyngeal bone triangular in outline (Stauffer and Boltz 1989: 9). Scales along side ctenoid with 30-33 lateral-line scales. First gill arch with 9-12 rakers on ceratobranchial, 2-3 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 8).

Breeding males with light blue ground color and 6 vertical gray bars; head dark blue with 1 light blue interorbital bar, yellow gular and branchiostegal rays. Dorsal fin blue with gray flecks; anal fin blue with 3-5 yellow ocelli; P₂ fins black anteriorly fading to yellow/brown posteriorly; P₁ black (Stauffer and Boltz 1989).

Distribution.—*Metriaclima xanstomachus* was originally thought to be endemic to the Maleri Islands (Ribbink et al. 1983, Stauffer and Boltz 1989); however, analysis of shape and color patterns showed that the population inhabiting Kanjedza Island is also *M. xanstomachus*. The first principal components of the meristic data were plotted against the sheared second principal components of the morphometric data (Fig. 21). The minimum polygons formed by the populations inhabiting Nakantenga Island (one of the three Maleri islands) and Kanjedza Island were significantly ($P < 0.05$) different. Variables that had the highest loadings on the principal components of the meristic data were teeth rows in the upper jaw (0.248), teeth rows in the lower jaw (0.244), and number of scale rows on cheek (0.238), while those with the highest loadings on the sheared second

principal components of the morphometric data were snout length (-0.421), caudal peduncle length (0.378), and preorbital depth (-0.304). There is clearly non-overlapping morphometrics for the two populations of *M. xanstomachus*. The specimens from Nakantenga Island are all larger than those from Kanjedza Island; thus, differences observed may be attributed to allometric growth. For example, when horizontal eye diameter/head length is plotted against head length allometric growth is indicated (Fig. 22). There are certainly links between the *Metriaclima* populations at the Maleri Islands with those at Kanjedza Island. For example *M. barlowi* occurs at both localities and there is a form with a red dorsal fin at both islands, although in the latter case, we regard the two red-top forms as distinct species (see below). It may be that the two populations of *M. xanstomachus* represent semi-species (*sensu* Mayr) or are, in fact, heterospecific.

Material Examined.—PSU 3060, 5; Nakantenga Island, Lake Malaŵi, Malaŵi, Africa; 3-7 m, March, 1991; PSU 3061, 20; Kanjedza Island, Lake Malaŵi, Malaŵi, Africa; 1-4 m, March, 1988.

Metriaclima pyrsonotos Stauffer, Bowers, Kellogg and McKay, n. sp. (Fig. 23)

Pseudotropheus zebra 'red dorsal', Ribbink et al. 1983: 162; Konings 1990: 454 (in part).

HOLOTYPE.—PSU 3062, adult male, 74.1 mm, Nakantenga Island (Maleri Islands), Lake Malaŵi, Africa, 2-4 m, March, 1991 (Figs. 23 & 24).

PARATYPES.—PSU 3063, 8; USNM 341926, 4; ANSP 176200, 3; MFU 7, 4; (56.9 - 76.6 mm), data as for holotype.

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The red dorsal fin in combination with black bars on a blue ground color distinguish this form from all other members of the genus except for *Metriaclima sandaracinos* (Mpanda Island and Kanjedza Island) and *Metriaclima emmiltos* (Chilumba), which also have red dorsal fins. *Metriaclima pyrsonotos* differs from all the other red top BB forms in that the vertical black lateral bars infiltrate the proximal portion of the dorsal fin. In general, *M. pyrsonotos* has fewer teeth in the outer row of the left lower jaw (mode - 7) than *M. emmiltos* from Chilumba (mode - 9), and *M. sandaracinos* from Kanjedza (mode - 10), or Mpanda (mode - 12) islands (Table 9).

Description.—Jaws isognathous (Fig. 23); teeth on jaws in 2-3 rows; majority of teeth in outer rows bicuspid, with a few posterior unicuspid teeth; those in inner rows tricuspid; 7 teeth in out-

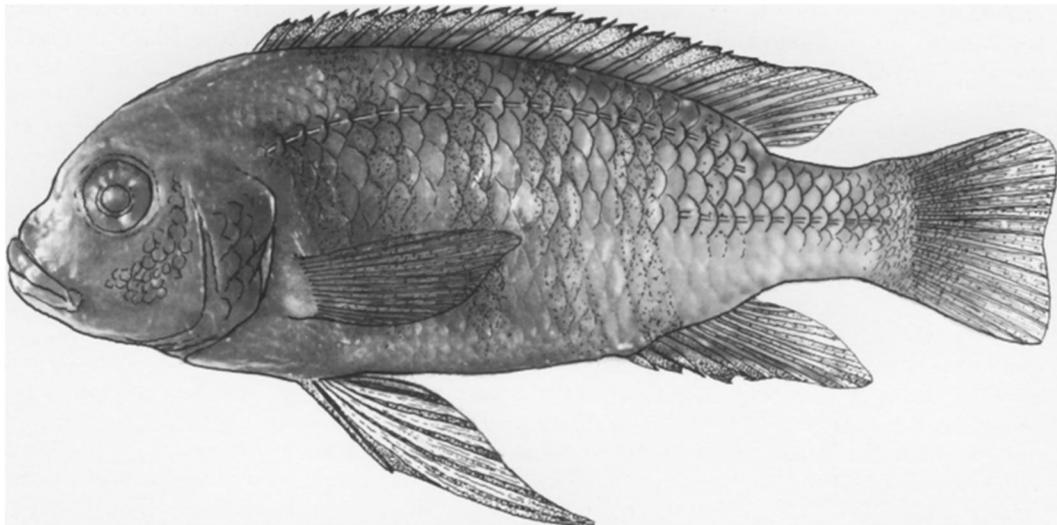


Fig. 23. *Metriaclima pyrsonotos*, HOLOTYPE, PSU 3062, adult male, 74.1 mm SL.

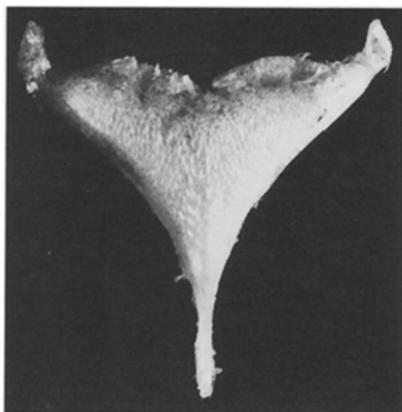


Fig. 24. Lower pharyngeal bone of the type specimen of *Metriaclima pyrsonotos*, PSU 3062.

er row of left lower jaw of holotype, 4-10 in paratypes. Dorsal fin with 17 spines in the holotype and 16-18 in paratypes; dorsal-fin rays 8 in holotype and 8-10 in paratypes. Pectoral fins with 13 rays in holotype and 12-14 in paratypes; anal fin with 3 spines and 7 rays in holotype and 6-8 in paratypes. Lower pharyngeal bone triangular in outline (Fig. 24). Scales along side ctenoid; holotype with 31 lateral-line scales and 30-32 in paratypes. First gill arch with 10-14 rakers on the ceratobranchial, 2-3 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 9).

Breeding males have a light blue ground coloration laterally with 5-6 black vertical bars anterior

to the caudal peduncle; belly anterior to the P_2 's black fading to light blue posteriorly; head black with 2 light interorbital bars; dorsal fin red/orange with vertical lateral bars of side sometimes penetrating the fin; light blue lappets; caudal fin blue with some specimens having an orange cast; anal fin blue with 1-4 yellow ocelli; pelvic fins black with white leading edges. Females blue/gray laterally with faint barring. Some individuals almost entirely black; head black with gray interorbital bars; dorsal fin with brown cast; anal fin and pelvic fins black.

Distribution.— Endemic to the Maleri islands where it has been observed at both Nakantenga and Maleri islands. Ribbink et al. (1983) postulated that it was originally restricted to Nakantenga Island, but was introduced to Maleri Island. The minimum polygon clusters formed by the *M. pyrsonotos* and *M. sandaracinos* inhabiting Mpanda and Kanjedza islands (see below) were significantly ($P < 0.05$) different (Fig. 25). Variables that had the highest loadings on the sheared second principal components were snout length (0.473), pre-orbital depth (0.373), and caudal peduncle length (-0.332), while those having the highest loadings on the meristic data were number of teeth on the left lower jaw (-0.366), number of gill rakers on the ceratobranchial (0.308), and number of gill rakers on the epibranchial (0.273).

Etymology.— The name *pyrsonotos*, from the Greek, meaning red-backed to note the red dorsal fin.

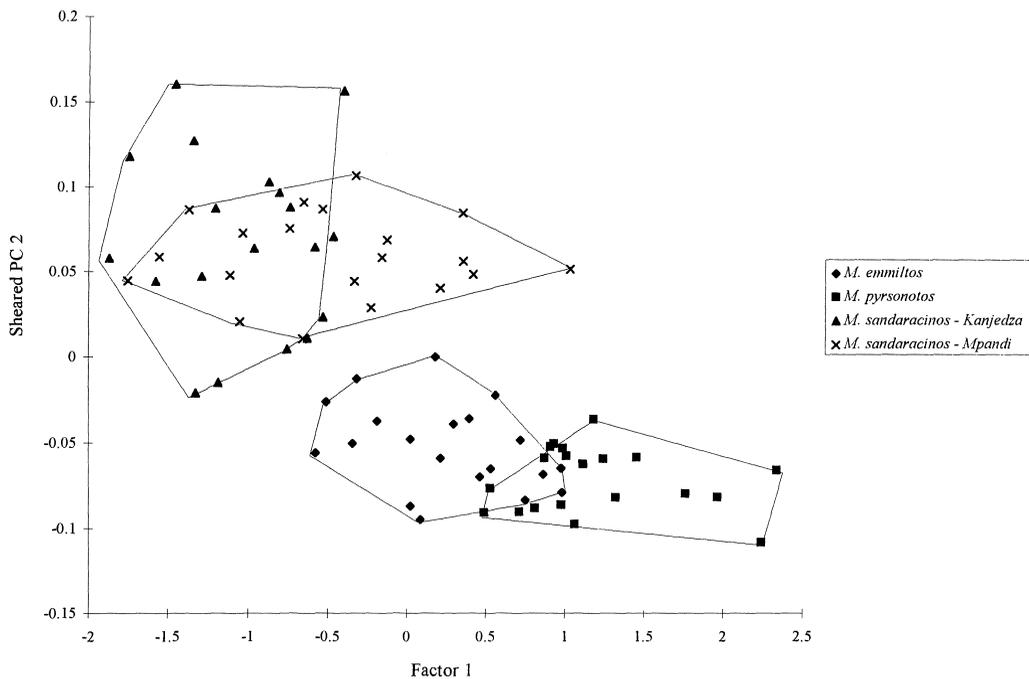


Fig. 25. Plot of the sheared second principal components (morphometric data) and the first factor score (meristic data) for *Metriaclima pyrsonotos*, *Metriaclima sandaracinos*, and *Metriaclima emmiltos*.

Metriaclima sandaracinos Stauffer, Bowers, Kellogg and McKaye, n. sp. (Fig. 26)

Pseudotropheus zebra 'red dorsal', Konings 1990: 454 (in part).

HOLOTYPE.—PSU 3064, adult male, 70.9 mm, Mpanda Island (Nkudzi Bay), Lake Malaŵi, Africa, 1-3 m, February 1991, (Figs. 26, 27).

PARATYPES.—PSU 3065, 7; USNM 341927, 4; ANSP 176201, 4; MFU 9, 4; (55.0 - 73.1 mm); data as for holotype. PSU 3066, 7; USNM 341928, 4; ANSP 176202, 4; MFU 8, 4; (54.0 - 69.0 mm); Kanjedza Island, Lake Malaŵi, Malaŵi, Africa, January, 1991.

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The red/orange dorsal fin in combination with black bars on a blue ground color distinguish this form from all other members of the genus except for the red dorsal BB forms inhabiting Chilumba and Nakantenga islands. The vertical black lateral bars do not extend into the dorsal fin as they do in *M. pyrsonotos*. In general, *Metriaclima sandaracinos*, has a greater number of teeth in the outer row of the left lower jaw (Kanjedza Island mode - 10; Mpanda Island mode - 12) than *M. pyrsonotos* (mode - 7) from Nakantenga Island or *M. emmiltos* from Chilumba (mode - 9). The

mean snout length expressed as percent HL of *M. sandaracinos* (Kanjedza Island mode - 34.6, Mpanda Island mode - 34.4) differs from that found in *M. pyrsonotos* (32.2) and from *M. emmiltos* Chilumba (mode - 32.9).

Description.—Jaws isognathous (Fig. 25); teeth on jaws in 3-4 rows; majority of teeth in outer rows bicuspid, with a few unicuspid posterior teeth; those in inner rows tricuspid; 9 teeth in outer row of left lower jaw of holotype, 7-13 in paratypes; dorsal-fin 9 in holotype and 8-10 in paratypes. Pectoral fins with 13 rays in holotype and 12-17 in paratypes; anal fin with 3 spines and 7 anal rays in holotype and 6-8 in paratypes. Lower pharyngeal bone triangular in outline (Fig. 26). Scales along side ctenoid; holotype with 32 lateral-line scales and 29-32 in paratypes. First gill arch with 8-13 rakers on the ceratobranchial, 2-3 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 9).

Laterally, the dorsal one-half of breeding males has a blue ground color; ventral one-half is orange/brown ground color; 6-7 black vertical bars. Head black with two light blue interorbital bars and green highlights on opercle; gular brown/orange. Dorsal fin red with scattered blue highlights in membranes between spines; caudal fin brown fading to red posteriorly; anal fin blue/gray with 3 yellow ocelli; pectoral-fin spine and first ray

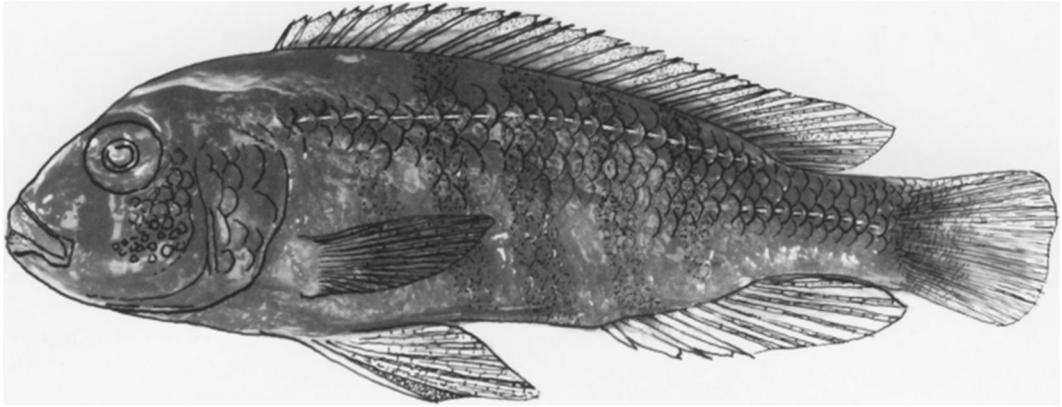


Fig. 26. *Metriaclima sandaracinos*, HOLOTYPE, PSU 3064, adult male, 70.9 mm SL.

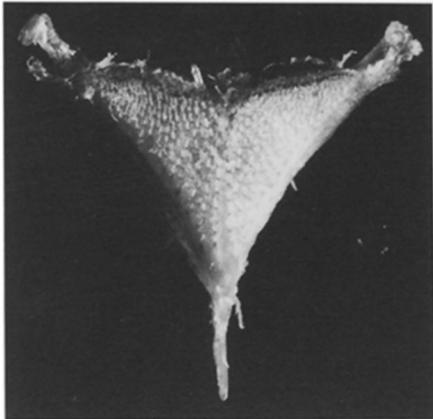


Fig. 27. Lower pharyngeal bone of the type specimen of *Metriaclima sandaracinos*, PSU 3064.

black, remainder red/orange; pelvic fins clear. Females brown laterally with 7 dark vertical bars. Head brown. Dorsal fin brown with orange lappets; caudal fin brown/black; anal fin brown/black with posteriad distal portion of membrane orange, no ocelli; pectoral-fin rays black, membranes clear; pelvic-fin spine and first ray black, remainder dark orange.

Distribution.—Occupies the rocky shores of Kanjedza Island and Chirombo Bay, and Mpanda Island and the rock outcroppings of Nkudzi Bay. The minimum polygon clusters formed by *M. sandaracinos*, *M. pyrsonotos* and *M. emmiltos* were significantly ($P < 0.05$) different (Fig. 25). Variables that had the highest loadings on the sheared second principal components were snout length (0.473), preorbital depth (0.373), and caudal peduncle length (-0.332), while those having the highest loadings on the meristic data were number of teeth on the left lower jaw (-0.366), number of gill rakers on the ceratobranchial (0.308), and number of gill

rakers on the epibranchial (0.273).

Etymology.—The name *sandaracinos*, from the Greek, meaning orange-colored to note the orange coloration of the dorsal fin.

Metriaclima emmiltos Stauffer, Bowers, Kellogg and McKaye, n. sp. (Fig. 28)

Pseudotropheus zebra 'red dorsal', Konings 1990:454 (in part).

HOLOTYPE.—PSU 3067, adult male, 84.1 mm, Mpanga Rocks, Chilumba, Lake Malaŵi, Malaŵi, Africa, 1-3 m, April, 1991 (Figs. 28 & 29).

PARATYPES.—PSU 3068, 7; USNM 341929, 4; ANSP 176203, 4; MFU 10, 4; (59.3 - 84.2 mm); data as for holotype.

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The red/orange dorsal fin in combination with black bars on a blue ground color distinguish this form from all other members of the genus except for *M. pyrsonotos* and *M. sandaracinos*, from Nakantenga and Kanjedza and Mpanda islands, respectively. The vertical black lateral bars do not extend into the dorsal fin as they do in *M. pyrsonotos*. In general, *M. emmiltos* has fewer teeth in the outer row of the left lower jaw (mode - 9), than the populations of *M. sandaracinos*. The mean snout length expressed as percent HL of *M. emmiltos* (34.9) differs from that found in *M. sandaracinos* (Kanjedza Island mean - 34.6, Mpanda Island mean - 34.4). The minimum polygon clusters formed by *M. emmiltos*, *M. sandaracinos* and *M. pyrsonotos* were significantly ($P < 0.05$) different (Fig. 25). Variables that had the highest loadings on the sheared second principal components were snout length (0.473), preorbital depth (0.373), and caudal peduncle length (-0.332), while

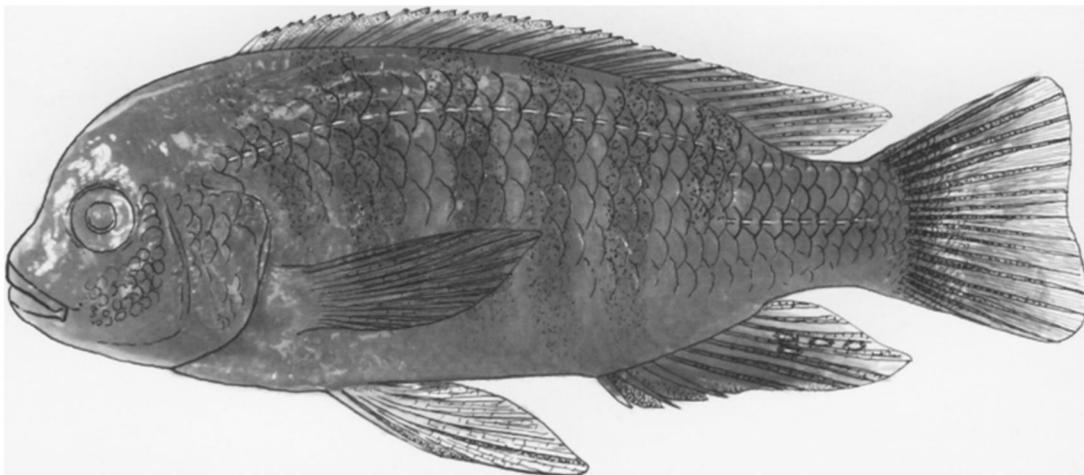


Fig. 28. *Metriaclima emmiltos*, HOLOTYPE, PSU 3067, adult male, 84.1 mm SL.

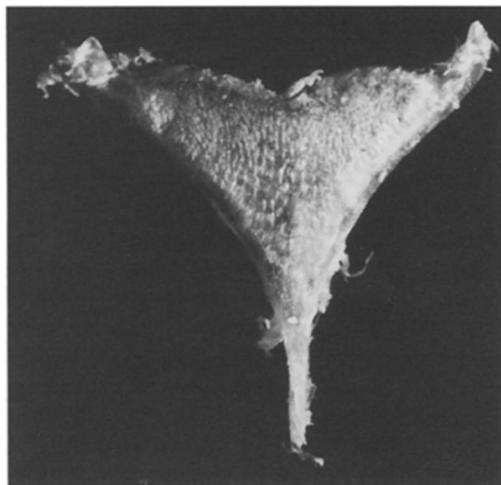


Fig. 29. Lower pharyngeal bone of the type specimen of *Metriaclima emmiltos*, PSU 3067.

those having the highest loadings on the meristic data were number of teeth on the left lower jaw (0.366), number of gill rakers on the ceratobranchial (0.308), and number of gill rakers on the epibranchial (0.273).

Description.—Jaws isognathous (Fig. 28); teeth on jaws in 2-3 rows; majority of teeth in outer rows bicuspid, with a few unicuspid posterior teeth; those in inner rows tricuspid; 9 teeth in outer row of left lower jaw of holotype, 8-12 in paratypes. Dorsal fin with 17 spines in the holotype and 17-18 in paratypes; dorsal-fin rays 9 in holotype and 8-10 in paratypes. Pectoral fins with 13 rays in holotype and 12-13 in paratypes; anal fin with 3 spines and 7 rays in holotype and 6-8 in paratypes. Lower pharyngeal bone triangular in outline (Fig. 29). Scales along side ctenoid; holo-

type with 31 lateral-line scales and 30-32 in paratypes. First gill arch with 10-14 rays on the ceratobranchial, 2-3 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 9).

Laterally, breeding males are dark blue dorsally, fading to light blue ventrally with 7 dark vertical bars. Head dark blue with two light blue interorbital bars; green highlights on cheek and opercle with dark blue opercular spot; gular pale blue. Dorsal fin orange with light blue lappets; caudal fin orange rays with blue membranes; anal fin dark blue/gray anteriorly fading to pale blue posteriorly with 6-7 ocelli; pectoral fins with black rays and clear membranes; spine and first two rays of pelvic fin black, remainder clear. Some females similarly colored, but flecked with green highlights and pale green interorbital bars; some females with brown ground color; no ocelli on anal fin.

Distribution.—Inhabits Mpanga Rocks at Chilumba.

Etymology.—The name *emmiltos*, from the Greek, meaning red-tinged to note the color of the dorsal fin.

Metriaclima mbenjii Stauffer, Bowers, Kellogg and McKaye, n. sp. (Fig. 30)

Pseudotropheus 'zebra mbenjii', Konings 1990: 452.

HOLOTYPE.—PSU 3069, adult male, 88.0 mm, Mbenji Island, Lake Malaŵi, Malaŵi, Africa, January, 1991 (Figs. 30 & 31).

PARATYPES.—PSU 3070, 3; USNM 341930, 2; ANSP 176204, 2; MFU 29, 2; (72.4 - 88.3 mm) data as for holotype. PSU 3071, 10; (71.6 - 81.9 mm); Mbenji Island, Lake Malaŵi, Malaŵi, Africa, April, 1991; PSU 3072, 4; (72.9 - 84.1); Mbenji Island, Lake Malaŵi, Malaŵi, Africa, April, 1991.

Diagnosis.—The moderately sloped head, swol-

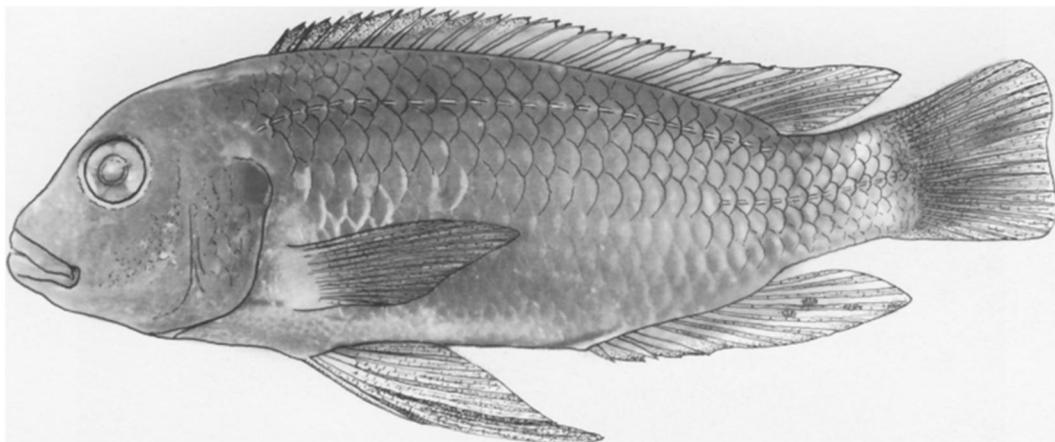


Fig. 30. *Metriaclima mbenjii*, HOLOTYPE, PSU 3069, adult male, 88.0 mm SL.



Fig. 31. Lower pharyngeal bone of the type specimen of *Metriaclima mbenjii*, PSU 3069.

len rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The pale blue ground coloration with very faint vertical bars, in conjunction with a red dorsal fin (Fig. 32a), delimits *M. mbenjii* from all other *Metriaclima* species except for *Metriaclima greshakei* (Meyer and Foerster). The first principal components of the meristic data were plotted against the sheared second principal components of the morphometric data for *M. mbenjii* and *M. greshakei* (Fig. 33). There was no overlap in the minimum polygon clusters formed by *M. greshakei* with that formed by *M. mbenjii*. Variables that had the highest loadings on the sheared second principal components were snout length (-0.439), distance between the posterior anal-fin insertion and the dorsal caudal-fin insertion (0.419), and caudal

peduncle length (0.373); while those with the highest loadings on the principal components of the meristic data were teeth rows on the upper jaw (0.471), scale rows on cheek (0.463), and teeth rows on the lower jaw (0.427).

Description.—Jaws isognathous (Fig. 30); teeth on jaws in 2-4 rows; majority of teeth in outer rows bicuspid, with a few posterior unicuspid teeth; those in inner rows tricuspid; 12 teeth in outer row of left lower jaw of holotype, 4-12 in paratypes. Dorsal fin with 18 spines in the holotype and 17-18 in paratypes; dorsal-fin rays 8 in holotype and 8-10 in paratypes. Pectoral fin with 14 rays in holotype and 12-14 in paratypes; anal fin with 3 spines and 6-8 rays. Lower pharyngeal bone triangular in outline (Fig. 31). Scales along side ctenoid; holotype with 31 lateral-line scales and 30-32 in paratypes. First gill arch with 11-13 rakers on ceratobranchial, 2-3 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 10).

Most breeding males have a light blue ground coloration with 6-8 faint vertical bars, and white belly; head below eye dark blue/gray; dorsal to eye, pale blue with one dark blue/gray interorbital bar, green opercular spot, and white gular. Dorsal fin red orange with blue lappets; caudal fin with blue rays and orange membranes; anal fin with orange proximal membranes, clear mid-fin membranes, and blue tips; anal spines blue; posterior anal-fin membranes red orange with 3 yellow ocelli; P_2 spine and first ray blue/gray with white leading edge, remainder clear; P_1 membranes red/orange proximally, clear distally. A few breeding males' dorsal one-half has a orange ground color with dark blue blotches (Fig. 32b), and ventral one-half a blue ground coloration, scales are outlined in orange with blue blotches;



Fig. 32a. *Metriaclima mbenjii*, blue form, from Mbenjii Island.



Fig. 32b. *Metriaclima mbenjii*, orange-blotch form, from Mbenjii Island.

head dorsal to eyes is orange with dark blue blotches and 2 light blue interorbital bars; ventral to eyes is gray with purple, blue, and green highlights, gular light blue/purple. Dorsal fin orange with light blue and dark blue blotches with several small orange spots in rayed portion of the membranes; caudal fin orange with light blue and dark blue blotches; anal fin orange proximally and clear distally with three yellow ocelli; P_2 clear with occasional orange spots; P_1 with pale orange rays

and clear membranes. Most females with brown ground color laterally with green highlights and 6-8 vertical bars and gray belly; head brown with faint green interorbital bar; dorsal fin brown; caudal fin light red/orange distally; anal fin gray with 3 pale yellow ocelli; P_2 spine and first ray with black, remainder clear; P_1 clear. Some females are orange laterally with blue highlights and spots with blue/green belly; head orange with blue/green opercle; dorsal and caudal fins orange

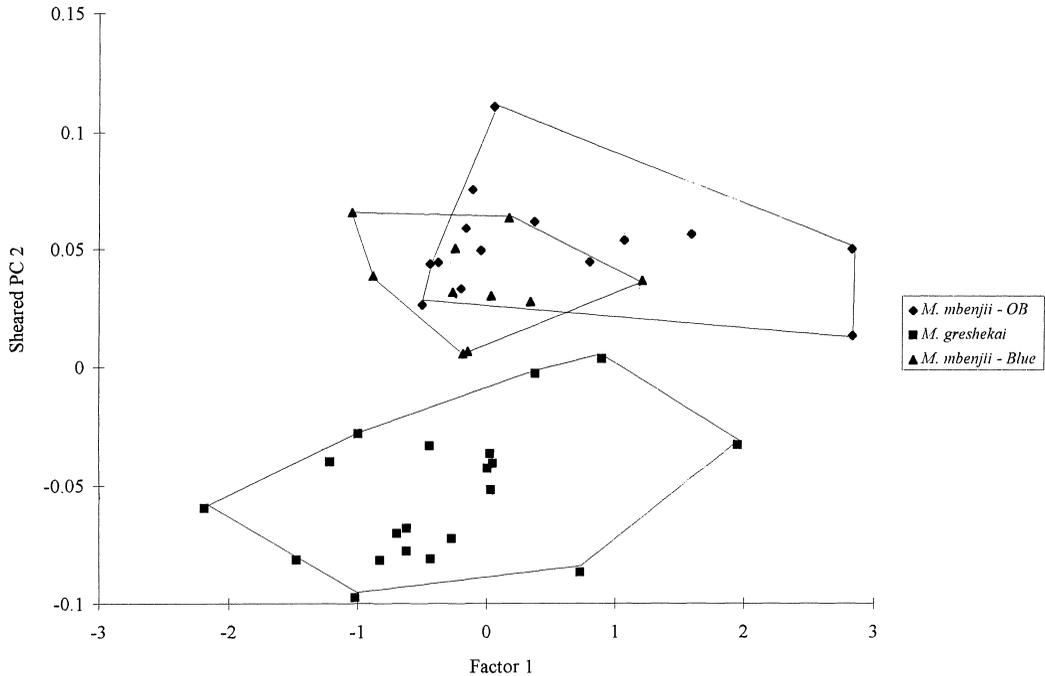


Fig. 33. Plot of the sheared second principal components (morphometric data) and the first factor score (meristic data) for *Metriaclima mbenjii*, both the orange-blotch and blue forms, and *Metriaclima greshakei*.

with dark orange spots scattered throughout; anal fin orange anteriorly and distally, clear proximally, and 7-9 ocelli located posteriorly; P_2 with first 2 membranes orange and the remainder clear with orange spots; P_1 pale orange with distal portion of some membranes black.

Distribution.—*Metriaclima mbenjii* is endemic to Mbenji Island.

Etymology.—The name referring to the fact that *M. mbenjii* is endemic to Mbenji Island.

***Metriaclima greshakei* (Meyer and Foerster)**

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The pale blue ground coloration with very faint vertical bars in conjunction with a red dorsal fin, delimits *M. greshakei* from all other *Metriaclima* species except for *M. mbenjii*. The first principal components of the meristic data were plotted against the sheared second principal components of the morphometric data for *M. mbenjii* and *M. greshakei* (Fig. 33). There was no overlap in the minimum polygon clusters formed by *M. greshakei* with that formed by *M. mbenjii*. Variables that had the highest loadings on the sheared second principal components were snout length (-0.439), distance between the posterior anal-fin insertion and the dorsal caudal-fin insertion (0.419), and

caudal peduncle length (0.373); while those with the highest loadings on the principal components of the meristic data were teeth rows on the upper jaw (0.471), scale rows on cheek (0.463), and teeth rows on the lower jaw (0.427).

Description.—Jaws isognathous; teeth on jaws in 2-3 rows; majority of teeth in outer rows bicuspid, with a few posterior unicuspid teeth; those in inner rows tricuspid; 3-12 teeth in outer row of left lower jaw. Dorsal fin with 17-18 spines and 8-9 rays. Pectoral fin with 11-14 rays; anal fin with 3 spines and 6-7 rays. Lower pharyngeal bone triangular in outline. Scales along side ctenoid with 30-33 lateral-line scales. First gill arch with 8-12 rakers on the ceratobranchial, 2-3 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 10).

Breeding males have a blue/gray ground color dorsally, fading to gray ventrally; live males are cobalt with 6-8 faint vertical bars; head blue/gray with blue opercle, green highlights and a white gular. Dorsal fin is dark rust colored proximally, and orange/red distally with white lappets; caudal-fin rays are white with orange/red membranes; anal fin clear with 7 yellow ocelli; P_2 with white leading edge, clear rays, and gray/black membranes. Females similarly colored, but sometimes have a brown/rust ground color and the anal fin has as many as 10 ocelli.

Distribution.—*Metriaclima greshakei* is restricted

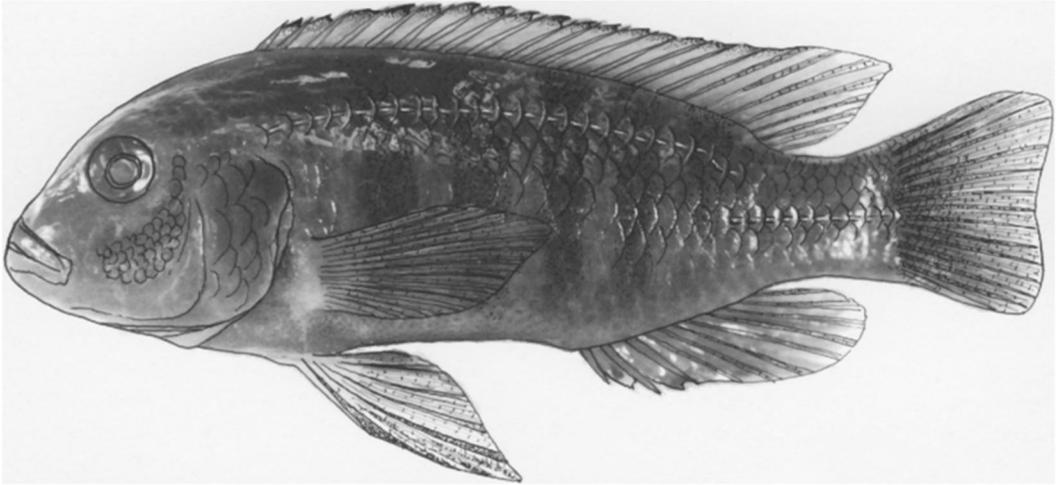


Fig. 34. *Metriaclima thapsinogen*, HOLOTYPE, PSU 3074, adult male, 86.4 mm SL.

to the rock reefs south of Boadzulu Island, Lake Malaŵi (Konings 1990).

Material examined.—PSU 3073, 20; (60.5 - 94.1 mm); Makokola Reef off southwestern end of Boadzulu Island, Lake Malaŵi, Malaŵi, Africa, 25-35 m, May, 1991.

Metriaclima thapsinogen Stauffer, Bowers, Kellogg and McKaye, n. sp. (Fig. 34)

HOLOTYPE.—PSU 3074, adult male 86.4 mm, Eccles Reef, Lake Malaŵi, Malaŵi, Africa, March, 1995, (Figs. 34 & 35).

PARATYPES.—PSU 3075, 8; USNM 341931, 2; ANSP 176205 2; MFU 30, 2; (65.5 - 86.4 mm), data as for holotype.

Diagnosis.—The moderately sloped head, swollen rostral tip of the neurocranium, isognathous jaws, and the presence of bicuspid teeth in the outer rows of the jaws place this species in *Metriaclima*. The blue ground coloration with distinct vertical bars in conjunction with the orange dorsal fin and yellow chin delimits *M. thapsinogen* from all other species in *Metriaclima*.

Description.—Jaws isognathous (Fig. 34); teeth on jaws in 2-4 rows; majority of teeth in outer rows bicuspid, with a few posterior unicuspid teeth; those in inner rows tricuspid; 9 teeth in outer row of left lower jaw of holotype, 7-11 in paratypes. Pectoral fin with 14 rays in holotype, 13-15 rays in paratypes. Lower pharyngeal bone triangular in outline (Fig. 35). Scales along side ctenoid; holotype with 31 lateral-line scales and 30-32 in paratypes. First gill arch with 11-13 rakers on the ceratobranchial, 2-3 on epibranchial, and 1 between the epibranchial and ceratobranchial (Table 11).

Breeding males have a blue ground color with

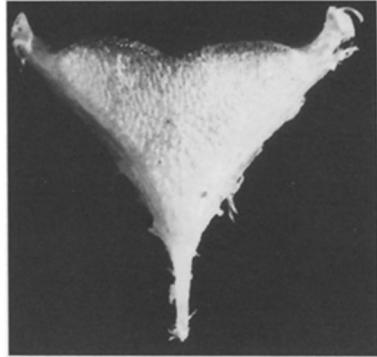


Fig. 35. Lower pharyngeal bone of the type specimen of *Metriaclima thapsinogen*, PSU 3074.

6 black vertical bars; head dark blue with 2 light blue interorbital bars, opercle with green highlights, and yellow gular. Dorsal fin orange with blue lappets; caudal fin gray in proximal seven-eighths, distal one-eighth orange; anal fin gray with 2 yellow ocelli; P₂ orange/brown; P₁ with black rays and clear membranes. Females green laterally with scales outlined in yellow; head gray with 2 green interorbital bars and pale yellow gular; dorsal fin red; caudal fin gray; anal fin proximal one-quarter gray, distal three-quarters orange/brown with no ocelli; P₂ orange/brown; P₁ with gray rays and clear membranes.

Distribution.—*Metriaclima thapsinogen* was collected only at Eccles Reef.

Etymology.—The name *thapsinogen* was respelled from the Greek *thapsinogenion*, meaning yellow chin to note the yellow color of the gular and branchiostegal rays.

DISCUSSION

We agree with Mayden and Wood (1995) and Mayden (in press), that the Evolutionary Species Concept, sensu Wiley (1978) is the only valid theoretical concept; however it is non-operational and must be used in conjunction with other surrogate species concepts (Stauffer et al. 1997). When delimiting sympatric species, differentiation of morphological traits, including color patterns, are considered to be indicative of reproductive isolation (biological species concept; Mayr and Ashlock 1991) or specific mate-recognition system (recognition species concept; Paterson 1993). The designation of allopatric populations as either being conspecific or heterospecific is more problematical.

As indicated by Lewis (1982), the acquisition of reproductive isolation without significant morphological change makes it difficult to delimit African haplochromine cichlids. Additionally, the use of starch gel electrophoresis has been inconclusive for delimiting species (Kornfield 1978), although DNA sequencing of mtDNA may be adequate for distinguishing among Lake Malawi cichlids in some lineages (Bowers et al. 1994). Rapid speciation of Malawian cichlids, however, may have prevented sorting of mitochondrial lineages, permitting distantly related species to share mtDNA polymorphisms derived from a common ancestor (Moran and Kornfield 1993). Many morphologically and genetically similar species have been separated based on breeding coloration and behavioral characteristics (Ribbink et al. 1983, McKaye and Stauffer 1986, Stauffer et al. 1993). For example, behavioral observations were used to hypothesize that the blue-black color form (*M. zebra*) was reproductively isolated from the blue color morph (*M. callainos*) at Nkhata Bay (Holzberg 1978, Schroder 1980).

Many of the forms described herein, were first hypothesized to be undescribed species based on differences in color pattern. Unique color patterns were used in conjunction with the discontinuity of morphological differences to determine specific status. For example, if a series of allopatric populations demonstrated gradual variation throughout its range (i.e. *M. zebra*; Figs. 6a, 6b, 6c) they were considered to be conspecific. If however, similarly colored forms exhibited discontinuities in morphological characteristics throughout their range, they were regarded as heterospecific populations (i.e. *M. pyrsonotos*, *M. sandaracinos*, *M. emmiltos*; Fig. 25).

The combination of the following: 1) presence of many small scales in the nape region, 2) preference for boulder and rocky substrate, and 3) and

the reduction of the left ovary is evidence which aligns the genus, *Metriaclima*, with the other groups of rock-dwelling cichlids of Lake Malawi. The presence of bicuspid teeth in the anterior portion of the outer rows of both the upper and lower jaws distinguishes *Metriaclima* from *Cyathochromis*, *Cynotilapia*, *Gephyrochromis*, and *Labidochromis*. The isognathous jaws of *Metriaclima* delimits it from *Genyochromis*, and its terminal mouth discriminates *Metriaclima* from *Labeotropheus*. Within what was historically considered to be *Pseudotropheus*, the moderately sloped ethmo-vomerine block and swollen rostral tip to the neurocranium separates *Metriaclima* from the *P. elongatus*, *P. tropheops*, and *P. williamsi* complexes. Described species that are not discussed in this paper, but which are characterized by a moderately sloped ethmo-vomerine block and swollen rostral tip, and thus belong to *Metriaclima* include: *Metriaclima aurora*, *Metriaclima barlowi*, *Metriaclima elegans*, *Metriaclima estherae*, *Metriaclima hajomaylandi*, *Metriaclima lombardoi*, *Metriaclima lanisticola*, *Metriaclima livingstonii*, and *Metriaclima porsus*.

Within *Metriaclima*, the species described herein represent those that have a blue lateral ground color with black vertical bars, or have secondarily lost these bars and appear to be solid blue. This blue/black color pattern is present in many of the other genera of rock-dwelling cichlids, which inhabit Lake Malawi, including *Labidochromis zebroides* Lewis, *Petrotilapia* "likoma barred" (Ribbink et al. 1983), *Cynotilapia afra* (Gunther), *Pseudotropheus elongatus* Fryer, *Pseudotropheus* cf. *williamsi* 'namalenge', *Pseudotropheus microstoma* Trewavas (*P. tropheops* complex), and *Labeotropheus trewavasae* Fryer. The blue/black color pattern can also be found in many of the sand-dwelling fishes such as *Protomelas similis* (Trewavas), *Copadichromis cyaneus* (Trewavas), and *Trematocranus microstoma* Trewavas. Thus, Stauffer et al. (1995) speculated that the blue/black color is pleisomorphic based on either the commonality principle (Watrous and Wheeler 1981) or outgroup comparisons (Smith and Koehn 1971).

Metriaclima zebra is considered to be the most primitive species in the genus. Certainly it is the most widespread, ranging from Crocodile Rocks at the southern end of Lake Malawi to Chilumba, which is located in the north. Breeding males exhibit the blue/black color pattern, and there are no other pigmentation patterns (e.g. red dorsal fin, yellow throat, extension of lateral vertical bars onto the dorsal fin), which are interpreted as apomorphic characters.

Surely, allopatric speciation and subsequent

dispersal has occurred within *Metriaclima*. For example, the occurrence of *M. malabbranchion* at both Mitande Rocks and Domwe Island at Cape MacClear, can be explained by dispersal. It is much more difficult, however, to believe that the species with a red dorsal fin, *M. emmiltos*, which is endemic to Chilumba in the northern part of the lake is more closely related to other species with red dorsal fins (i.e. *M. sandaracinos* and *M. pyrsonotos*) than it is to the *M. zebra* population with which it is sympatric.

Metriaclima elegans, *M. lanisticola*, *M. livingstonii*, *M. pursus* are the only described mbuna species, which have secondarily invaded the sand. All of these species are associated with empty snail shells (*Lanistes* spp.) either as adults or during their ontogeny. This behavior character may in fact be an apomorphic character, in which case these species are more closely related to each other than to other sympatric *Metriaclima* species, or it may be due to convergence. A detailed analysis of this group must be completed, which includes at least two undescribed species endemic to Nakantenga and Likoma islands.

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LITERATURE CITED

- Barel, C., M. van Oijen, F. Witte, and E. Witte-Maas. 1977. An introduction to the taxonomy and morphology of the haplochromine Cichlidae from Lake Victoria. *Neth. J. Zool.* 27: 333-389.
- Bookstein, F., B. Chernoff, R. Elder, J. Humphries, G. Smith and R. Strauss. 1985. Morphometrics in Evolutionary Biology. Academy of Natural Sciences, Spec. Publ. 15, Philadelphia, PA.
- Bowers, N. J., T. D. Kocher, and J. R. Stauffer, Jr. 1994. Intra- and inter-specific mitochondrial DNA sequence variation within two species of rock-dwelling cichlids (Teleostei: Cichlidae) from Lake Malaŵi, Africa. *Molecular Phylogenetics and Evolution* 3: 75-82.
- Bowers, N. J. and J. R. Stauffer, Jr. 1997. Eight new species of rock-dwelling cichlids of the genus *Melanochromis* (Teleostei: Cichlidae) from Lake Malaŵi, Africa. *Ichthyol. Explor. Freshwaters* 8: 49-70.
- Fryer, G. 1959. The trophic interrelationships and ecology of some littoral communities in Lake Nyasa, with especial reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. *Proc. Zool. Soc. Lond.* 132: 153-281.
- Fryer, G. and T. D. Iles. 1972. The cichlid fishes of the Great Lakes of Africa. TFH Publications, Neptune, USA.
- Holzberg, S. 1978. A field and laboratory study of the behaviour and ecology of *Pseudotropheus zebra* (Boulenger), an endemic cichlid of Lake Malaŵi, Africa. *Zeitschr. Zool. Syst. Evolutg. Forsch.* 16: 171-187.
- Humphries, J., F. Bookstein, B. Chernoff, G. Smith, R. Elder, and S. Poss. 1981. Multivariate discrimination by shape in relation to size. *Systematic Zoology* 30: 291-308.
- Konings, A. 1990. Cichlids and all the other fishes of Lake Malaŵi. T.F.H. Publications, Inc., Neptune City, New Jersey.
- Konings, A. 1995. Malaŵi cichlids in their natural habitat. Cichlid Press, Germany.
- Kornfield, I. 1978. Evidence for rapid speciation in African cichlid fishes. *Experientia* 34: 335-336.
- Lewis, D. S. C. 1982. Problems of species definition in Lake Malaŵi cichlid fishes (Pisces: Cichlidae). *Ichthyological Bulletin of the J. L. B. Smith Institute of Ichthyology* 23: 1-5.
- Mayden, R. L. in press. A hierarchy of species concepts: the deouement in the saga of the species problem. In: M. F. Claridge, H. A. Dawah, and M. R. Wilson (eds.). *The units of biodiversity - species in practice*. Systematics Association, London.
- Mayden, R. L. and R. M. Wood. 1995. Systematics, species concepts, and the evolutionarily significant unit in biodiversity and conservation biology. *Amer. Fish. Soc. Sym.*, 17: 58-113.
- Mayr, E. and P. D. Ashlock. 1991. Principles of systematic zoology. McGraw-Hill, New York.
- McKaye, K. R., T. Kocher, P. Reinthal, R. Harrison, and I. Kornfield. 1984. Genetic evidence for allotropic and sympatric differentiation among color morphs of a Lake Malaŵi cichlid fish. *Evolution* 31: 215-219.
- McKaye, K. R. and J. R. Stauffer, Jr. 1986. Description of a gold cichlid, *Pseudotropheus barlowi* (Teleostei: Cichlidae), from Lake Malaŵi, Africa. *Copeia* 1986: 870-875.
- Meyer, M. K. and W. Foerster. 1984. Un nouveau *Pseudotropheus* du lac Malaŵi avec des remarques sur le complexe *Pseudotropheus-Melanochromis* (Pisces, Perciformes, Cichlidae). *Revue fr. Aquariol.* 10: 107-112.
- Moran, P. and I. Kornfield. 1993. Retention of an ancestral polymorphism in the mbuna species flock

- (Pisces: Cichlidae) of Lake Malaŵi. *Molecular Biology and Evolution* 10: 1015-1029.
- Moran, P., I. Kornfield, and P. Reinthal. 1994. Molecular systematics and radiation of the haplochromine cichlids (Teleostei: Cichlidae of Lake Malaŵi. *Copeia* 1994: 274-288.
- Oliver, M. 1984. Systematics of African fishes: determination of the most primitive taxon, and studies on the haplochromines of Lake Malaŵi (Teleostei: Cichlidae). Ph.D. Dissertation, Yale University, New Haven, CT.
- Oliver, M. L. and P. V. Loiselle. 1972. A new genus and species of cichlid of the mbuna group (Pisces: Cichlidae) from Lake Malaŵi. *Revue de Zoologie et de Botanique Africaines* 85: 309-320.
- Paterson, H. E. H. 1993. Evolution and the recognition concept of species. In: S. F. McEvey (ed.). *Collected writings of H. E. H. Paterson*. Johns Hopkins University Press, Baltimore, Maryland.
- Reyment, R., R. Blackith, and N. Cambell. 1984. *Multivariate Morphometrics*. Academic Press, New York, NY.
- Ribbink, A. J., B. A. Marsh, A. C. Marsh, A. C. Ribbink and B. J. Sharp. 1983. A preliminary survey of the cichlid fishes of the rocky habitats in Lake Malaŵi. *S. Afr. J. Sci.* 18:149-310.
- Schroder, J. H. 1980. Morphological and behavioural differences between the BB/OB and B/W colour morphs of *Pseudotropheus zebra* Boulenger (Pisces: cichlidae) *Ztschr. Zool. Syst. Evolutg. Forsch.* 18: 69-76.
- Smith, G. R. and A. K. Koehn. 1971. Phenetic and cladistic studies of biochemical and morphological characteristics of *Catostomus*. *Systematic Zoology* 20:282-297.
- Staeck, W. 1980. *Pseudotropheus heteropictus* n. sp. Aus dem Malaŵi-See (Pisces: Cichlidae). *Senckenbergiana Biol.* 60: 159-162.
- Stauffer, J. R., Jr. 1988. Three new rock-dwelling cichlids (Teleostei: Cichlidae) from Lake Malaŵi, Africa. *Copeia* 1988: 663-668.
- Stauffer, J. R. 1991. Description of a facultative cleanerfish (Teleostei: Cichlidae) from Lake Malaŵi, Africa. *Copeia*. 1991: 141-147.
- Stauffer, J. R., Jr. and J. M. Boltz. 1989. Description of a rock-dwelling cichlid (Teleostei: Cichlidae) from Lake Malaŵi, Africa. *Proc. Biol. Soc. Wash.* 102: 8-13.
- Stauffer, J. R., Jr., J. J. Bowers, K. R. McKaye, and T. D. Kocher. 1995. Evolutionarily significant units among cichlid fishes: The role of behavioral studies. *Amer. Fish. Soc. Sym.* 17:227-244.
- Stauffer, J. R., Jr. and E. Hert. 1992. *Pseudotropheus callainos*, a new species of mbuna (Cichlidae), with analyses of changes associated with two intra-lacustrine transplantations in Lake Malaŵi, Africa. *Ichthyol. Explor. Freshwaters* 3(3):253-264.
- Stauffer, J. R., Jr., C. H. Hocutt, and R. L. Mayden. 1997. *Pararhinichthys*, a new monotypic genus of minnows (Teleostei: Cyprinidae) of hybrid origin from eastern North America. *Ichthyol. Explor. Freshwaters* 7: 327-336.
- Stauffer, J. R., Jr., T. J. LoVullo, and K. R. McKaye. 1993. Three new sand-dwelling cichlids from Lake Malaŵi, Africa, with a discussion of the status of the genus *Copadichromis* (Teleostei: Cichlidae). *Copeia* 1993: 1017-1027.
- Trewavas, E. 1935. A synopsis of the cichlid fishes of Lake Nyasa. *Ann. Mag. Nat. Hist.* (10)16:65-118.
- Watrous, L. E. and Q. D. Wheeler. 1981. The out-group comparison method of character analysis. *Systematic Zoology* 30:1-11.
- Wiley, E. O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology* 27: 17-26.

[TABLES 1-11 FOLLOW]

Table 1. Morphometric and meristic values of *Merristiema zebra* holotype and populations from Mazinzi Reef (N = 13), Crocodile Rocks (N = 19), Roadzulu Island (N = 24), Thumbi East Island (N = 20), Songwe Hill (N = 13), Mitande Rocks (N = 20), Nkhata Bay (N = 16), 5 km North of Nkhata Bay (N = 15), and Chitande Rocks (N = 16). Morphometric and meristic values of the *Merristiema zebra* type are also listed.

	<i>M. zebra</i>				Mazinzi Reef				Crocodile Rocks				Roadzulu Island				Thumbi East Island			
	Mean	Standard Deviation	Range	Mode	Mean	Standard Deviation	Range	Mode	Mean	Standard Deviation	Range	Mode	Mean	Standard Deviation	Range	Mode	Mean	Standard Deviation	Range	Mode
Standard length, mm	83.3	73.0	63.7-88.4	73.2	73.2	9.0	56.1-91.9	74.3	8.8	61.2-89.6	72.8	6.2	55.5-80.0							
Head length, mm	26.5	23.7	20.7-28.2	24.0	24.0	2.8	18.8-30.2	24.6	2.6	19.6-28.3	23.5	1.9	17.8-26.2							
Percent of standard length																				
Head length	31.8	32.5	31.6-34.0	32.8	32.8	0.6	31.3-33.5	33.2	1.4	30.5-35.7	32.3	0.8	30.4-33.7							
Snout to dorsal-fin origin	35.2	35.0	33.4-36.5	34.3	34.3	0.8	33.2-36.1	34.4	1.2	31.6-36.2	34.3	1.0	32.1-36.0							
Snout to pelvic-fin origin	35.2	28.9	26.0-34.8	29.0	29.0	3.6	21.4-36.2	30.8	3.8	24.7-36.8	28.8	2.5	21.4-31.0							
Pectoral-fin length	23.8	26.6	24.5-29.3	27.4	27.4	2.9	19.7-33.0	27.7	1.5	24.3-30.8	28.4	1.4	23.3-31.6							
Pelvic-fin length	36.0	35.8	24.8-50.6	38.2	38.2	9.7	26.6-57.1	42.5	9.1	28.3-59.2	37.0	4.1	29.4-44.9							
Dorsal-fin base length	62.1	59.9	56.1-62.3	59.8	59.8	1.0	57.9-61.6	60.9	1.3	57.6-63.8	60.5	1.5	58.3-63.8							
Anterior dorsal to anterior anal	57.9	51.5	47.0-53.3	53.1	53.1	1.1	51.6-55.0	53.3	1.8	50.0-57.3	51.3	1.8	48.1-54.4							
Posterior dorsal to posterior anal	17.2	16.0	15.0-17.0	16.6	16.6	0.8	15.3-17.8	16.6	0.9	14.7-18.2	15.0	0.7	13.4-16.3							
Anterior dorsal to posterior anal	66.4	62.9	58.7-64.4	64.4	64.4	1.1	62.7-66.1	64.5	1.2	62.5-67.1	63.5	1.4	61.0-66.3							
Posterior dorsal to anterior anal	32.4	30.2	28.6-33.0	30.4	30.4	1.0	28.8-32.4	31.6	1.0	29.8-33.3	29.6	0.9	28.3-31.1							
Posterior dorsal to ventral caudal	17.9	18.4	16.7-21.0	18.2	18.2	0.6	17.2-19.7	18.6	1.0	16.1-20.9	17.1	0.9	14.9-18.9							
Posterior anal to dorsal caudal	19.7	20.6	19.4-22.8	19.5	19.5	0.7	18.4-20.9	20.9	0.8	18.9-22.0	19.4	0.7	18.2-20.7							
Anterior dorsal to pelvic-fin origin	36.6	35.8	33.5-38.6	37.0	37.0	1.1	35.1-39.1	38.0	2.4	32.9-42.2	34.4	1.5	30.1-36.4							
Posterior dorsal to pelvic-fin origin	58.0	58.6	56.5-62.4	56.5	56.5	1.2	54.7-58.6	56.9	1.5	54.5-59.4	55.9	1.5	52.3-58.1							
Percent of head length																				
Horizontal eye diameter	30.6	32.4	29.7-34.8	29.6	29.6	1.2	27.7-32.5	30.6	2.2	25.9-35.0	33.0	1.7	29.2-36.1							
Vertical eye diameter	29.4	32.0	29.8-34.7	30.0	30.0	1.1	28.4-31.9	30.4	2.4	24.4-36.0	33.4	1.7	28.9-35.5							
Snout length	40.0	35.1	32.2-38.7	34.4	34.4	2.0	30.7-37.6	36.4	2.6	30.8-40.0	34.8	2.1	31.2-39.3							
Postorbital head length	38.9	38.3	36.5-39.7	41.2	41.2	0.9	39.7-43.1	38.3	1.3	35.9-40.9	36.9	1.1	34.7-39.5							
Preorbital depth	21.9	20.9	18.6-24.0	21.4	21.4	1.2	19.5-23.4	21.8	1.6	18.5-25.1	20.5	1.2	18.45-22.55							
Lower-jaw length	39.6	37.5	35.5-40.4	36.2	36.2	1.3	33.5-38.1	38.6	2.5	34.4-43.5	37.0	2.5	33.5-42.3							
Cheek depth	25.3	23.8	18.6-27.9	27.3	27.3	1.7	25.1-30.2	25.6	2.7	21.2-30.7	24.2	1.8	21.9-29.2							
Head depth	93.2	93.8	81.6-101.0	95.4	95.4	2.4	92.0-102.1	100.3	5.0	90.6-109.3	92.3	4.7	81.2-102.2							
Counts																				
Lateral-line scales	30	31	30-32	31	31	84.2	30-31	30	45.8	29-32	32	75.0	31-33							
Pored scales posterior to lateral line	2	2	1-3	2	2	78.9	0-2	2	66.7	1-3	2	70.0	0-3							
Scale rows on cheek	5	3	3-5	5	5	73.7	4-5	4	50.0	3-5	4	55.0	4-5							
Dorsal-fin spines	18	18	16-18	17	17	94.7	16-17	17	70.8	16-18	18	70.0	16-19							
Dorsal-fin rays	8	8	8-9	9	9	89.5	8-9	9	79.2	8-10	9	65.0	8-9							
Anal-fin spines	3	3	3-4	3	3	100.0	3-3	3	100.0	3-3	3	100.0	3-3							
Anal-fin rays	8	7	8-6	8	8	94.7	7-8	7	87.5	7-8	7	90.0	7-8							
Pectoral-fin rays	13	13	13-14	14	14	52.6	13-14	13	58.3	12-14	13	85.0	12-14							
Pelvic-fin rays	5	5	5-5	5	5	100.0	5-5	5	100.0	5-5	5	100.0	5-5							
Gill rakers on first ceratobranchial	12	10	9-11	11	11	57.9	11-13	11	37.5	10	12	40.0	9-12							
Gill raker on first epibranchial	3	2	2-3	3	3	78.9	2-3	2	58.3	1	3	75.0	2-3							
Teeth in outer row of left lower jaw	12	12	9-15	10	10	42.1	9-13	10	29.2	8-12	11	30.0	10-14							
Teeth rows on upper jaw	4	3	3-3	3	3	84.2	2-3	3	62.5	2-3	3	100.0	3-3							
Teeth rows on lower jaw	5	3	3-4	3	3	100.0	3-3	3	54.2	2-3	3	100.0	3-3							

TABLE 1 (continued)

	Songwe Hill			Mirande Rocks			Nkhata Bay			5 km North of Nkhata Bay		
	Mean	Standard Deviation	Range	Mean	Standard Deviation	Range	Mean	Standard Deviation	Range	Mean	Standard Deviation	Range
Standard length, mm	70.9	6.4	56.2-80.0	78.6	8.9	57.7-90.6	70.4	7.3	57.0-84.2	70.7	7.3	60.2-83.6
Head length, mm	23.3	2.1	18.6-27.5	24.3	3.0	18.2-28.1	22.3	2.0	18.7-25.7	22.4	1.9	19.9-25.8
Percent of standard length												
Head length	32.9	0.7	31.9-34.3	31.0	0.9	29.1-33.1	31.8	0.8	30.5-33.0	31.7	1.0	30.4-33.5
Snout to dorsal-fin origin	35.3	1.0	33.9-37.7	34.3	1.2	32.0-36.2	34.2	0.7	32.8-35.5	34.1	1.1	32.1-36.7
Snout to pelvic-fin origin	28.8	2.6	22.3-32.7	30.3	3.8	21.7-35.8	27.1	2.6	22.4-31.3	27.9	2.3	24.4-31.8
Pectoral-fin length	27.6	1.3	25.3-30.7	26.6	2.3	21.8-30.9	28.6	3.1	26.5-30.2	26.8	2.0	22.1-29.6
Pelvic-fin length	41.7	4.4	34.2-49.1	39.8	6.9	29.5-52.1	31.3	3.1	26.2-35.9	32.1	4.3	24.7-43.0
Dorsal-fin base length	60.2	1.8	57.4-63.2	61.8	1.4	59.5-65.5	61.7	1.6	58.9-64.1	59.7	1.5	56.6-62.2
Anterior dorsal to anterior anal	51.5	1.7	47.7-53.9	52.2	1.3	49.5-54.3	51.4	1.5	49.1-53.3	52.7	1.3	49.9-54.7
Posterior dorsal to posterior anal	15.2	0.5	14.4-16.1	16.5	1.1	14.6-17.9	15.4	0.5	14.5-16.3	15.7	0.8	14.1-17.3
Anterior dorsal to posterior anal	63.4	1.1	61.8-65.4	65.1	1.2	63.4-68.2	64.7	1.7	62.2-67.4	63.7	1.2	61.6-66.2
Posterior dorsal to anterior anal	29.7	1.2	28.2-32.5	31.7	1.0	29.8-33.3	31.0	1.0	29.0-32.4	29.0	0.9	27.0-30.5
Posterior dorsal to ventral caudal	17.7	1.3	16.1-20.1	18.4	1.0	17.0-20.2	17.7	0.9	16.1-19.4	17.2	0.5	16.4-18.2
Posterior anal to dorsal caudal	19.8	0.8	18.5-20.8	21.9	1.1	19.9-24.6	20.6	0.7	19.0-21.9	18.9	0.5	18.0-20.1
Anterior dorsal to pelvic-fin origin	34.9	1.3	32.8-36.4	36.2	1.9	33.5-40.2	34.2	1.0	32.0-36.0	35.3	0.9	33.5-37.2
Posterior dorsal to pelvic-fin origin	56.3	1.6	53.1-58.4	57.0	1.3	54.0-59.5	56.5	1.5	54.0-59.2	56.3	1.0	54.5-57.7
Percent of head length												
Horizontal eye diameter	32.9	1.0	31.7-34.9	32.9	1.1	30.3-34.8	33.3	1.0	31.8-35.1	32.0	1.4	30.3-35.1
Vertical eye diameter	32.8	1.5	29.9-35.2	32.7	1.3	30.1-35.2	34.1	1.8	32.7-36.2	31.8	1.1	30.2-34.0
Snout length	35.4	1.7	31.9-37.8	33.6	2.7	29.5-40.5	32.7	1.8	29.7-35.6	34.0	1.7	31.2-37.5
Postorbital head length	38.0	1.1	35.9-39.5	39.4	1.2	37.8-42.6	38.7	0.8	37.4-40.2	39.6	0.9	38.1-41.0
Preorbital depth	20.3	1.5	17.7-22.5	21.1	1.4	17.8-23.6	21.2	1.2	19.2-22.9	22.2	1.3	20.1-24.0
Lower-jaw length	38.1	2.4	33.4-40.7	40.8	2.7	36.8-47.2	39.0	2.0	32.5-40.8	38.0	1.5	35.8-41.0
Cheek depth	23.9	1.6	21.2-27.2	27.4	1.8	24.3-30.3	27.7	2.0	24.8-31.5	27.9	1.4	25.3-30.1
Head depth	94.9	5.3	87.6-104.1	102.9	4.6	91.2-107.7	94.1	3.0	89.0-99.3	92.3	4.6	81.6-99.2
Counts	Mode	% Freq.	Range	Mode	% Freq.	Range	Mode	% Freq.	Range	Mode	% Freq.	Range
Lateral-line scales	31	61.5	30-33	31	40.0	30-33	31	56.3	30-32	31	66.7	31-32
Pored scales posterior to lateral line	3	53.8	2-3	2	50.0	0-3	2	75.0	0-2	2	53.3	0-2
Scales rows on cheek	3	53.8	3-5	4	65.0	3-5	4	75.0	4-5	5	60.0	4-6
Dorsal-fin spines	18	61.5	17-18	17	55.0	17-18	18	56.3	17-19	18	53.3	17-18
Dorsal-fin rays	9	76.9	8-9	8	50.0	8-10	9	75.0	7-9	9	66.7	8-9
Anal-fin spines	3	100.0	3-3	3	95.0	3-4	3	100.0	3-3	3	100.0	3-3
Anal-fin rays	7	84.6	6-7	7	90.0	6-7	7	87.5	6-8	8	86.7	7-8
Pectoral-fin rays	13	76.9	13-15	13	95.0	13-14	13	75.0	13-14	14	53.3	13-14
Pelvic-fin rays	5	100.0	5-5	5	100.0	5-5	5	100.0	5-5	5	100.0	5-5
Gill rakers on first ceratobranchial	11	69.2	8-12	11	35.0	11-14	12	50.0	10-13	12	46.7	10-12
Teeth in outer row of left lower jaw	2	61.5	2-3	3	75.0	2-3	3	56.3	2-3	3	60.0	2-3
Teeth rows on upper jaw	10	46.2	8-13	9	25.0	4-13	12	43.8	7-13	11	53.3	9-12
Teeth rows on lower jaw	3	92.3	2-3	3	65.0	2-4	3	81.3	3-4	3	53.3	3-5
	3	100.0	3-3	3	65.0	2-4	3	93.8	2-3	3	80.0	3-4

Table 2. Ranges of morphometric and meristic values of *Metraclima heteroptictus* paratypes (N = 2).

	Chitande Rocks			Paratypes Range
	Mean	Standard Deviation	Range	
Standard length, mm	69.6	8.1	61.2-84.6	74.0-85.7
Head length, mm	22.1	2.4	19.1-25.8	22.2-24.6
Percent of standard length				
Head length	31.8	0.7	30.4-32.9	28.1-29.5
Snout to dorsal-fin origin	33.8	0.7	32.7-35.6	30.6-31.1
Snout to pelvic-fin origin	26.4	2.9	22.5-32.1	35.8-36.4
Pectoral-fin length	27.5	1.6	25.1-29.7	14.1-17.5
Pelvic-fin length	34.7	4.2	29.3-43.6	19.4-28.5
Dorsal-fin base length	60.3	0.8	58.8-61.7	59.2-62.3
Anterior dorsal to anterior anal	51.2	1.2	48.1-53.0	51.1-53.3
Posterior dorsal to posterior anal	15.5	0.6	14.0-16.2	14.7-16.0
Anterior dorsal to posterior anal	63.4	0.7	62.2-64.1	64.2-64.5
Posterior dorsal to anterior anal	28.6	0.8	27.3-30.0	28.8-29.9
Posterior dorsal to ventral caudal	17.6	0.5	16.7-18.4	15.0-17.2
Posterior anal to dorsal caudal	19.3	0.7	17.8-20.6	18.8-20.1
Anterior dorsal to pelvic-fin origin	34.2	0.2	33.4-34.9	34.0-34.8
Posterior dorsal to pelvic-fin origin	55.6	1.4	52.1-57.5	56.7-57.7
Percent of head length				
Horizontal eye diameter	34.1	1.2	31.2-36.8	28.0-28.2
Vertical eye diameter	33.8	0.8	31.8-35.0	28.1-28.4
Snout length	32.4	1.4	30.6-36.1	36.5-37.7
Postorbital head length	40.1	0.8	38.7-41.1	38.8-38.9
Preorbital depth	21.5	1.1	19.5-23.5	19.4-20.2
Lower-jaw length	40.9	1.0	38.9-43.0	37.4-37.4
Cheek depth	28.5	1.3	26.0-30.2	30.1-31.0
Head depth	93.1	1.9	90.7-97.1	97.7-101.5
Counts	Mode	% Freq.	Range	Range
Lateral-line scales	31	56.3	31-32	32-32
Pored scales posterior to lateral line	2	100.0	2-2	2-2
Scale rows on cheek	4	81.3	4-5	5-5
Dorsal-fin spines	17	75.0	17-18	18-18
Dorsal-fin rays	9	87.5	8-9	9-10
Anal-fin spines	3	100.0	3-3	3-3
Anal-fin rays	8	75.0	7-8	8-9
Pectoral-fin rays	14	68.8	12-14	13-13
Pelvic-fin rays	5	100.0	5-5	5-5
Gill rakers on first ceratobranchial	11	62.5	10-12	12-12
Gill raker on first epibranchial	3	56.3	2-3	2-2
Teeth in outer row of left lower jaw	12	56.3	12-14	14-16
Teeth rows on upper jaw	3	62.5	2-3	6-6
Teeth rows on lower jaw	2	56.3	2-3	5-6

TABLE 1 (concluded)

Table 3. Morphometric and meristic values of *Metriacisma malabanchion* holotype and populations from Mirande Rocks (N = 20), Namalenge Island (N = 20), Domwe Island (N = 20), Mumbo Island (N = 20), and Zimbabwe Rocks (N = 20).

	Holotype	Mirande Rocks			Namalenge Island			Domwe Island		
		Mean	Standard Deviation	Range	Mean	Standard Deviation	Range	Mean	Standard Deviation	Range
Standard length, mm	85.7	70.7	4.6	64.2-81.5	75.7	5.9	64.3-86.6	76.8	11.1	55.3-88.6
Head length, mm	27.9	22.2	1.3	20.2-25.4	24.3	1.9	20.5-26.6	23.5	3.4	17.1-26.9
Percent of standard length										
Head length	32.5	31.4	0.8	30.2-33.1	32.1	1.0	30.7-34.2	30.7	0.6	29.2-31.5
Snout to dorsal-fin origin	33.8	34.3	1.2	31.6-36.4	34.3	1.1	32.1-36.6	32.8	1.0	30.8-34.6
Snout to pelvic-fin origin	33.7	26.8	1.8	23.8-31.0	29.9	2.8	24.8-33.5	27.8	4.2	20.2-32.4
Pectoral-fin length	31.1	28.8	1.2	26.6-31.2	27.6	2.3	19.3-30.0	29.1	2.5	20.4-33.4
Pelvic-fin length	45.8	33.1	3.9	28.2-43.0	37.7	4.8	28.2-46.8	38.2	6.1	25.6-49.6
Dorsal-fin base length	60.5	61.5	1.5	57.6-63.6	59.9	1.2	58.3-62.3	60.0	0.9	57.5-61.3
Anterior dorsal to anterior anal	52.1	53.3	1.2	50.8-56.4	52.3	1.4	49.5-54.2	50.4	1.0	48.6-52.4
Posterior dorsal to posterior anal	17.2	15.8	1.1	14.2-18.3	15.9	0.6	14.2-16.8	15.5	0.4	14.7-16.4
Anterior dorsal to posterior anal	63.7	64.8	1.2	62.0-66.4	64.3	1.0	62.7-66.2	63.3	0.8	61.7-64.9
Posterior dorsal to anterior anal	30.2	29.5	1.2	26.9-31.3	29.8	1.2	27.1-32.5	28.5	0.8	26.4-30.0
Posterior dorsal to ventral caudal	17.7	17.5	0.7	16.1-18.7	17.9	0.7	16.3-19.2	17.1	0.4	16.4-18.1
Posterior anal to dorsal caudal	18.3	19.2	0.7	18.0-20.3	19.0	0.5	17.9-19.7	18.5	0.8	16.8-20.3
Anterior dorsal to pelvic-fin origin	36.0	35.4	1.3	33.1-38.2	36.2	1.5	33.2-38.6	32.4	1.6	27.9-34.5
Posterior dorsal to pelvic-fin origin	57.4	57.8	1.3	55.8-60.4	56.6	1.2	54.8-58.6	58.8	1.5	56.0-61.0
Percent of head length										
Horizontal eye diameter	30.3	33.2	1.6	37.0-41.9	31.3	1.1	28.6-33.4	31.9	0.9	29.8-33.5
Vertical eye diameter	29.9	33.4	2.2	30.5-37.9	31.4	0.8	30.1-32.7	31.5	0.9	30.1-33.0
Snout length	36.4	32.8	1.3	30.4-35.0	34.1	1.3	31.2-36.1	33.0	2.1	28.5-36.7
Postorbital head length	36.4	39.8	1.6	37.0-41.9	39.9	1.2	37.3-42.3	39.4	1.2	37.6-41.4
Precorbital depth	17.5	21.1	1.0	18.3-25.5	21.9	0.8	20.3-23.3	20.3	1.2	17.4-21.9
Lower-jaw length	35.8	35.2	1.8	31.6-37.5	38.4	1.1	36.2-41.0	36.1	1.0	34.0-37.7
Cheek depth	26.1	26.6	1.7	22.6-29.4	27.6	1.5	24.7-30.5	26.2	1.9	21.9-28.4
Head depth	93.4	92.4	4.3	82.4-99.8	96.1	4.0	87.7-103.0	87.1	3.4	80.4-92.7
Counts		Mode	% Freq.		Mode	% Freq.		Mode	% Freq.	
Lateral-line scales	32	32	55.0	32-33	31	55.0	30-32	33	65.0	31-33
Pored scales posterior to lateral line	2	2	85.0	1-2	2	60.0	0-2	2	65.0	0-3
Scale rows on cheek	4	4	100.0	4-4	5	55.0	3-5	4	45.0	3-6
Dorsal-fin spines	18	18	85.0	17-19	17	60.0	16-18	18	75.0	17-19
Dorsal-fin rays	8	9	95.0	9-10	9	70.0	8-9	9	75.0	8-10
Anal-fin spines	3	3	100.0	3-3	3	95.0	3-4	3	100.0	3-3
Anal-fin rays	8	7	55.0	7-9	8	90.0	7-8	8	90.0	7-9
Pectoral-fin rays	12	14	50.0	13-14	14	60.0	12-14	13	50.0	12-14
Pelvic-fin rays	5	5	100.0	5-5	5	100.0	5-5	5	100.0	5-5
Gill rakers on first ceratobranchial	13	10	75.0	10-12	11	50.0	11-13	12	50.0	10-12
Gill raker on first epibranchial	3	3	85.0	2-3	3	70.0	2-4	3	85.0	2-4
Teeth in outer row of left lower jaw	9	13	35.0	9-14	12	40.0	7-13	11	40.0	10-14
Teeth rows on upper jaw	3	3	70.0	3-4	4	40.0	2-5	3	65.0	3-4
Teeth rows on lower jaw	3	3	65.0	3-4	3	90.0	3-4	3	80.0	3-4

TABLE 3 (concluded)

	Mumbo Island			Zimbabwe Rocks		
	Mean	Standard Deviation	Range	Mean	Standard Deviation	Range
Standard length, mm	85.2	3.20	76.8-91.5	95.8	6.1	78.2-105.4
Head length, mm	26.5	1.1	24.2-28.2	30.7	2.1	24.2-34.0
Percent of standard length						
Head length	31.1	0.8	29.3-32.5	32.0	0.9	30.9-34.5
Snout to dorsal-fin origin	33.0	1.0	30.5-34.5	35.1	0.9	33.4-37.8
Snout to pelvic-fin origin	32.3	1.5	28.4-34.6	37.50	2.3	29.8-40.1
Pectoral-fin length	30.2	1.7	27.3-33.6	28.3	1.6	26.0-31.2
Pelvic-fin length	39.9	3.4	30.8-45.8	39.9	4.7	31.6-48.9
Dorsal-fin base length	60.8	1.1	58.7-63.1	62.6	1.6	60.4-66.0
Anterior dorsal to anterior anal	51.1	1.1	49.0-53.4	54.2	1.3	51.0-56.3
Posterior dorsal to posterior anal	16.7	0.5	15.6-17.8	17.0	0.9	15.4-18.8
Anterior dorsal to posterior anal	64.3	0.9	62.9-65.8	66.1	1.5	63.5-69.2
Posterior dorsal to anterior anal	30.1	1.0	28.4-31.7	33.1	1.3	31.2-35.7
Posterior dorsal to ventral caudal	17.8	1.0	16.6-20.1	18.6	1.2	16.1-20.8
Posterior anal to dorsal caudal	19.1	0.9	17.5-20.5	19.8	0.9	17.1-21.2
Anterior dorsal to pelvic-fin origin	34.7	1.4	32.8-37.6	38.7	1.8	34.3-41.1
Posterior dorsal to pelvic-fin origin	58.4	1.1	55.7-60.0	57.7	1.7	54.5-60.8
Percent of head length						
Horizontal eye diameter	31.8	1.4	29.1-33.8	30.0	1.1	27.6-31.7
Vertical eye diameter	31.7	1.3	29.8-33.7	29.4	1.4	26.2-31.3
Snout length	34.5	1.6	31.8-37.7	33.0	3.3	20.6-35.3
Postorbital head length	39.6	1.1	36.4-41.4	39.6	0.9	38.2-40.8
Preorbital depth	19.5	1.5	16.7-22.0	21.5	1.2	18.7-23.1
Lower-jaw length	37.5	1.5	34.0-40.9	41.0	2.0	36.0-44.2
Cheek depth	27.6	1.4	24.2-30.1	27.9	1.2	26.0-30.6
Head depth	94.9	3.7	88.4-100.9	101.3	6.0	91.0-113.0
Counts	Mode	% Freq.	Range	Mode	% Freq.	Range
Lateral-line scales	32	70.0	32-34	32	50.0	31-34
Pored scales posterior to lateral line	2	50.0	0-3	2	60.0	1-3
Scale rows on cheek	4	50.0	3-5	4	80.0	4-6
Dorsal-fin spines	18	50.0	17-19	18	65.0	16-18
Dorsal-fin rays	9	70.0	8-10	9	70.0	8-10
Anal-fin spines	3	100.0	3-3	3	100.0	3-3
Anal-fin rays	8	80.0	7-9	8	80.0	7-9
Pectoral-fin rays	13	85.0	12-14	13	80.0	12-14
Pelvic-fin rays	5	100.0	5-5	5	100.0	5-5
Gill rakers on first ceratobranchial	13	65.0	12-14	12	50.0	12-14
Gill raker on first epibranchial	3	80.0	2-4	3	100.0	3-3
Teeth in outer row of left lower jaw	7	30.0	3-10	10	35.0	7-12
Teeth rows on upper jaw	3	75.0	2-3	3	100.0	3-3
Teeth rows on lower jaw	3	70.0	2-3	3	100.0	3-3

Table 4. Morphometric and meristic values of the type series of *Metriaclicma chrysomallos* (N = 20). Mean, standard deviation, and range include the holotype.

	Holotype	Mean	Standard Deviation	Range
Standard length, mm	84.8	76.7	11.1	61.0-89.6
Head length, mm	26.6	24.2	3.2	18.6-27.8
Percent of standard length				
Head length	31.4	31.7	1.0	29.1-33.0
Snout to dorsal-fin origin	34.9	34.5	0.9	32.8-36.9
Snout to pelvic-fin origin	33.4	29.3	4.0	23.2-33.9
Pectoral-fin length	28.9	28.1	1.6	24.4-31.2
Pelvic-fin length	73.3	33.8	5.3	24.6-41.8
Dorsal-fin base length	62.0	61.8	1.8	59.7-65.5
Anterior dorsal to anterior anal	50.7	50.9	1.6	48.1-54.1
Posterior dorsal to posterior anal	16.8	16.5	0.6	15.6-17.5
Anterior dorsal to posterior anal	64.1	64.3	1.7	62.3-67.2
Posterior dorsal to anterior anal	31.6	31.9	1.1	29.9-33.7
Posterior dorsal to ventral caudal	17.5	17.7	0.6	16.6-19.0
Posterior anal to dorsal caudal	19.7	20.3	0.7	19.0-21.3
Anterior dorsal to pelvic-fin origin	36.2	35.2	1.6	32.6-37.4
Posterior dorsal to pelvic-fin origin	56.2	17.7	0.6	16.6-19.0
Percent of head length				
Horizontal eye diameter	32.8	31.9	1.2	29.8-34.3
Vertical eye diameter	30.2	32.1	1.3	30.1-34.9
Snout length	35.7	32.5	1.9	28.7-35.8
Postorbital head length	38.6	38.6	0.9	36.7-40.0
Preorbital depth	19.6	19.5	1.7	16.8-22.6
Lower-jaw length	35.3	39.3	1.5	35.3-41.4
Cheek depth	26.2	26.0	2.0	22.5-30.6
Head depth	94.6	96.8	4.2	88.1-102.4
Counts		Mode	% Freq.	Range
Lateral-line scales	32	32	90.0	31-33
Pored scales posterior to lateral line	2	2	80.0	0-2
Scaic rows on cheek	4	4	80.0	3-4
Dorsal-fin spines	17	18	55.0	17-18
Dorsal-fin rays	9	9	75.0	8-10
Anal-fin spines	3	3	100.0	3-3
Anal-fin rays	7	7	85.0	6-8
Pectoral-fin rays	13	13	100.0	13-13
Pelvic-fin rays	5	5	100.0	5-5
Gill rakers on first ceratobranchial	13	13	50.0	11-14
Gill raker on first epibranchial	3	3	65.0	2-3
Teeth in outer row of left lower jaw	13	8	25.0	6-13
Teeth rows on upper jaw	3	3	60.0	2-3
Teeth rows on lower jaw	3	3	75.0	2-3

Table 5. Morphometric and meristic values of the type series of *Metriaclicma phaeos* (N = 8). Mean, standard deviation, and range include the holotype.

	Holotype	Mean	Standard Deviation	Range
Standard length, mm	85.1	77.9	8.1	68.3-86.5
Head length, mm	25.9	24.0	2.5	20.4-27.1
Percent of standard length				
Head length	30.5	30.8	0.6	29.8-31.7
Snout to dorsal-fin origin	35.3	35.3	1.0	34.1-36.8
Snout to pelvic-fin origin	34.1	31.0	2.9	27.5-35.6
Pectoral-fin length	27.6	27.1	1.2	24.8-29.1
Pelvic-fin length	38.0	34.8	5.3	28.4-43.8
Dorsal-fin base length	59.8	59.0	1.1	57.8-61.0
Anterior dorsal to anterior anal	51.3	50.2	0.8	49.0-51.3
Posterior dorsal to posterior anal	13.9	14.5	0.7	13.3-15.7
Anterior dorsal to posterior anal	62.2	62.6	1.1	61.0-64.1
Posterior dorsal to anterior anal	28.4	29.4	0.8	28.4-30.9
Posterior dorsal to ventral caudal	16.5	17.0	0.6	15.9-17.9
Posterior anal to dorsal caudal	18.7	18.8	0.4	18.4-19.5
Anterior dorsal to pelvic-fin origin	33.9	34.0	1.0	32.6-35.5
Posterior dorsal to pelvic-fin origin	54.8	55.0	1.1	53.3-56.6
Percent of head length				
Horizontal eye diameter	30.8	30.9	2.0	27.7-32.9
Vertical eye diameter	31.4	30.4	1.7	27.8-33.3
Snout length	43.2	41.4	2.0	37.9-44.7
Postorbital head length	41.2	40.8	1.1	38.8-42.6
Preorbital depth	23.9	23.8	1.3	21.6-26.3
Lower-jaw length	44.5	42.3	1.8	38.7-44.5
Cheek depth	31.7	29.5	1.9	26.3-31.7
Head depth	104.8	100.1	4.4	92.8-105.3
Counts		Mode	% Freq.	Range
Lateral-line scales	31	32	53.6	31-32
Pored scales posterior to lateral line	1	2	55.6	1-3
Scale rows on cheek	4	5	55.6	4-5
Dorsal-fin spines	17	17	66.7	17-18
Dorsal-fin rays	9	9	100.0	9-9
Anal-fin spines	4	3	88.9	3-4
Anal-fin rays	8	8	100.0	8-8
Pectoral-fin rays	14	14	77.8	14-15
Pelvic-fin rays	5	5	100.0	5-5
Gill rakers on first ceratobranchial	13	12	66.7	11-13
Gill raker on first epibranchial	3	3	77.8	2-4
Teeth in outer row of left lower jaw	12	12	44.4	11-13
Teeth rows on upper jaw	4	3	55.6	3-4
Teeth rows on lower jaw	3	3	88.9	3-4

Table 6. Morphometric and meristic values of the type series of *Metriacrima cynemarginatus* (N = 18). Mean, standard deviation, and range include the holotype.

	Holotype	Mean	Standard Deviation	Range
Standard length, mm	73.9	66.7	9.9	51.9-80.4
Head length, mm	22.4	20.7	2.9	16.0-24.8
Percent of standard length				
Head length	30.2	31.0	0.8	29.8-32.6
Snout to dorsal-fin origin	31.8	32.5	1.1	30.4-34.1
Snout to pelvic-fin origin	28.5	25.1	4.0	18.6-31.3
Pectoral-fin length	26.1	26.5	1.0	25.5-29.4
Pelvic-fin length	29.7	27.6	2.0	23.4-30.9
Dorsal-fin base length	60.5	61.3	1.6	58.8-64.2
Anterior dorsal to anterior anal	49.0	49.1	4.4	32.0-51.9
Posterior dorsal to posterior anal	15.5	15.7	0.7	14.5-16.9
Anterior dorsal to posterior anal	62.4	63.6	1.6	61.4-66.3
Posterior dorsal to anterior anal	28.0	28.5	1.1	26.1-30.6
Posterior dorsal to ventral caudal	16.2	17.3	0.8	15.6-18.9
Posterior anal to dorsal caudal	20.4	20.2	0.9	18.4-21.7
Anterior dorsal to pelvic-fin origin	29.9	30.6	1.8	27.4-32.9
Posterior dorsal to pelvic-fin origin	55.9	56.7	1.1	54.8-58.4
Percent of head length				
Horizontal eye diameter	34.5	35.50	2.1	33.0-39.8
Vertical eye diameter	34.8	34.8	1.5	32.3-37.6
Snout length	33.1	31.1	1.7	28.5-34.1
Postorbital head length	37.4	39.0	1.4	36.4-41.3
Preorbital depth	16.2	16.2	1.6	12.3-18.8
Lower-jaw length	31.5	35.2	1.4	31.5-37.3
Cheek depth	23.3	23.3	2.4	18.6-26.7
Head depth	87.7	87.2	4.0	78.2-92.5
Counts		Mode	% Freq.	Range
Lateral-line scales	32	32	61.1	31-33
Pored scales posterior to lateral line	0	2	33.3	0-3
Scale rows on cheek	5	5	44.4	3-5
Dorsal-fin spines	17	18	72.2	17-18
Dorsal-fin rays	9	9	72.2	8-10
Anal-fin spines	3	3	100.0	3-3
Anal-fin rays	8	8	77.8	7-8
Pectoral-fin rays	13	13	50.0	11-15
Pelvic-fin rays	5	5	94.4	4-5
Gill rakers on first ceratobranchial	10	11	61.1	10-12
Gill raker on first epibranchial	2	3	88.9	2-3
Teeth in outer row of left lower jaw	12	8	33.3	8-12
Teeth rows on upper jaw	3	3	100.0	3-3
Teeth rows on lower jaw	3	3	88.9	2-3

Table 7. Morphometric and meristic values of the type series of *Metriclinima benetos* (N = 19) and *M. callainos* (N = 20). Mean, standard deviation, and range of *M. benetos* includes the holotype.

	<i>M. benetos</i>			<i>M. callainos</i>		
	Holotype	Mean	Standard Deviation	Mean	Standard Deviation	Range
Standard length, mm	81.4	71.6	5.4	68.5	5.9	60.5-80.1
Head length, mm	25.9	22.8	1.6	20.9	1.8	18.3-23.8
Percent of standard length						
Head length	31.8	31.9	0.7	30.8-33.0	0.7	29.2-31.6
Snout to dorsal-fin origin	33.0	33.7	0.9	32.8-35.7	1.1	30.6-34.6
Snout to pelvic-fin origin	30.8	27.6	2.3	23.4-32.2	2.2	22.1-28.9
Pectoral-fin length	25.1	24.6	1.9	18.9-27.3	1.5	22.0-28.6
Pelvic-fin length	37.4	39.6	4.4	30.5-45.8	3.9	24.0-36.4
Dorsal-fin base length	60.3	61.0	2.1	56.1-66.4	1.8	59.9-66.6
Anterior dorsal to anterior anal	49.2	49.8	1.2	47.3-52.4	1.5	46.5-54.3
Posterior dorsal to posterior anal	14.8	15.3	0.9	13.8-17.1	0.8	14.2-16.8
Anterior dorsal to posterior anal	62.7	62.8	1.3	60.2-64.8	1.5	62.0-67.4
Posterior dorsal to anterior anal	29.1	29.2	1.4	26.9-32.3	1.0	27.2-30.8
Posterior dorsal to ventral caudal	17.3	17.8	1.4	14.9-20.2	0.9	16.8-19.9
Posterior anal to dorsal caudal	19.8	20.9	1.0	19.5-22.8	1.2	19.8-24.2
Anterior dorsal to pelvic-fin origin	33.5	22.3	1.4	30.3-35.6	1.5	29.9-35.1
Posterior dorsal to pelvic-fin origin	57.3	57.4	1.9	54.1-60.7	1.2	53.9-58.4
Percent of head length						
Horizontal eye diameter	33.0	33.0	1.3	29.1-34.9	1.6	28.5-34.2
Vertical eye diameter	31.4	32.4	1.3	30.4-35.8	1.5	29.7-35.3
Snout length	35.3	34.4	1.6	32.5-37.6	2.6	28.8-37.2
Postorbital head length	38.1	38.7	1.2	35.8-40.6	1.4	37.8-42.6
Precorbital depth	21.8	20.1	1.1	18.0-21.8	1.3	20.1-25.0
Lower-jaw length	38.9	36.9	1.6	33.5-39.6	2.0	34.9-43.3
Cheek depth	27.8	25.4	2.1	20.9-29.0	3.4	21.3-33.5
Head depth	93.7	94.2	3.8	87.4-103.0	8.2	63.2-103.9
Counts		Mode	% Freq.	Mode	% Freq.	Range
Lateral-line scales	29	30	42.1	31	65.0	30-32
Pored scales posterior to lateral line	2	2	57.9	0-3	2	85.0
Scale rows on cheek	3	4	84.2	3-5	4	100.0
Dorsal-fin spines	16	17	73.7	16-18	18	85.0
Dorsal-fin rays	9	9	78.9	8-10	9	75.0
Anal-fin spines	3	3	100.0	3-3	3	100.0
Anal-fin rays	7	7	78.9	6-8	7	95.0
Pectoral-fin rays	13	13	84.2	12-14	14	65.0
Pelvic-fin rays	5	5	100.0	5-5	5	100.0
Gill rakers on first ceratobranchial	10	10	57.9	9-12	11	75.0
Gill raker on first epibranchial	2	2	89.5	2-3	2	65.0
Teeth in outer row of left lower jaw	9	12	31.6	9-13	14	40.0
Teeth rows on upper jaw	4	3	73.7	3-4	4	95.0
Teeth rows on lower jaw	4	4	63.2	3-4	4	75.0

Table 8. Morphometric and meristic values of *Metriaclima xanstormachus* from Nakantenga Island (N = 5) and Kanjedza Island (N = 20).

	Nakantenga Island			Kanjedza Island		
	Mean	Standard Deviation	Range	Mean	Standard Deviation	Range
Standard length, mm	80.3	2.9	77.0-83.3	64.1	4.1	55.2-70.7
Head length, mm	25.5	1.0	24.6-26.8	21.1	1.4	18.2-23.6
Percent of standard length						
Head length	31.8	0.3	31.4-32.2	33.0	0.7	32.1-34.3
Snout to dorsal-fin origin	32.5	0.9	31.6-33.6	33.9	0.9	32.4-35.6
Snout to pelvic-fin origin	30.7	1.4	29.0-32.1	25.6	1.8	21.5-28.4
Pectoral-fin length	26.7	1.6	24.0-28.1	27.3	1.9	22.1-30.0
Pelvic-fin length	36.1	2.1	33.1-38.8	36.3	5.6	25.2-44.6
Dorsal-fin base length	61.6	1.0	60.3-62.8	58.9	1.4	56.2-61.1
Anterior dorsal to anterior anal	53.3	2.4	49.8-55.5	51.4	1.2	49.7-54.2
Posterior dorsal to posterior anal	15.3	0.5	14.5-15.8	14.6	0.6	13.7-16.0
Anterior dorsal to posterior anal	64.8	0.6	64.4-65.8	62.4	1.0	60.6-63.9
Posterior dorsal to anterior anal	28.5	0.6	27.8-29.2	28.2	1.0	26.4-30.3
Posterior dorsal to ventral caudal	18.1	0.5	17.4-18.6	17.1	0.8	15.7-18.8
Posterior anal to dorsal caudal	19.3	0.8	18.7-20.7	18.2	0.8	17.2-19.8
Anterior dorsal to pelvic-fin origin	36.8	1.3	35.2-38.6	34.6	1.1	32.4-36.8
Posterior dorsal to pelvic-fin origin	57.0	0.7	56.0-57.9	57.4	1.3	55.7-59.9
Percent of head length						
Horizontal eye diameter	26.3	1.9	24.4-29.4	32.1	1.7	30.0-36.4
Vertical eye diameter	26.0	1.8	24.1-28.2	31.8	1.3	29.5-34.6
Snout length	39.0	0.7	38.4-40.1	33.7	1.4	31.1-36.0
Postorbital head length	40.0	1.0	39.0-41.1	39.8	0.8	38.4-42.0
Precorbital depth	25.2	1.6	22.5-26.4	39.8	0.8	38.4-42.0
Lower-jaw length	39.5	1.4	37.1-40.7	35.9	1.8	32.8-38.8
Cheek depth	28.0	1.9	25.4-30.3	27.7	1.4	24.3-30.5
Head depth	97.5	3.1	94.3-101.5	83.7	2.7	79.9-88.4
Counts	Mode	% Freq.	Range	Mode	% Freq.	Range
Lateral-line scales	31	60.0	31-32	31	50.0	30-33
Pored scales posterior to lateral line	2	80.0	1-2	2	70.0	0-2
Scale rows on cheek	5	80.0	4-5	5	55.0	4-6
Dorsal-fin spines	17	60.0	17-18	17	70.0	16-18
Dorsal-fin rays	9	80.0	8-9	9	70.0	8-10
Anal-fin spines	3	100.0	3-3	3	100.0	3-3
Anal-fin rays	7	100.0	7-7	8	90.0	7-8
Pectoral-fin rays	14	60.0	13-14	14	55.0	12-14
Pelvic-fin rays	5	100.0	5-5	5	100.0	5-5
Gill rakers on first ceratobranchial	10	60.0	10-11	11	70.0	9-12
Gill raker on first epibranchial	2	100.0	2-2	3	65.0	2-3
Teeth in outer row of left lower jaw	10	60.0	9-10	10	65.0	9-11
Teeth rows on upper jaw	4	60.0	3	4	65.0	3-4
Teeth rows on lower jaw	3	60.0	3-4	4	50.0	3-5

Table 9. Morphometric and meristic values of the type series of *Metriciactima emmilotos* (N = 20), *M. pyrsonotos* (N = 20), and *M. sandaracinos* which includes populations from Mpandi Island (N = 20) and Kanjedza Island (N = 19). Mean, standard deviation, and range of all populations includes the holotype.

	<i>M. emmilotos</i>				<i>M. pyrsonotos</i>			
	Holotype	Mean	Standard Deviation	Range	Holotype	Mean	Standard Deviation	Range
Standard length, mm	84.1	72.8	8.0	59.3-84.2	74.1	66.2	7.2	56.9-76.6
Head length, mm	27.2	23.0	2.4	18.6-27.2	22.6	20.8	2.2	18.2-23.6
Percent of standard length								
Head length	32.3	31.7	0.9	30.4-32.8	30.5	31.6	0.7	30.5-32.6
Snout to dorsal-fin origin	35.8	34.5	0.8	33.4-35.8	34.8	34.7	1.5	32.0-37.0
Snout to pelvic-fin origin	32.8	27.5	3.1	22.8-32.8	27.4	24.8	2.9	32.0-37.1
Pectoral-fin length	28.9	28.3	1.2	26.0-30.2	26.3	27.8	1.6	25.6-30.9
Pelvic-fin length	35.2	31.8	3.1	27.8-38.4	32.6	33.5	4.9	26.8-44.6
Dorsal-fin base length	62.3	62.2	1.0	60.7-65.5	62.3	62.7	1.1	60.8-66.0
Anterior dorsal to anterior anal	54.7	52.9	1.7	50.2-56.2	53.4	53.9	1.3	51.9-55.9
Posterior dorsal to posterior anal	17.4	16.5	0.8	15.3-17.6	16.6	17.0	0.9	16.0-18.8
Anterior dorsal to posterior anal	66.4	65.1	1.3	62.5-67.8	64.6	66.1	0.9	64.6-68.4
Posterior dorsal to anterior anal	33.1	32.1	1.2	29.9-33.7	32.9	33.0	1.2	30.6-35.4
Posterior dorsal to ventral caudal	18.7	18.4	0.7	17.2-19.5	19.1	18.6	1.2	17.2-21.5
Posterior anal to dorsal caudal	21.2	21.4	0.8	20.2-22.5	21.8	21.4	0.7	20.2-22.3
Anterior dorsal to pelvic-fin origin	38.8	35.8	2.0	31.6-38.9	38.4	37.7	1.5	35.3-41.5
Posterior dorsal to pelvic-fin origin	57.0	56.9	1.1	54.7-58.7	57.4	58.5	1.3	56.0-60.7
Percent of head length								
Horizontal eye diameter	30.2	31.8	1.7	29.3-34.7	33.8	32.8	1.3	31.2-35.3
Vertical eye diameter	30.4	32.5	1.7	29.9-36.5	33.4	33.1	0.9	31.8-35.3
Snout length	34.9	32.9	1.8	29.1-35.2	32.9	32.2	1.1	29.7-34.2
Postorbital head length	40.0	38.8	0.1	37.3-40.2	37.7	39.5	1.1	37.0-40.8
Preorbital depth	21.2	20.1	1.0	18.6-21.7	21.6	20.1	1.2	18.1-21.6
Lower-jaw length	35.3	39.0	1.6	35.3-41.6	40.4	39.5	1.4	37.5-42.5
Cheek depth	27.9	26.8	2.3	22.7-32.4	29.5	27.9	2.2	23.1-31.7
Head depth	104.8	99.7	5.7	90.5-110.2	113.7	105.3	5.0	97.0-115.4
Counts		Mode	% Freq.	Range		Mode	% Freq.	Range
Lateral-line scales	31	31	55.0	30-32	31	31	80.0	30-32
Pored scales posterior to lateral line	2	2	50.0	0-2	2	2	70.0	0-2
Scale rows on cheek	4	4	95.0	4-5	5	4	80.0	3-5
Dorsal-fin spines	17	17	55.0	17-18	17	17	80.0	16-18
Dorsal-fin rays	9	9	60.0	8-10	8	9	85.0	8-10
Anal-fin spines	3	3	100.0	3-3	3	3	100.0	3-3
Anal-fin rays	6	7	85.0	6-8	7	7	90.0	6-8
Pectoral-fin rays	13	13	95.0	12-13	13	13	85.0	12-14
Pelvic-fin rays	5	5	100.0	5-5	5	5	100.0	5-5
Gill rakers on first ceratobranchial	12	13	45.0	10-14	11	12	45.0	10-14
Gill raker on first epibranchial	3	3	65.0	2-3	3	3	95.0	2-3
Teeth in outer row of left lower jaw	9	9	45.0	8-12	7	7	35.0	4-10
Teeth rows on upper jaw	3	3	100.0	3-3	3	3	90.0	2-3
Teeth rows on lower jaw	3	3	100.0	3-3	2	2	50.0	2-3

TABLE 9 (concluded)

	<i>M. sandaracina</i> - Nipantdi Island			<i>M. sandaracina</i> - Kanjedza Island			
	Holotype	Mean	Standard Deviation	Range	Mean	Standard Deviation	Range
Standard length, mm	70.9	64.9	4.8	55.0-73.1	62.7	4.4	54.0-69.0
Head length, mm	23.2	21.7	1.5	18.6-24.4	21.1	1.4	18.7-23.4
Percent of standard length							
Head length	32.7	33.5	0.8	32.3-35.3	33.5	1.1	32.3-35.6
Snout to dorsal-fin origin	34.9	35.7	0.8	34.8-37.3	35.00	1.9	30.5-38.3
Snout to pelvic-fin origin	28.1	26.2	2.3	21.8-30.6	25.0	2.0	20.9-28.9
Pectoral-fin length	26.5	26.0	1.8	22.3-30.2	30.1	6.3	21.4-43.3
Pelvic-fin length	38.1	35.7	4.5	24.9-42.0	31.8	4.9	23.5-40.5
Dorsal-fin base length	59.2	59.8	1.4	57.9-63.0	60.0	1.8	55.7-62.6
Anterior dorsal to anterior anal	51.3	52.9	0.9	51.3-54.6	52.0	1.4	48.0-53.7
Posterior dorsal to posterior anal	14.3	15.2	0.6	14.2-16.1	14.8	0.8	13.9-16.0
Anterior dorsal to posterior anal	58.0	62.5	1.8	58.0-64.5	62.8	1.3	59.1-65.0
Posterior dorsal to anterior anal	28.1	29.5	0.9	28.0-31.2	28.7	1.1	27.0-30.7
Posterior dorsal to ventral caudal	16.8	17.4	0.8	15.0-18.7	17.7	1.2	16.2-20.3
Posterior anal to dorsal caudal	20.1	20.3	1.0	18.9-22.3	19.4	1.7	16.8-23.4
Anterior dorsal to pelvic-fin origin	35.1	35.5	1.5	33.0-38.2	34.2	1.5	31.3-36.9
Posterior dorsal to pelvic-fin origin	52.8	54.7	0.8	52.8-56.0	56.0	1.5	52.7-58.4
Percent of head length							
Horizontal eye diameter	31.8	33.1	1.0	30.8-34.5	31.6	2.8	25.6-35.7
Vertical eye diameter	34.0	33.8	1.3	31.7-36.7	31.3	2.9	26.6-35.5
Snout length	32.5	34.4	1.7	30.9-36.6	34.6	2.0	30.8-37.8
Postorbital head length	38.4	37.8	1.2	35.5-39.7	38.0	1.2	36.0-39.5
Preorbital depth	20.7	20.7	1.2	17.7-22.5	19.7	1.7	16.7-22.8
Lower-jaw length	35.9	35.8	1.2	33.3-37.7	36.9	1.4	34.4-39.2
Cheek depth	27.4	24.8	2.1	21.5-27.7	23.3	2.1	20.0-27.1
Head depth	94.4	91.8	2.7	84.9-96.2	85.2	6.2	74.8-94.6
Counts		Mode	% Freq.	Range	Mode	% Freq.	Range
Lateral-line scales	32	31	45.0	30-32	31	42.0	29-32
Pored scales posterior to lateral line	2	2	65.0	0-2	2	63.0	0-2
Scale rows on cheek	5	5	85.0	4-5	3	42.0	3-5
Dorsal-fin spines	17	17	80.0	13-18	17	84.0	16-18
Dorsal-fin rays	9	9	85.0	8-10	9	58.0	8-9
Anal-fin spines	3	3	100.0	3-3	3	100.0	3-3
Anal-fin rays	7	7	95.0	7-8	7	95.0	6-7
Pectoral-fin rays	13	13	75.0	12-17	13	89.0	12-14
Pelvic-fin rays	5	5	100.0	5-5	5	100.0	5-5
Gill rakers on first ceratobranchial	11	11	50.0	9-13	10	42.0	8-12
Gill raker on first epibranchial	3	3	60.0	2-3	2	68.0	2-3
Teeth in outer row of left lower jaw	9	12	35.0	7-12	10	37.0	10-13
Teeth rows on upper jaw	3	3	95.0	3-4	3	89.0	3-4
Teeth rows on lower jaw	3	3	95.0	3-4	3	89.0	3-4

Table 10. Morphometric and meristic values of the type series of *Metrictima mbenjii* (N = 24) and *M. greshkai* (N = 20). Mean, standard deviation, and range of *M. mbenjii* include the holotype.

	<i>M. mbenjii</i>			<i>M. greshkai</i>			
	Holotype	Mean	Standard Deviation	Range	Mean	Standard Deviation	Range
Standard length, mm	88.0	79.0	5.6	71.0-88.3	77.6	9.6	60.5-94.1
Head length, mm	26.3	24.6	1.8	21.5-27.5	25.9	3.0	19.9-31.3
Percent of standard length							
Head length	29.9	31.2	0.6	29.9-32.0	33.4	0.9	31.2-34.9
Snout to dorsal-fin origin	32.8	34.6	0.9	32.8-36.9	36.1	1.1	34.1-38.0
Snout to pelvic-fin origin	32.8	30.1	2.5	26.3-34.8	31.3	4.0	23.8-38.2
Pectoral-fin length	26.1	27.5	2.1	23.9-31.2	28.4	1.7	25.6-31.1
Pelvic-fin length	33.9	32.0	4.0	26.7-39.3	34.4	3.4	29.6-44.2
Dorsal-fin base length	59.0	61.7	1.6	57.8-63.8	60.8	1.4	58.0-63.4
Anterior dorsal to anterior anal	56.3	53.5	1.8	50.0-57.7	52.8	1.3	50.6-55.7
Posterior dorsal to posterior anal	15.4	16.5	0.7	15.3-17.8	15.7	0.7	14.4-16.8
Anterior dorsal to posterior anal	65.1	64.9	1.4	61.8-67.1	64.0	1.5	62.2-67.2
Posterior dorsal to anterior anal	30.4	31.3	1.2	29.4-33.5	30.6	1.1	28.5-32.2
Posterior dorsal to ventral caudal	17.0	18.6	0.9	17.0-20.1	17.5	0.4	16.6-18.5
Posterior anal to dorsal caudal	21.6	21.6	0.7	20.1-22.6	19.7	0.8	18.4-21.4
Anterior dorsal to pelvic-fin origin	33.4	36.1	1.4	32.9-38.3	38.1	1.2	36.0-40.5
Posterior dorsal to pelvic-fin origin	57.1	57.1	1.5	54.3-60.2	57.0	4.8	37.6-60.6
Percent of head length							
Horizontal eye diameter	32.7	33.7	1.3	30.7-35.8	31.3	1.5	29.1-33.3
Vertical eye diameter	30.9	34.1	1.6	30.9-38.2	31.5	1.8	28.5-34.4
Snout length	35.8	34.6	1.8	31.3-37.7	35.9	1.6	33.3-39.1
Postorbital head length	38.5	38.3	1.4	36.0-42.2	37.3	1.0	35.2-38.7
Preorbital depth	23.2	21.5	1.4	18.3-24.2	21.6	1.2	19.3-24.4
Lower-jaw length	41.4	40.3	1.7	37.3-43.4	36.4	1.1	33.9-38.4
Cheek depth	25.3	27.8	1.5	25.3-30.8	25.4	1.8	21.0-28.8
Head depth	100.4	102.2	3.7	95.9-109.2	98.0	4.5	91.3-109.4
Counts		Mode	% Freq.	Range	Mode	% Freq.	Range
Lateral-line scales	31	31	66.7	30-32	31	60.0	30-33
Pored scales posterior to lateral line	2	2	54.2	1-3	2	85.0	1-2
Scale rows on cheek	4	4	83.3	4-5	4	85.0	4-5
Dorsal-fin spines	18	18	50.0	17-18	17	55.0	17-18
Dorsal-fin rays	8	9	54.2	8-10	9	55.0	8-9
Anal-fin spines	3	3	100.0	3-3	3	100.0	3-3
Anal-fin rays	7	7	87.5	6-8	7	95.0	6-7
Pectoral-fin rays	14	13	54.2	12-14	13	70.0	11-14
Pelvic-fin rays	5	5	100.0	5-5	5	100.0	5-5
Gill rakers on first ceratobranchial	11	12	66.7	11-13	11	60.0	8-12
Gill raker on first epibranchial	3	3	75.0	2-3	2	65.0	2-3
Teeth in outer row of left lower jaw	12	12	37.5	4-12	10	25.0	3-12
Teeth rows on upper jaw	3	3	83.3	3-4	3	80.0	2-3
Teeth rows on lower jaw	3	3	83.3	2-4	3	95.0	2-3

Table 11. Morphometric and meristic values of the type series of *Metriclinia thapsinogen* (N = 15). Mean, standard deviation, and range include the holotype.

	Holotype	Mean	Standard Deviation	Range
Standard length, mm	86.4	77.7	7.1	65.5-86.4
Head length, mm	28.4	24.9	2.4	20.8-28.4
Percent of standard length				
Head length	32.9	32.0	0.8	30.8-33.0
Snout to dorsal-fin origin	33.9	33.7	0.7	32.5-35.0
Snout to pelvic-fin origin	34.0	29.9	2.5	25.5-34.0
Pectoral-fin length	29.1	27.6	2.1	21.5-29.7
Pelvic-fin length	31.1	30.8	2.6	26.9-37.3
Dorsal-fin base length	59.3	59.8	1.1	58.0-62.3
Anterior dorsal to anterior anal	50.4	52.1	1.3	50.4-53.7
Posterior dorsal to posterior anal	16.1	16.3	0.6	15.4-17.4
Anterior dorsal to posterior anal	62.6	63.8	1.3	61.7-66.8
Posterior dorsal to anterior anal	30.5	30.0	1.3	27.9-32.1
Posterior dorsal to ventral caudal	17.1	17.8	0.5	17.1-19.0
Posterior anal to dorsal caudal	19.1	19.3	0.6	18.4-20.3
Anterior dorsal to pelvic-fin origin	34.5	35.4	1.5	32.9-38.9
Posterior dorsal to pelvic-fin origin	55.6	56.5	1.8	53.8-59.7
Percent of head length				
Horizontal eye diameter	29.5	30.0	1.0	28.4-31.1
Vertical eye diameter	28.3	29.7	1.0	28.1-31.2
Snout length	35.4	33.4	2.2	30.1-36.8
Postorbital head length	41.0	41.6	0.7	40.4-43.0
Preorbital depth	19.6	19.6	1.6	17.5-22.7
Lower-jaw length	34.0	36.9	1.9	34.0-39.2
Cheek depth	27.1	28.0	1.4	25.7-30.8
Head depth	93.8	95.9	2.8	90.2-100.5
Counts		Mode	% Freq.	Range
Lateral-line scales	31	31	80.0	30-32
Pored scales posterior to lateral line	1	1	40.0	0-2
Scale rows on cheek	5	5	60.0	4-5
Dorsal-fin spines	17	17	66.7	16-18
Dorsal-fin rays	9	9	66.7	8-9
Anal-fin spines	3	3	100.0	3-3
Anal-fin rays	8	8	80.0	7-9
Pectoral-fin rays	14	14	66.7	13-15
Pelvic-fin rays	5	5	100.0	5-5
Gill rakers on first ceratobranchial	12	12	66.7	11-13
Gill raker on first epibranchial	3	3	60.0	2-3
Teeth in outer row of left lower jaw	9	8	46.7	7-11
Teeth rows on upper jaw	3	3	86.7	2-3
Teeth rows on lower jaw	3	3	73.3	2-4