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**TAXONOMIC ANALYSIS OF THE *METRIACLIMA ZEBRA* SPECIES COMPLEX IN
LAKE MALAŪI WITH FIVE NEW SPECIES DESCRIPTIONS**

A Dissertation in

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by

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ABSTRACT

Lake Malaŵi is an African rift lake sharing borders with Malaŵi, Tanzania, and Mozambique and is known for its speciose haplochromine cichlids – most notably, the endemic rock-dwelling cichlids known as mbuna. One of the larger genera of mbuna is *Metriaclima*, a group consisting of approximately 75 species which is diagnosed by its feeding behavior and several morphological characteristics including the presence of bicuspid teeth in the outer row of both the upper and lower jaws. The members of genus are found in clear waters at sediment-free rocky coasts and do not have a continuous distribution around the lake. *Metriaclima zebra*, the type species for genus *Metriaclima*, was described based on a single specimen. While the collection location of this holotype is not known, based on the travel records of its collector, it is likely the specimen originates from Likoma Island.

This study included the morphological analysis of 1006 specimens of *Metriaclima* belonging to seventy collections from around Lake Malaŵi. Morphometric differences were analyzed using sheared principal component analysis (SPCA) of the morphometric data and principal component analysis (PCA) of the meristic data. The relationships among several color forms of *Metriaclima* were investigated and the holotype was compared to specimens from in and around Likoma Island to test the hypothesis that the location of origin for the type material is Likoma Island. The holotype was found to be morphologically similar to Likoma Island populations. Additionally, a distinctive yellow breasted *M. zebra* from Lumessi, Mozambique and *Metriaclima* sp. ‘blue blaze’ were regarded as conspecific with *M. zebra* based on the morphological analysis.

This investigation resulted in the description of the following five new species belonging to the *M. zebra* species complex: *M. pambazuko*, *M. lundoensis*, *M. midomo*, *M. tarakiki*, and *M. nigrodorsalis*. These species were distinguished and described based on color patterns, and

morphometric, meristic, and ecological differences. These new species were compared and distinguished from sympatric *Metriaclima* species and nearby populations of *Metriaclima* having similar color and pigmentation pattern and ecological niches. Lastly, a dichotomous key to the species of *Metriaclima* is presented.

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Chapter 1

Introduction

The cichlid fishes of East Africa represent the largest and best known case of explosive radiation in modern vertebrates. This radiation is concentrated in the three Great Lakes of Africa – lakes Tanganyika, Malaŵi, and Victoria. The Lake Malaŵi radiation produced the greatest number of endemic species of the three lakes, making it the most speciose lake in the world (Greenwood 1974).

Lake Malaŵi contains four to six species of the tilapiine tribe and an estimated 850 to 1500 haplochromine cichlid species, approximately 470 of which have been described and 2 of which are not endemic (Stauffer et al. 1997; Snoeks 2000; Konings 2001; Turner et al. 2001; Genner et al. 2004). Two major lineages exist within the haplochromines, the smaller, mostly rock-dwelling cichlids (often called mbuna) and the mostly pelagic and sand-dwelling cichlids. The endemic Malaŵi cichlid species are monophyletic, having one common ancestor (Kornfield et al. 1985; Meyer et al. 1990; Kornfield 1991; Moran et al. 1994).

The formation of Lake Malaŵi is estimated to have begun 8.6 million years ago, with deep-water conditions established around 4.5 million years ago (Ebinger et al. 1993; Delvaux 1995). The current Malaŵian radiation is estimated to be between 570,000 and 1 million years old (Meyer et al. 1990; Moran et al. 1994; Sturmbauer et al. 2001). The monophyly and recent radiation of haplochromine cichlids has limited their genetic diversity.

It is generally agreed that Lake Malaŵi was colonized by a generalized cichlid, probably similar to the recent *Astatotilapia calliptera* (Konings 2007). The diversification of the haplochromine cichlids has proceeded in three major bursts of cladogenesis (Danley & Kocher 2001). The first divergent event resulted in two major lineages –the sand- and rock-dwellers. The second radiation is responsible for the diversification of mbuna genera and is associated with

refinement of the trophic apparatus. The final major divergence led to species differing in reproductive characters, such as color patterns (Albertson et al. 1999; Danley & Kocher 2001). Research aimed at understanding speciation of African cichlids is ongoing and it is likely that refinement of molecular techniques will allow for a better understanding of this topic in the future.

The driving mechanisms for the explosive radiation of the haplochromine cichlids are unknown (Stauffer et al. 2005). The two most widely proposed methods of speciation are allopatric speciation (Fryer 1959; Fryer & Iles 1972; Greenwood 1984), which may have resulted from lake level fluctuations, and sympatric speciation driven by intrinsic isolating mechanisms (McKaye & Stauffer 1986; Turner & Burrows 1995; Oppen et al. 1998; Takahashi et al. 2001; Genner & Turner 2005). In both the allopatric and sympatric models, sexual selection fueled the rapid radiation. The significant youth of this diverse species flock may support the hypothesis that some mode of divergence other than the traditionally accepted model of allopatry has operated in Lake Malaŵi (Kornfield & Smith 2000). Sexual selection has long been argued as a mechanism that might drive speciation (Seehausen & van Alphen 1999; Seehausen et al. 1999; Kellogg et al. 2000; Turner 2000). Smith & Kornfield (2002) suggest speciation, marked by divergence in male color, may be extremely rapid and that many cryptic species, bearing similar color patterns, may be derived from independent origins. Rocky outcrops and islands in the southern portion of Lake Malaŵi, which are believed to have been dry due to low lake levels within the last 200-300 years, are inhabited by endemic species and unique color forms found nowhere else in the lake, suggesting that distinctive color forms, and even valid species, have evolved *in situ* within the last 200 years (Owen et al. 1990).

The importance of male breeding coloration in the speciation and maintenance of cichlid species in the Great Lakes of Africa is universally accepted (Barlow 1974; Barel et al. 1977; Greenwood 1981; Bowers & Stauffer 1993; Stauffer et al. 1995, 1997; Smith & Kornfield 2002).

Biologists agree that female mate choice can act as a strong driving force in runaway speciation, where the average female preference for a specific male trait (i.e. coloration) differs between two allopatric populations (Barlow 1981, 2000; Stauffer et al. 2006). Speciation by sexual selection on variation in male breeding coloration has been proposed to explain the rapid evolution of rock-dwelling haplochromine cichlids (Turner & Burrows 1995; van Doorn et al. 1998; Seehausen & van Alphen 1999, Kidd et al. 2006). Seehausen et al. (1999) suggest the force of sexual selection has allowed distinctive male breeding coloration to arise and evolve quickly.

Rock-dwelling Cichlids

Lake Malaŵi is well known for its endemic, small, rock-dwelling haplochromine cichlid fishes known as mbuna. They are the dominant fishes in rocky shores and all share the presence of many small scales in the nape, cheek and chest region and a reduction of the left ovary (Trewavas 1935; Fryer 1959). Most mbuna inhabit rocky areas which are discontinuous around the periphery of the lake and islands (Fryer & Iles 1972), but some others have reinvaded the sandy habitats. Markert et al. (1999) suggested the sandy bottoms and deep waters surrounding these rocky areas may act as strong barriers to dispersal of mbuna. Mbuna have severely restricted gene flow between disjunct habitats because of their restriction to rocky areas and lack of a pelagic dispersal phase, as seen in coral reef fishes. For this reason, numerous allopatric populations exist (Owen et al. 1990).

Most mbuna exhibit sexual dimorphism, with males typically attaining more intense breeding color and larger size. In most populations, territorial males have brighter, more dramatic coloration while females typically retain the juvenile coloration. Male breeding coloration is normally only expressed when a sexually mature male is defending a territory or a position in the hierarchy (Nelissen 1985), and a drabber male breeding coloration may be seen in some females

displaying aggression, often while mouthbrooding (Konings 2007). Physiological and anatomical evidence strongly suggests that mbuna have color vision and therefore, researchers agree that male breeding coloration plays a role attracting females for breeding (Stuaffer et al. 2002b). Jordan et al. (2006) documented the presence of several spectral classes of cone photoreceptors in cichlids and suggested color vision is important for both foraging and mate selection behavior. For these reasons, biologists agree female mate choice has been a driving force in the creation of uniquely-colored populations and in the evolution of these species (Barlow 1991, Andersson 1994). Many mbuna populations exhibit geographical variations in mostly male breeding coloration with little intra-population variation such that every location is characterized by a unique set of colors and markings (Ribbink et al. 1983; Ribbink 1986).

Mbuna are maternal mouthbrooders, and as such, only females carry the eggs and fry in their mouths and choose their temporary mate. Observations of mate choice and assortative mating experiments of mbuna have shown that female choice is influenced by male color patterns (Oppen et al. 1998; Pauers et al. 2004; Kidd et al. 2006). Most species of rock-dwelling cichlids have males that defend territories (locations that include small caves, rock crevices, rock surfaces, or the water column) where the spawning site is located and where females are attracted to spawn.

Rock-dwelling cichlids of Lake Malaŵi are well known for their adaptive feeding abilities. Mbuna exhibit a variety of feeding specializations and include algae-feeders, piscivores, planktivores, fin-biters, scale-eaters, and sand-sifters (Konings 2007). Although feeding specializations exist, many trophic specialists opportunistically feed on other items when available, such as plankton during the frequent blooms. Based on molecular data, Albertson et al. (1999) suggested adaptations in trophic morphology likely played a role in the early history of the lake, but has probably not led to the recent species diversity.

Genus Metriaclima

Metriaclima is a genus comprised of rock-dwelling cichlids endemic to Lake Malaŵi. The type species of this genus is *M. zebra*. The taxonomic status of *M. zebra* and the genus *Metriaclima* has been re-evaluated several times. Boulenger (1899) originally described *M. zebra* in the genus *Tilapia* based on a single specimen (BMNH 1891.12.17.7). Regan (1922) later moved *M. zebra* to the newly formed genus *Pseudotropheus*. Of the dozen genera of mbuna currently recognized, the genus *Pseudotropheus* is the most diverse and widespread (Stauffer & Kellogg et al. 2000; Konings & Stauffer 2006). Ribbink et al. (1983) recognized three species groups and three species complexes within *Pseudotropheus*, one of which was then referred to as the *P. zebra* species complex, a probable monophyletic group. The polyphyletic genus *Pseudotropheus* also contains several recognized and diverse groupings including: the *P. elongatus*, *P. williamsi*, and the *P. aggressive* complex, and a group of miscellaneous forms.

Meyer and Foerster (1984) proposed the name *Maylandia* as a subgenus of *Pseudotropheus* to include members of the *P. zebra* species complex. The proposal of *Maylandia* was not accompanied by either a diagnosis or a description of a character that would distinguish it from other taxa (a requirement of the International Code of Zoological Nomenclature); thus *Maylandia* was declared a nomen nudum (Stauffer et al. 1997; Konings & Geerts 1999). Stauffer et al. (1997) elevated the members of the *P. zebra* species complex to a newly diagnosed genus, *Metriaclima*.

The following three morphological characteristics were originally used to diagnose the genus *Metriaclima*: 1) The presence of bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws; 2) The moderately-sloped ethmo-vomerine block with a swollen rostral tip (Figure 1.0); and 3) The lower jaw forming a 45° angle with a line that connects the tip of the snout to the hypural plates (Stauffer et al. 1997). The morphological characteristics of the

ethmo-vomerine block reflect the manner in which these fishes browse the substrate. For this reason, the diagnosis of *Metriaclima* was expanded by Konings & Stauffer (2006) to include several feeding behavior characteristics. Members of *Metriaclima* feed at almost perpendicular angles to the substrate (Konings 1995; Stauffer & Posner 2006) and are capable of aligning the teeth of both the upper and lower jaws by abducting the jaws to a 180°-angle opening. Members of *Metriaclima* prefer aufwuchs, including diatoms and algal strands, as their primary food source and are adapted to brush loose aufwuchs from between filamentous algae. While closing the mouth from a 180°-angle, the teeth collect loose material by combing through the algae anchored to the substrate (Fryer 1959). These so-called bites into the substrate follow in rapid succession.



Figure 1.0: Left image: Cranium of *Metriaclima zebra* illustrating a moderately sloped ethmo-vomerine block (angle of ethmo-vomerine block is 34° with parasphenoid) with a swollen rostral tip. Right image: Cranium of *Tropheops tropheops*, illustrating a steeply sloped ethmo-vomerine block (angle of ethmo-vomerine block is 85° with parasphenoid) and lack of a swollen rostral tip (taken from Konings and Stauffer 2006).

Konings and Stauffer (2006) also included the following morphological characters in their expanded diagnosis of *Metriaclima*: 4) The lower jaw is often slightly longer and thicker than the upper jaw; 5) A large part of the upper dental arcade is normally exposed when the mouth is closed; 6) The tips of the teeth in the premaxilla and dentary are in a V-shaped line with the anterior most in upper and lower jaw furthest apart; and 7) The bicuspid teeth in the outer row

along the side of the jaws does not follow the contour of the jaw and the lateral teeth are rotated so that the plane of their two-pronged tips runs parallel with those in the anterior part of the jaw.

Presence of bicuspid teeth with both tips of equal length in the anterior portion of the outer row on both the upper and lower jaws distinguishes *Metriaclima* from many mbuna genera including the following: *Cyathochromis*, *Cynotilapia*, *Genyochromis*, *Gephyrochromis*, *Iodotropheus*, *Labeotropheus*, *Labidochromis*, *Petrotilapia*, and part of *Melanochromis*. Two horizontal stripes along the flanks of members of *Melanochromis*, distinguish them from *Metriaclima*. The species of *Melanochromis*, *Tropheops*, and *Pseudotropheus* lack a swollen rostral tip of the ethmo-vomerine block.

The original description of *Metriaclima* included the following species that were previously grouped in *Pseudotropheus*: *M. zebra* (Boulenger), *M. heteropictus* (Staeck), *M. callainos* (Stauffer & Hert), *M. xanstomachus* (Stauffer & Boltz), *M. greshakei* (Meyer & Foerster), *M. aurora* (Burgess), *M. barlowi* (McKaye & Stauffer), *M. elegans* (Trewavas), *M. estherae* (Konings), *M. hajomaylandi* (Meyer & Scharl), *M. lombardoi* (Burgess), *M. lanisticola* (Burgess), *M. livingstonii* (Boulenger), and *M. pursus* (Stauffer). The same publication also included the description of ten new species belonging to *Metriaclima* (*M. melabbranchion*, *M. chrysomallos*, *M. phaeos*, *M. cyneusmarginatus*, *M. benetos*, *M. pyrsonotos*, *M. sandaracinos*, *M. emmiltos*, *M. mbenjii*, and *M. thapsinogen*). More recently, Konings & Stauffer (2006) added a new species to the genus, *M. flavifemina*, which inhabits the rock-sand interface in the southern portion of Lake Malaŵi, and removed *P. heteropictus*. Konings and Stauffer (2006) also re-described *M. zebra* to include a population lacking lateral bars. *Metriaclima elegans* and *M. livingstonii* will not be considered as belonging to *Metriaclima* herein as recent information suggests *M. elegans* and *M. livingstonii* instead belong to the genus *Pseudotropheus* (Jay Stauffer, Jr. and Ad Konings, personal communication). Konings (1999) synonymized *M. melabbranchion* with *M. zebra* on grounds of lacking morphological differences with latter species with which it

was supposed to be sympatric, and *M. pursus* was synonymized with *M. lanisticola* (Konings, 2007) for lack of distinguishing morphological characters and close geographic proximity of populations of latter species. Lastly, Konings (2007) synonymized the red-top zebras described by Stauffer et al. (1997) as *M. sandaracinos* and *M. thapsinogen* with *M. pyrsonotos*. This was based on genetic similarities (Smith & Kornfield, 2002), the results of mate choice experiments by George Turner (unpublished), close geographic proximity of populations, and on the absence of fixed color differences. Lastly Konings (2007) moved *Pseudotropheus fainzilberi* to the genus *Metriaclima*.

Metriaclima may possibly be the most species-rich of all mbuna species complexes as Konings (2007) recognizes at least 75 different species within the genus. Groups within this genus are often referred to as species, but are sometimes also called populations of a single or a few species. Knight and Turner (2004) suggest that some of these groups may be incipient species – populations undergoing differentiation that, in time, may eventually become separate species. This genus contains many endemic species. These groups tend to differ from each other principally in one or more elements of the male breeding coloration. Species richness of *Metriaclima* may be attributed to the restriction of these species to islands and reefs, and to the force of allopatric speciation. Pauers et al. (2008) argue male-male aggression may also be a diversifying force in the speciation of mbuna.

Members of *Metriaclima* can exhibit polychromatism where populations contain so-called orange (O) and orange blotch (OB) color morphs as well as normally colored individuals (Fryer & Iles 1972; Ribbink et al. 1983; Konings 2001) (Figure 1.1). Fryer and Iles (1972) suggested the evolution of these morphs is only possible in species where mate recognition is based not just on male coloration but also on shape and behavior of the male. The orange color is the result of a lack of black pigment, and this mutation is frequently observed in African cichlids (Konings 2001). OB morphs can occur in both sexes, but are much less common in males, which

are referred to as “marmalade cats” in the aquarium trade. Konings (2001) suggested an OB male is poorly recognized as a potential mate by females and therefore is very unproductive. The orange morph is comparatively rarer than the OB morph among females. Konings (2001) suggested some OB morphs may have the advantage of being much less conspicuous against the rocky background of their habitats than their normal-colored counterparts, other O or OB morphs are at a disadvantage.



Figure 1.1: Orange blotch (OB) female *M. zebra* from Gome Rock, Lake Malaŵi, Malaŵi (top) and OB male *M. zebra* from Masinje, Lake Malaŵi, Malaŵi (bottom). Photos by Ad Konings.

Konings (2007) divided the members of this genus inhabiting the sediment-free rocky habitat into three groups, namely the classic zebra, the cobalt zebra, and the large zebra species complex. The members of these groups are found in clear waters at sediment-free rocky coasts

and do not have a continuous distribution around the lake. The classic zebra group consists of fishes having blue and black lateral bars, referred to as “BB zebra” (Fryer & Iles 1972). Based on polymorphic genetic loci (AFLPs), the BB *zebra* complex is deeply divided into a southeast and a northwest/central East clade, where most populations are most closely related to proximate populations of different core color patterns than phenotypically highly similar yet geographically distant populations (Allender et al. 2003). For example, some of the BB *zebra* populations are more closely related to other members of *Metriaclima* (i.e., *M. fainzilberi*, *M. estherae*, and *M. xanstomachus*), which differ in color pattern to BB *zebra*, than to what were thought to be conspecific BB *zebra* populations from elsewhere in the lake.

Metriaclima zebra

Metriaclima zebra (Boulenger 1899) is considered to be the most primitive and most widespread species within the genus (Stauffer et al. 1997) and was among the first mbuna ever exported from the lake (Konings 2007). *Metriaclima zebra* is found from Cape Manulo to Kande Island, around Namalenje Island, the Nankumba peninsula, Boadzulu Island, and from Makanjila Point to Mala Point, from Mbamba Bay to Lundu, and from Lumbila to Ikombe on the eastern shore (Konings 2007; see Figure 1.2 & 1.3). It also exhibits significant geographical color variation (Konings & Stauffer 2006). Over twenty geographical color variants are currently recognized (Konings 2001). Some of these populations have not yet been resolved convincingly to the species level (Konings & Stauffer 2006). Differences in morphometrics and meristics among populations are well documented and can be attributed to clinal variation (Stauffer et al. 1997; Konings & Stauffer 2006).

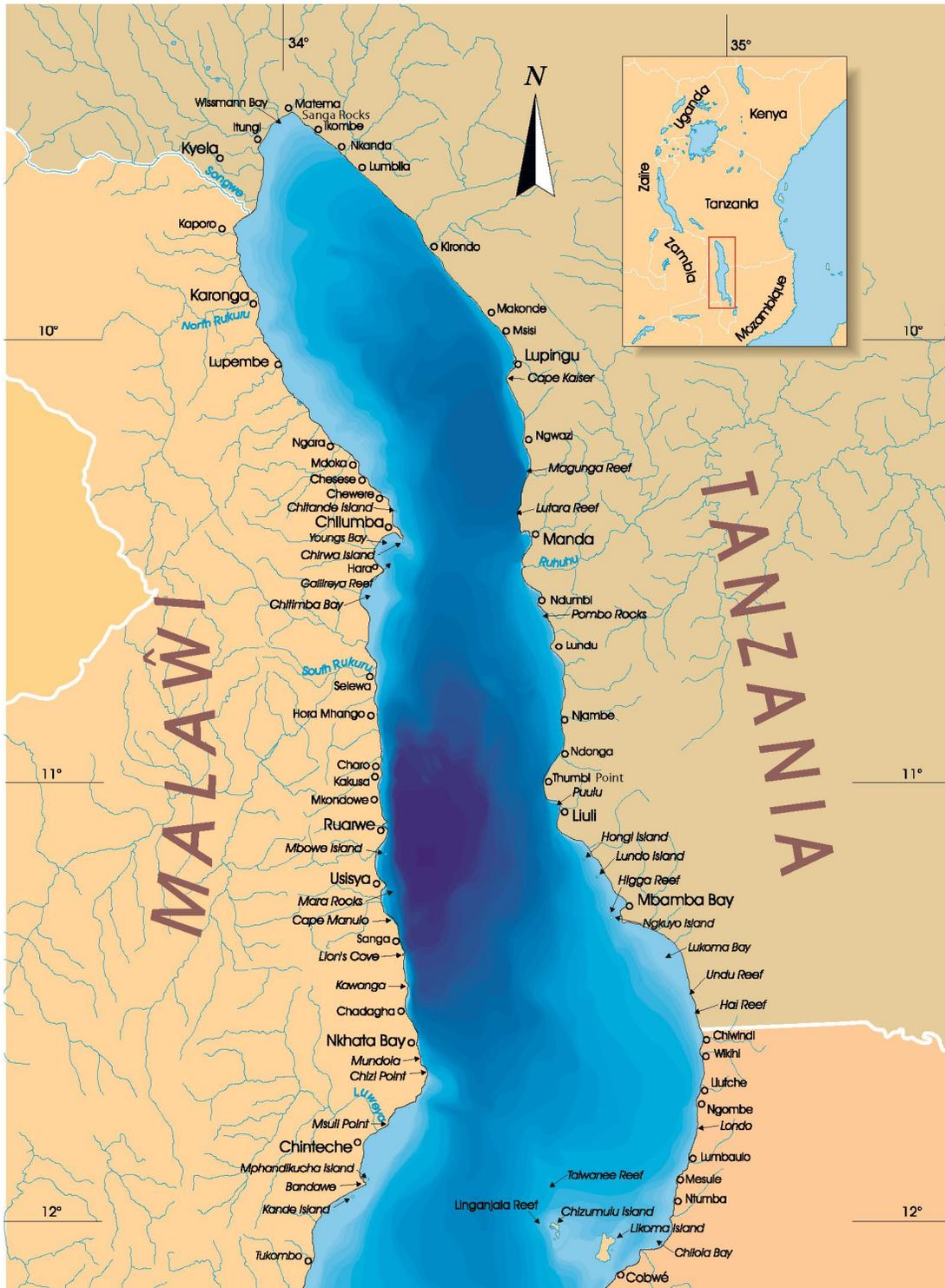


Figure 1.2: Map of northern Lake Malaŵi, Africa



Figure 1.3: Map of southern Lake Malaŵi, Africa

Metriaclima zebra is used to describe many populations of mbuna distributed throughout Lake Malaŵi that are blue-black barred (BB) and a least one form, from the Maleri Islands, that lacks the distinct black bars of the holotype (Konings and Stauffer 2006). The live breeding males of *M. zebra* can be distinguished from all other members of *Metriaclima* except from *M. callainos* on the basis of the following color traits: light blue ground coloration with or without distinct black lateral bars, light blue dorsal fin lacking pigmentation (e.g., the absence of the following on the dorsal fin: extension of lateral bars, submarginal or marginal band, yellow ocellated spots on the trailing part of the dorsal fin), lack of yellow pigmentation on the gular and head, and a light blue anal fin. The blue and white female color morphs of *Metriaclima callainos* distinguish it from *M. zebra*. Females of *M. zebra* are distinguished from most other members of *Metriaclima* by having a gray/blue to blue/brown ground color and lacking yellow pigment in the unpaired fins.

Classification

The delimitation of haplochromine species in Lake Malaŵi is especially difficult owing to the recent speciation, vast diversity, similarity in morphological and genetic traits among taxa, and the plethora of allopatric populations. The diversity of Lake Malaŵi's ichthyofauna greatly depends upon one's taxonomic viewpoint. In an area of similarly rich endemism in Mexico, the species concept employed greatly influenced the estimates of avian beta diversity (Peterson & Navarro-Siguenza 1999). Genner et al. (2004) investigated the effect of allopatric populations on estimates of species richness and found that of the 34 species of *Tropheops* identified by Ribbink et al. (1983), only seven taxa would be counted toward a minimum estimate of regional species richness if allopatric populations were excluded from the diversity measure. They identified 101

endemic species using the biological species concept and 249 endemic species using the phylogenetic species concept.

The habitat of mbuna, rocky “islands” separated by sandy stretches and deep water, allows for many allopatric populations. While the specific status of sympatric taxa is relatively simple to ascertain, by either direct observation of reproductive behavior or indirect genetic comparisons, the status of allopatric taxa is exceedingly difficult to determine (Lewis 1982). Very few studies have tested the specific status of allopatric populations of mbuna, until recently. Laboratory testing of assortative mating between allopatric color variants of *M. zebra* illustrated that females differentiate among males of different populations (Knight & Turner 2004). The authors suggest that some races of BB *zebra* represent incipient geographical species diverging under sexual selection exerted by female choice of male breeding color.

Live Coloration

Live coloration is an important characteristic for Malaŵi cichlid taxonomists to use when describing species and in many cases male coloration is the primary trait used to delimit species (e.g., Marsh 1983; Ribbink et al. 1983; Bowers & Stauffer 1993, Stauffer et al. 1995, 1997b). It is used in cichlid communication and intensifies during mate selection (i.e., breeding season), and thus, it is an essential component of the specific mate recognition system (SMRS; Paterson 1978) of mbuna (Fryer & Iles 1972, Greenwood 1974; Ribbink et al. 1983; Stauffer & Boltz 1989; Kidd et al. 2006). Coloration is an important attribute for intraspecific interactions and is likely to be more strongly shaped by sexual selection rather than survival; therefore, coloration may act as a reproductive barrier without concordant morphological differences (Meyer 1993). Male color patterns can influence the variance in male reproductive success (Wickler 1962; Hert 1991). While non-visual cues (e.g., olfactory cues) were important for species recognition of *M.*

emmitos (Plenderleith et al. 2005), Kidd et al. (2006) found that female *M. zebra* and *M. benetos* can identify conspecific males using only visual clues.

In the last 25 years, the use of coloration in species delimitation, particularly within lakes Malaŵi and Victoria, has been adopted, based on the assumption that male breeding colors are important in mate recognition and thus act as prezygotic barriers to gene flow (Ribbink et al. 1983; Seehausen 1996; Konings 2001). Fryer (1959) proposed that color differences could be used to delimit species, in the absence of morphological differences, because these color differences may act as significant barriers to interbreeding. Recent studies of cichlid fishes in lakes Malaŵi and Victoria have emphasized the importance of male courtship colors in the definition of species (e.g. Ribbink et al. 1983; Seehausen 1996; Turner 1996). Interestingly, most color variation among Lake Malaŵi mbuna and the Lake Victoria cichlids appears highly repetitive and can be broken down into a small number of core color patterns that are similar between the lakes. As suggested by Allender et al. (2003), these core color patterns have been acquired several times in parallel between and within genera and therefore, similar color forms cannot simply be assumed to be conspecific (Genner & Turner 2005).

The use of coloration as a tool for the delimitation of polychromatic species or intraspecific color variants is more difficult. Smith & Kornfield (2002) found species-level phenotypic (i.e., color) convergence in populations of *Metriaclima* (suggestive of convergent origin of the same color pattern in two different populations of the same species complex of Lake Malaŵi), implying that also allopatric populations with similar coloration cannot be assumed to be conspecific. Similarly, Allender et al. (2003) concluded geographically proximate species of *Metriaclima* possessing different color patterns were more closely related to one another than distant species with the same or with different color patterns.

Morphological data

Historically, morphological data have been used as the primary technique to describe cichlids (Stiassny 1991). Surprisingly, allopatric forms can diverge morphologically very quickly as was documented by Stauffer & Hert (1992) where the morphology of a translocated population of *Metriaclima callainos* differed considerably from its native population after a separation of only 20 years. For this reason, the use of morphometrics alone to resolve species differences of non-neighboring populations, in cases where a genetic exchange between the populations in question is not naturally feasible, is inadvisable in many cases.

Molecular data

Molecular methods have proven useful in detecting supraspecific relationships among cichlids, but until recently, these methods were not capable of detecting differences between closely related populations (Kornfield 1984; Moran et al. 1994). Due to the recent speciation of Lake Malaŵi cichlids, many molecular techniques are inappropriate for the study of mbuna phylogeny due to the highly conservative nature of the markers examined. For example, sensitive molecular techniques such as microsatellite analysis often have to cope with high allelic diversity that may confound results and cause difficulties in interpretation (Arnegard et al. 1999; Danley et al. 2000; Smith & Kornfield 2002). The most useful molecular technique for detecting relationships among species and genera has proven to be the analysis of Amplified Fragment Length Polymorphism (AFLP), a DNA fingerprinting technique that allows for evaluation of the variation at a large number of loci. Studies of mbuna using AFLPs have proven successful in detecting both inter- and intraspecific variation (Albertson et al. 1999; Allender et al. 2003). Unfortunately, while molecular methods are useful in detecting specific status for sympatric

forms, they are less useful when investigating allopatric populations (Turner et al. 2001; Kornfield & Smith 2000) because sympatric species often can appear more closely related to one another than to their same species in neighboring populations. The low genetic diversity of this group of fishes (resulting from its recent speciation) limits the applicability of many molecular approaches to species identification of mbuna; therefore, molecular approaches were not employed in this study. To date no descriptions of Malaŵi cichlids have been published based on DNA analyses because no correlation between a genetic profile and a phylogenetic species could be made.

Behavioral data

Behavior has proven useful in the delimitation of Lake Malaŵi cichlid fishes (Ribbink et al. 1983; Stauffer et al. 1993, 1995, 2002b). While McElroy & Kornfield (1990) concluded courtship behavior of some male mbuna is not critical to species recognition and that little interspecific differentiation in behavioral expression exists among mbuna in general, more recent experimental work with newer methods suggests the opposite. Based on observations of remarkable ecological similarity among reproductively isolated taxa, Genner et al. (1999) proposed that ecological segregation is not necessary for the coexistence of Lake Malaŵi cichlids. The use of behavioral data as expressed in mate choice based on color patterns or bower shapes have been used to diagnose cichlid species (Stauffer et al. 2002b). The use of behavior in distinguishing species was limited by the fact that experimental conditions cannot mimic environmental heterogeneities, and laboratory artifacts may constrain mate choice and break down pre-zygotic barriers (Turner et al. 2001). Also, the absence of well-developed post-mating isolation in haplochromines (Crapon de Caprona 1986) has limited the use of laboratory testing for these fishes.

Species Concepts and Criteria Used to Delimit *Metriaclima*

To define species categories, one must begin by considering the philosophical approach to species (Ghiselin 1969) – whether to regard species as a taxonomic category that does not exist in nature (i.e., nominalist view) or whether species exist in nature and are not merely categories for a taxonomist’s convenience (Ghiselin 2002; Mayden 2002; Wiley 2002). Herein species are considered ontological individuals – they are historical, temporal, and spatial identities, real individuals rather than classes, and exist regardless of whether or not sufficient data exist to recognize them (Ghiselin 1974; Wiley 1978; Frost & Kluge 1994).

More than 20 species concepts have been proposed (Mayden 1997) and taxonomists typically rely upon the concept that is most appropriate for a given situation. The evolutionary species concept (ESC) as amended by Wiley (1978) from the work of Simpson (1961) is the only concept available for the widespread use across taxa. Wiley’s (1978, p. 18) species definition states that “a species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate”. Unfortunately, the ESC is non-operational owing to its reliance on a well resolved phylogeny (Mayden 1997; Stauffer et al. 2002a).

There is considerable debate over the most appropriate species concept for the classification of fishes. In general, biologists studying sexually reproducing living organisms have used the biological species concept (BSC; Mayr 1942; Mayr and Ashlock 1991) but this approach is especially problematic for application to cichlids. The biological species concept considers species as groups of interbreeding natural populations that are reproductively isolated from other groups. The high morphological diversity (including coloration), the conservative bauplan, the low genetic divergence, and the abundance of allopatric populations among mbuna, make it difficult to diagnose species using morphological criteria alone (Stauffer et al. 2006).

Cichlid descriptions prior to the 1980s were primarily based on morphological traits of preserved museum specimens (Barel et al. 1977; Turner 2000). Since that time, numerous other techniques have been applied to the delineation of species in Lake Malaŵi. Stauffer and McKaye (2001) recommend a combination of morphological, genetic, and behavioral data be used to diagnose these species. For example, Turner et al. (2001) find closer inspection of taxa defined on the basis of male breeding coloration often leads to the discovery of subtle differences in female color, morphology, microhabitat preferences, or diet.

I regarded species as ontological individuals as described above. Cichlids are easily seen as ontological individuals as observational data show that species-specific breeding in sympatry is based on the recognition of their conspecifics (i.e., the recognition of individuals in nature). In concept, I adhered first to the ESC, whereby I aimed to identify species which form a single lineage on an independent evolutionary trajectory. As this species concept is non-operational, I employed criteria associated with other concepts to serve as surrogates in identifying evolutionary species. This approach has been coined as integrative taxonomy as defined by Dayrat (2005, p.407) “the science that aims to delimit the units of life’s diversity from multiple and complementary perspectives (phylogeography, comparative morphology, populations genetics, ecology, development, behavior, etc.).”

These species were first recognized in nature and selectively captured based on color and pigmentation patterns and the species-specific breeding interactions (e.g. males courting females), thereby the biological species concept was employed during the collection of these fishes and assisted in indicating the independence of their evolutionary lineage. Secondly, feeding behavior of collected individuals and ecological niche (e.g., sediment free rocky habitat) was observed and noted. For example, it was documented that these fishes fed at nearly perpendicular angles to the substrate and were capable of aligning the teeth of both the upper and lower jaws by abducting the jaws to a 180°-angle. These behavioral criteria aided in the delimitation of the species and it

could be argued that the ecological species concept was, in part, employed. Lastly, morphological data collected on preserved individuals were used to compare populations in questions to sympatric *Metriaclima* and neighboring *Metriaclima* populations sharing similar color and pigmentation patterns. This provided criteria relevant to the morphological species concept. For the purposes of this study, species were regarded as groups of individuals that interbreed *in situ*, share color and pigmentation patterns and ecological niche, and are morphologically distinct from sympatric species and nearby populations exhibiting similar color patterns.

Study Goals, Objectives and Approach

Management and conservation of African fishes is impaired by the lack of taxonomic and distribution data of these fish resources (Stiassny 1996). Owing to the widespread recognition of *M. zebra* in scientific and popular literature, it is important to understand the distribution and extensive intraspecific variation of this species. It is also important to work towards identifying the type locality of *M. zebra*. For all of the aforementioned reasons, a morphological investigation of the taxonomic relationships of the various populations of the *M. zebra* species complex and the type specimen was conducted. My research objectives were to investigate morphological and meristic differences among an extensive collection of populations of *M. zebra*-like species in Lake Malaŵi, and if warranted, based on available data, diagnose new species in *Metriaclima*.

I used breeding coloration, feeding behaviors, and morphometric data to diagnose species. I define species as groups of individuals that interbreed *in situ*, share color patterns, and are morphologically distinct from sympatric species and nearby populations exhibiting similar color patterns.

Chapter 2

Methods and Materials

Materials Examined

Adult fishes used in the morphological investigation (excluding materials borrowed from the Natural History Museum, London) were collected by SCUBA divers who chased them into a monofilament net (7m X 1m; 1.5cm mesh). Necessary permits for the collection of fishes were acquired from the governments of Malaŵi, Mozambique, and Tanzania. These permits allowed for the collection of twenty specimens each of various undescribed fish species for taxonomic work. Fishes were collected and processed under the approval of the Animal Use and Care Committee at Pennsylvania State University (IACUC #24269). Fishes were anesthetized with clove oil, preserved in 10% formalin, and then placed in 70% ethanol for permanent storage in the PSUFM. Digital photographs of live specimens were taken by Ad Konings.

Both photographs and color/pigmentation notes of the type material for the newly described species are stored in The Pennsylvania State University Fish Museum (PSUFM) – catalogue numbers provided under species descriptions. Color notes and pigmentation patterns were recorded in the field at the time of capture for both territorial and non-territorial males, females, and juveniles by Jay R. Stauffer and Ad Konings. All color notes were taken on live breeding fishes. The color patterns were variable in all species examined, and in descriptions such variation was recorded by placing a slash between the two colors between which the specific patterns varies, i.e. blue/white was used to designate that the color ranges from blue to white. Behavioral notes including feeding angles and habitat were also recorded after capture.

Currently the PSUFM houses over 400 collections of *Metriaclima*. The majority of these collections contain members of the *M. zebra* complex. This is most likely the most extensive collections of these fishes. One thousand and six specimens from a total of seventy collections belonging to the *M. zebra* complex were examined as part of this study (see Appendix A). The selected collections are distributed throughout the lake (Figure 2.0); thus they should account for the proposed north-to-south colonization that was facilitated by rising water levels (Smith & Kornfield 2002). Three of the examined collections were borrowed from the Natural History Museum (London; BMNH), including the holotype for *M. zebra*.

Characters Examined

External counts and measurements follow Barel et al. (1977) and Konings & Stauffer (2006). When possible, twenty individuals were measured per collection. Twenty-four measurements and fourteen counts were made per fish (Table 2.0). Nine of these measurements were specific to the head region, owing to the observation of Fryer & Iles (1972), who found that most cichlids have restricted diversity in their body form with the exception of the head region. All counts and measures were done on the left side of the fish except for gill raker counts, which were performed on the right side of the fish to prevent damaging the measured side. Tables containing morphometric data show some measurements, as noted, presented in percent standard length (SL) or percent head length (HL) following Konings and Stauffer (2006).

Table 2.0: Morphometric and meristic characters examined in the morphological analysis. All fishes measured as noted in the Characters Examined section.

Morphometric Measure	Abbreviation
standard length	SL
head length	HL
snout length	SNL
post orbital head length	POHL
horizontal eye depth	HED
vertical eye depth	VED
premaxillary depth	PRE
cheek depth	CD
lower jaw length	LJL
head length	HD
body depth	BD
snout to dorsal fin insertion	SNDOR
snout to pelvic fin insertion	SNPEL
dorsal fin base length	DFBL
anterior of dorsal fin to anterior of anal fin	ADAA
anterior of dorsal fin to posterior of anal fin	ADPA
posterior of dorsal fin to anterior of anal fin	PDAA
posterior of dorsal fin to posterior of anal fin	PDPA
posterior of dorsal fin to ventral part of hypural plate	PDVC
posterior of anal fin to dorsal part of hypural plate	PADC
anterior of dorsal fin to insertion of pelvic fin	ADP2
posterior of dorsal fin to insertion of pelvic fin	PDP2
caudal peduncle length	CPL
least caudal peduncle depth	LCPD
Meristic Measure	Abbreviation
dorsal fin spines	DSPINES
dorsal fin rays	DRAYS
anal fin spines	ASPINES
anal fin rays	ARAYS
pelvic fin rays	P2RAYS
pectoral fin rays	P1RAYS
lateral line scales	LLS
pored scales post-lateral line	PSPLL
cheek scales	CS
upper gill rakers	GRLOW
lower gill rakers	GRUP
teeth on outer row of left lower jaw	TORLLJ
tooth rows on upper jaw	TRU
tooth rows on lower jaw	TRL

Analysis

Morphological data were analyzed using principal component analysis (PCA) and sheared principal component analysis (SPCA). Principal component analysis is a multivariate ordination technique commonly used for examining morphological variables and discerning among species (Humphries et al. 1981; Stauffer et al. 1997). Meristic data (counts) were analyzed using PCA of the correlation matrix. Differences in body shape were analyzed using SPCA with the covariance matrix factored (Humphries et al. 1981; Bookstein et al. 1985). Sheared principal component analysis ordines morphometric data independently of a main linear ordination (Reyment et al. 1984), allowing for mensural variables to be analyzed independent of size. The first principal component detects size differences of specimens while subsequent sheared principal components, being independent of size, detect shape differences (Humphries et al. 1981; Bookstein et al. 1985).

Differences among species were illustrated by plotting the sheared second principal components of the morphometric data against the first principal components of the meristic data. In the following chapters, the variation of the first principal component is expressed as a percentage and reflects size. The variation explained by the second principal component is provided also as a percentage but is presented as the “remaining” variation explained by the second principal component. The remaining variation percentage explained by the second principal component is based on the remaining difference left after the size is eliminated (i.e. first principal component explains 80% of the variation, so the second principal component explains a proportion of the remaining 20% remaining).

Minimum polygon clusters were drawn to encompass the points of a population on the principal components plots. A minimum polygon cluster is a closed figure on a two dimensional plot that includes the spatial data points of all individuals belonging to a particular group. An

ANOVA ($P < 0.05$) was used to determine if two minimum polygon clusters were significantly different along one or both axes. If more than two groups were included in the analysis and the mean multivariate scores of the clusters were significantly different along one axis, a Duncan's multiple range test ($P < 0.05$) was used to determine which clusters differ from each other on that axis.

Chapter 3

Results and Discussion

This study included the morphological analysis of 1006 specimens of *Metriaclima*. As a result of this investigation, five new species have been described – *M. pambazuko*, *M. lundoensis*, *M. midomo*, *M. tarakiki*, and *M. nigrodorsalis*. These species were distinguished and described based on color patterns, ecological data, and morphometric and meristic differences. These species were compared with sympatric *Metriaclima* species and with neighboring populations having similar color and pigmentation pattern and ecological niches; the newly described species could be distinguished from such populations. The descriptions of the five new species are presented in the following chapter.

In addition to the new descriptions, the relationships among several color forms of *Metriaclima* were investigated and the holotype was compared to specimens from in and around Likoma Island. A distinctive yellow breasted *M. zebra* from Lumessi, Mozambique and *Metriaclima* sp. ‘blue blaze’, which is distinguishable by a light blue blaze on the head and smaller body size (relative to most other *M. zebra* populations), were regarded as conspecific with *M. zebra* based on the morphological analysis. The holotype of *M. zebra* was found to morphologically resemble the Likoma Island population of *M. zebra*, suggesting that Likoma Island may be the type locality.

Metriaclima zebra, the type species for genus *Metriaclima*, was described based on a single specimen and the location for this holotype is not known. The holotype of *Metriaclima zebra* was collected by Miss M.E. Woodward and given to the British Museum of Natural History (London) by Miss McLaughlin in 1891. The type locality was recorded as Lake Nyassa. These two women were missionaries who resided on Likoma Island, Lake Malaŵi, Malaŵi from 1888

onward (Anderson-Morshhead, 1897). For this reason, Ad Konings (personal communication) suggested that the holotype of *M. zebra* was collected from Likoma Island.

A multivariate analysis of morphometric and meristic data of the holotype and populations of *M. zebra* from Likoma Island and nearby Chizumulu Island (Figure 3.0) was completed. The holotype, which was collected in 1891, is still in very good condition and therefore lends itself to this type of analysis. The plot of the first principal component of the meristic data versus the sheared second principal component of the morphometric data (Figure 3.1) shows that the holotype is morphologically similar to *M. zebra* from Likoma Island; therefore, it is possible the holotype was collected there. Although, morphologically, the holotype also resembles *M. zebra* from nearby Chizumulu Island, it is improbable that the holotype was collected there as *M. zebra* from Chizumulu Island either have a blue blaze or are entirely without lateral bars and holotype lacks a blue blaze and has lateral bars, similar to the *M. zebra* from Likoma Island. Additional sampling and investigation of localities around Likoma Island may help to confirm the precise type locality of *Metriaclima zebra*.



Figure 3.0: Map of Likoma and Chizumulu Islands, Lake Malaŵi illustrating collection locations in blue circles.

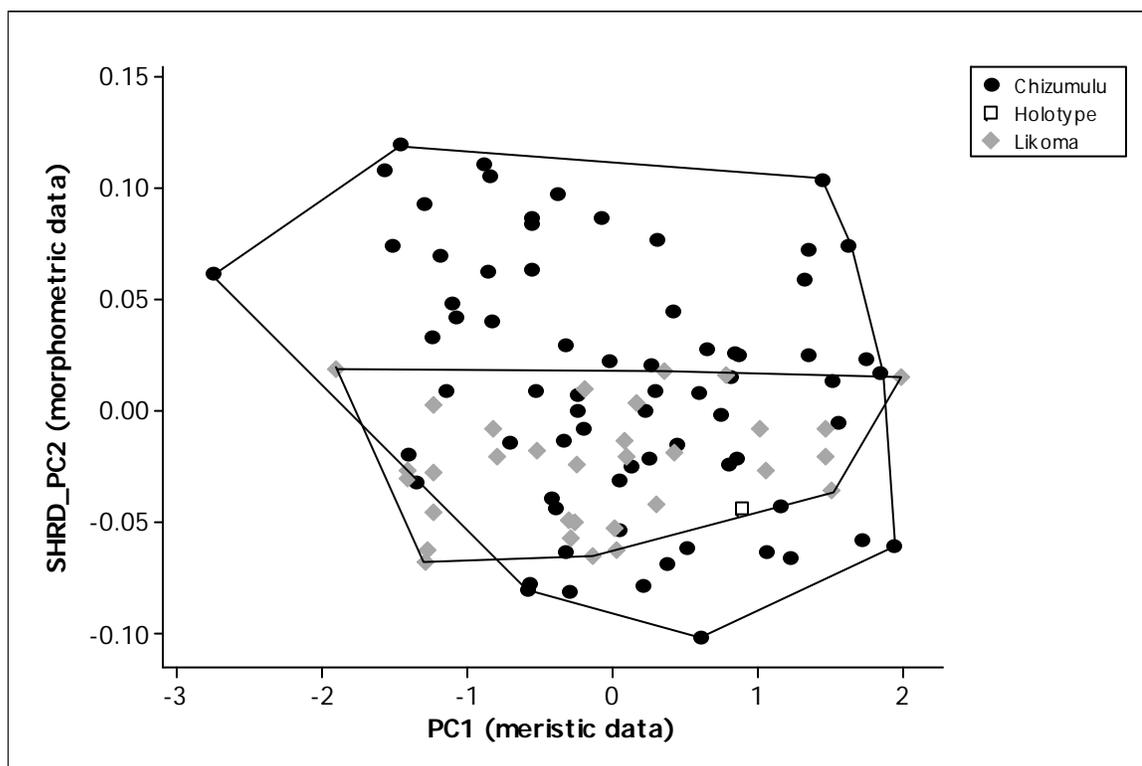


Figure 3.1: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. zebra* holotype, *M. zebra* from Likoma Island (see Appendix A, Accession #429, 517, 870, 942, & BMNH1971) and *M. zebra* from Chizumulu Island (see Appendix A, Accession #527, 678, 693, & 2061).

This study was successful in detecting morphological similarities between unique color forms of *M. zebra*. For example, *Metriaclima* sp. ‘blue blaze’ is known to inhabit Lundo Island, Londo Bay, the northern part of Chizumulu Island, and the mainland coast between Kirondo and Manda. The males of this form lack interorbital bars and appear to have a blue blaze on the head (Konings 2007). This form is not sympatric with *M. zebra*, either barred or unbarred. A multivariate analysis of morphometric and meristic data of *M. sp.* ‘blue blaze’ from Makonde and Manda, Tanzania and nearby *M. zebra* from Pombo Rocks, Thumbi Point, and Sanga Rocks, Tanzania suggested that this form, *M. sp.* ‘blue blaze’, is probably conspecific with *M. zebra*. The plot of the first principal component of the meristic data versus the sheared second principal component of the morphometric data (Figure 3.2) illustrates the two groups clearly overlap. The

morphometric data for these groups were not significantly different ($P > 0.05$, MANOVA). This finding is supported by mate choice experiments by Knight and Turner (2004) which found that *M. zebra* from Nkhata Bay and the *M. sp.* 'blue blaze' from Chizumulu Island did not exhibit any marked degree of assortative mating with respect to each other.

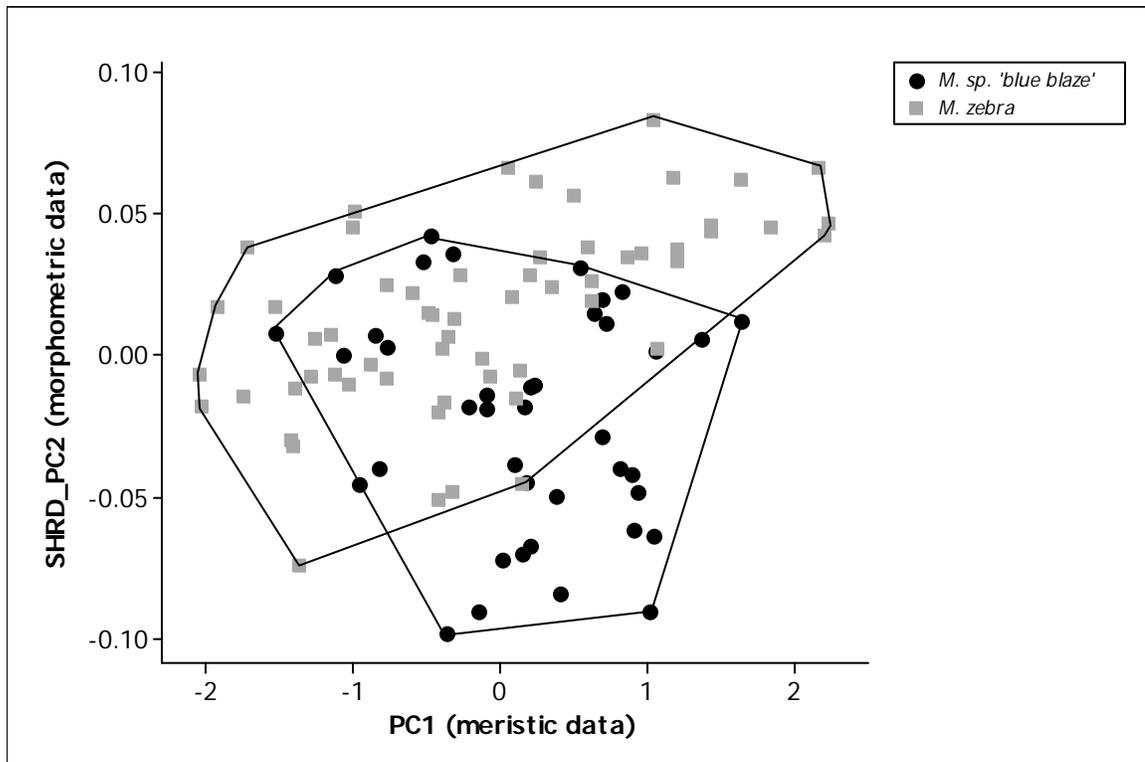


Figure 3.2: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. sp.* 'blue blaze' (see Appendix A, Accession #432 & 1551) and *M. zebra* from Tanzania (Accession #170, 176, & 529).

Additionally, a form of *M. zebra* from Lumessi, Mozambique that has a distinctive yellow breast was determined to be conspecific with *M. zebra*. The principal component analysis of yellow-breasted *M. zebra* at Lumessi and non-yellow-breasted *M. zebra* (Figure 3.3) suggests that *M. zebra* has variable color patterns which include a population with yellow breasts. There was overlap in the minimum polygon clusters formed by plotting the first principal component of the meristic data against the second sheared principal component of the morphometric data and

the morphometric data for these groups were not significantly different ($P > 0.05$, MANOVA).

Significant evidence does not exist to suggest that two color forms are heterospecific.

While this investigation was successful in diagnosing five new species and detecting morphological relationships among members of *M. zebra* species complex, there are many more species within this genus that need to be described and many more relationships, such as that of the red top zebras described by Stauffer et al. (1997), that need further investigation.

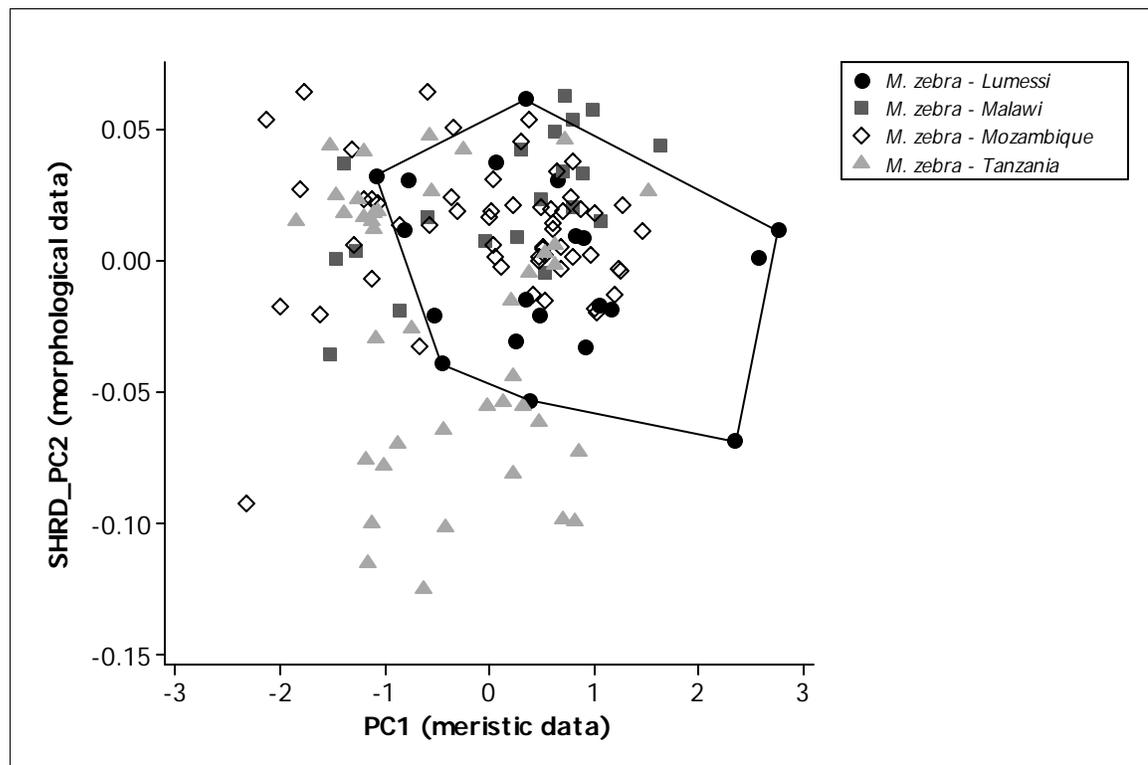


Figure 3.3: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. zebra* from Lumessi, Mozambique, Tanzania coast (see Appendix A, Accession # 176 & 1551), Mozambique coast (Accession #672, 677, & 699) and Gome Rock, Malaŵi (Accession #686).

Chapter 4

New Species of *Metriaclima*

Genus *Metriaclima* (Stauffer et al.)

The genus *Metriaclima* is diagnosed by the following morphological characteristics: 1) The presence of bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws; 2) The moderately-sloped ethmo-vomerine block with a swollen rostral tip; 3) The lower jaw forming a 45° angle with a line that connects the tip of the snout to the hypural plates (Stauffer et al. 1997); 4) The lower jaw is often slightly longer and thicker than the upper jaw; 5) A large part of the upper dental arcade is normally exposed when the mouth is closed; 6) The tips of the teeth in the premaxilla and dentary are in a V-shaped line with the anterior most in upper and lower jaw furthest apart; and 7) The bicuspid teeth in the outer row along the side of the jaws does not follow the contour of the jaw and the lateral teeth are rotated so that the plane of their two-pronged tips runs parallel with those in the anterior part of the jaw.

Presence of bicuspid teeth with both tips of equal length in the anterior portion of the outer row on both the upper and lower jaws distinguishes *Metriaclima* from many mbuna genera including the following: *Cyathochromis*, *Cynotilapia*, *Genyochromis*, *Gephyrochromis*, *Iodotropheus*, *Labeotropheus*, *Labidochromis*, *Petrotilapia*, and part of *Melanochromis*. Two horizontal stripes along the flanks of members of *Melanochromis*, distinguish them from *Metriaclima*. The species of *Melanochromis*, *Tropheops*, and *Pseudotropheus* lack a swollen rostral tip of the ethmo-vomerine block.

The genus contains the following species (as further explained in Chapter 1): *M. zebra* (Boulenger), *M. callainos* (Stauffer & Hert), *M. xanstomachus* (Stauffer & Boltz), *M. greshakei*

(Meyer & Foerster), *M. aurora* (Burgess), *M. barlowi* (McKaye & Stauffer), *M. estherae* (Konings), *M. hajomaylandi* (Meyer & Scharl), *M. lombardoi* (Burgess), *M. lanisticola* (Burgess), *M. chrysomallos* (Stauffer et al.), *M. phaeos* (Stauffer et al.), *M. cyneusmarginatus* (Stauffer et al.), *M. benetos* (Stauffer et al.), *M. pyrsonotos* (Stauffer et al.), *M. emmiltos* (Stauffer et al.), *M. mbenjii* (Stauffer et al.), *M. flavifemina* (Konings & Stauffer), and *M. fainzilberi* (Staeck).

Metriaclima pambazuko n. sp. (Figures 4.0-4.1)

HOLOTYPE.—PSU 4900, adult male, 61.3 mm, S 11°49.552' E 34°56.292, Londo Bay, Lake Malaŵi, Mozambique, Africa, February 2006, Konings & Stauffer (collectors).

PARATYPES.—PSU 4901, 19, (51.9-73.2 mm), same data as holotype; PSU 4902, 19, (59.3-75.9 mm), Hongi, Lake Malaŵi, Tanzania, January 2004; PSU 4903, 20, (61.8-74.7 mm), Lundo Island, Lake Malaŵi, Tanzania, January 2004.

Diagnosis.—The presence of 1) bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws; 2) moderately sloped ethmo-vomerine block with a swollen rostral tip; 3) lower jaw forming a 45° angle with a line that connects the tip of the snout to the hypural plate; 4) tips of the teeth in the premaxilla and dentary are in a V-shaped line with the anterior most in upper and lower jaw furthest apart; and 5) bicuspid teeth in the outer row along the side of the jaws do not follow the contour of the jaw and the lateral teeth are rotated so that the plane of their two-pronged tips runs parallel with those in the anterior part of the jaw place this species in *Metriaclima*. Additionally, *M. pambazuko* feeds at almost perpendicular angles to the substrate and is capable of aligning the teeth of both the upper and lower jaws by abducting the jaws to a 180°-angle opening in order to collect loose aufwuchs from the substrate.

The red/orange dorsal fin in combination with distinct black bars on a blue ground color and the absence of a yellow chin distinguishes this species from all other member of the genus except for *Metriaclima emmiltos* and *Metriaclima pyrsonotos*. The lateral bars of male *M. pambazuko* infiltrate the proximal portion of the dorsal fin, while the lateral bars of most males of *M. emmiltos* and *M. pyrsonotos* stop at the base of the dorsal fin. The anal fin of male *M. pambazuko* is black, while the anal fin of most male *M. pyrsonotos* and *M. emmiltos* is blue.

Female *M. pambazuko* have a light brown to beige ground color while those of *M. emmiltos* and *M. pyrsonotos* are dark brown to blue-brown. *M. pambazuko* has more teeth (13-23) in the outer row of the left lower jaw than *M. emmiltos* (8-12) and *M. pyrsonotos* (4-10) and has a larger distance between snout and pelvic-fin origin (range 35.3-44.2 %SL) than that of *M. emmiltos* (range 22.8-32.8 %SL). The head depth expressed as a percentage of head length of *M. pambazuko* (range 76.2-92.4) is generally less than that of *M. pyrsonotos* (range 90.5-110.2).



Figure 4.0: *Metriaclima pambazuko*, male, Londo Bay, Lake Malaŵi, Mozambique. Photo by Ad Konings.



Figure 4.1: *Metriaclima pambazuko*, female, Londo Bay, Lake Malaŵi, Mozambique. Photo by Ad Konings.

Description.—Morphometric and meristic data in Table 4.0. Teeth on jaws in 2-4 rows; majority of teeth in outer row bicuspid, some unicuspid; those in inner row tricuspid; 20 teeth in outer row of left lower jaw of holotype, 13-23 in paratypes. Dorsal fin with 16 spines in holotype, 16-18 in paratypes; dorsal-fin rays 10 in holotype and 8-10 in paratypes. Pectoral fin with 14 rays in holotype and 13-15 in paratypes; anal fin with 3 spines, 8 rays in holotype and 7-8 rays in paratypes. Scales along side ctenoid; holotype with 31 lateral-line scales and 29-32 in paratypes. First gill arch with 11-18 rakers on the ceratobranchial, 2-4 on epibranchial, and 1 between epibranchial and ceratobranchial.

Color notes and photos of live breeding adults catalogued under PSU 4926. Live breeding males with blue ground coloration and 5-7 distinct black bars. Caudal peduncle blue/black; breast white to black; belly gray/black. Head black with two blue interorbital bars; opercular spot gray/black; gular black. Dorsal fin proximally blue/gray/black and distally orange or completely orange; bars on side and proximal part of dorsal fin; dorsal fin with blue/white lappets. Proximal portion of caudal rays gray/black and distal portion orange; proximal half of caudal membranes black and distal half blue/gray. Anal fin black with 3-5 orange/yellow ocelli; white marginal band sometimes present. Pectoral fin with black/gray rays and clear membranes. Pelvic fin with blue, white, or yellow leading edge; remainder black.

Females with blue or brown ground coloration and approximately 5 gray bars; lateral scales brown with blue center. Caudal peduncle beige/brown; belly and breast white/gray. Head brown/gray; opercle with blue/green highlights; black opercular spot; gular gray. Dorsal fin proximally gray and distally orange/brown. Caudal fin rays gray; membranes clear. Anal fin gray with no ocelli or small yellow/orange ocelli. Pectoral fins with gray rays and clear membranes. Pelvic fins with first two membranes black/gray, remainder clear.

Table 4.0: Morphometric and meristic values for *Metriaclima pambazuko* from Londo Bay, Mozambique (PSU 4900-4901); Lundo Island, Tanzania (PSU 4903); and Hongi, Tanzania (PSU 4902). Min-Max includes holotype (N=59). Data per collection found in Appendix C.

Variable	Holotype	Mean	Std Dev	Min-Max
Standard length, mm	61.3	64.3	5.3	51.9-75.9
Head length, mm	19.5	20.4	1.7	16.8-24.0
Percent head length				
Snout length	31.4	33.9	1.7	30.1-37.9
Postorbital head length	39.3	40.0	1.3	37.3-43.3
Horizontal eye diameter	37.0	36.7	1.9	31.2-40.8
Vertical eye diameter	35.4	35.9	1.8	32.1-41.3
Preorbital depth	22.1	20.7	1.0	18.5-22.7
Cheek depth	24.3	25.3	1.8	22.3-30.8
Lower-jaw length	36.9	37.2	1.4	34.4-40.2
Head depth	81.4	84.3	4.1	76.2-92.4
Percent standard length				
Body depth	31.2	32.1	1.2	28.9-35.6
Snout to dorsal-fin origin	33.3	33.5	1.2	30.4-36.2
Snout to pelvic-fin origin	38.3	38.0	2.0	35.3-44.2
Dorsal-fin base length	59.4	60.2	1.6	56.8-63.7
Anterior dorsal to anterior anal	50.1	49.4	1.3	46.6-52.7
Anterior dorsal to posterior anal	62.3	62.7	1.3	59.4-66.6
Posterior dorsal to anterior anal	29.1	29.8	1.1	27.0-32.3
Posterior dorsal to posterior anal	15.9	16.2	0.7	14.9-17.9
Posterior dorsal to ventral caudal	18.4	18.3	0.7	16.5-20.9
Posterior anal to dorsal caudal	22.4	22.1	0.7	20.0-23.7
Anterior dorsal to pelvic-fin origin	36.3	35.6	1.5	32.1-38.6
Posterior dorsal to pelvic-fin origin	57.7	56.9	1.7	52.4-60.3
Caudal peduncle length	14.6	15.0	0.9	12.8-17.4
Least caudal peduncle depth	10.9	11.2	0.4	10.2-12.4
Counts				
		Mode	% Frequency	Min-Max
Dorsal-fin spines	16	17	76.3	16-18
Dorsal-fin rays	10	9	79.7	8-10
Anal-fin spines	3	3	100.0	3-3
Anal-fin rays	8	8	94.9	7-8
Pelvic-fin rays	5	5	100.0	5-5
Pectoral-fin rays	14	14	91.5	13-15
Lateral-line scales	31	31	49.2	29-32
Pored scales posterior to lateral line	1	1	67.8	0-1
Scale rows on cheek	4	4	74.6	3-6
Gillrakers on first ceratobranchial	12	12	54.2	11-18
Gillrakers on first epibranchial	3	3	59.3	2-4
Teeth in outer row of left lower jaw	20	17	18.6	13-23
Tooth rows on upper jaw	3	3	83.1	2-4
Tooth rows on lower jaw	3	3	81.4	2-4

Distribution.—*Metriaclima pambazuko* is known from Lundo and Hongi islands, Tanzania and from Londo Bay, Mozambique.

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

Remarks.— The coloration of *M. pambazuko* most closely resembles that of *Cynotilapia afra*; however, the presence of bicuspid teeth in the anterior portion of the outer row of both the upper and lower jaws distinguishes *Metriaclima* from *Cynotilapia*, a genus characterized by widely spaced, unicuspid teeth in the outer jaws. *Cynotilapia afra* and *M. pambazuko* are sympatric in Londo Bay, Mozambique as well as at the two islands, Lundo and Hongi, in Tanzania.

Although *Metriaclima pambazuko* shares the red/orange dorsal fin with other known red top BB zebras (*M. emmiltos* and *M. pyrsonotos*), the distribution of *M. pambazuko* is discontinuous with these species (*M. emmiltos* and *M. pyrsonotos* are from the western shores of Lake Malaŵi while *M. pambazuko* is found on the eastern shores); therefore, their heterospecificity is not in doubt.

In contrast, some populations of *M. zebra* and *M. fainzilberi* share similar color patterns and these species are sympatric with *M. pambazuko* or inhabit neighboring habitats. To test the heterospecificity of *M. pambazuko* with *M. zebra* and *M. fainzilberi*, a multivariate analysis of morphometric and meristic data from *M. pambazuko* and nearby and sympatric *M. zebra* and *M. fainzilberi* was conducted (Figure 4.2). This analysis supports the heterospecificity of these three species. The plot of the first principal component of the meristic data versus the sheared second principal component of the morphometric data (Figure 4.3) shows separation among the minimum polygon of *M. pambazuko*, *M. zebra* (from Chiwindi, Thumbi Point, and Londo Bay, Mozambique) and *M. fainzilberi* (from Londo Bay, Mozambique). Although there is some overlap of the minimum polygon clusters, these species are significantly different along the y-

axis, representing the second sheared principal component of the morphometric data ($P < 0.05$, Duncan's Multiple Range Test). Size accounted for 87% and the second principal component for 27% of the remaining variation. Variables with the highest loadings on the sheared second principal component in decreasing order are cheek depth (-0.79), premaxillary depth (-0.41), and posterior of dorsal fin to posterior of anal fin (0.28). The first principal component of the meristic data accounts for 23% of the total variation. Variables with the highest standardized scoring coefficients on the first principal component of the meristic data in decreasing order are dorsal spines (0.44), tooth rows lower jaw (0.41), and pectoral rays (0.35).

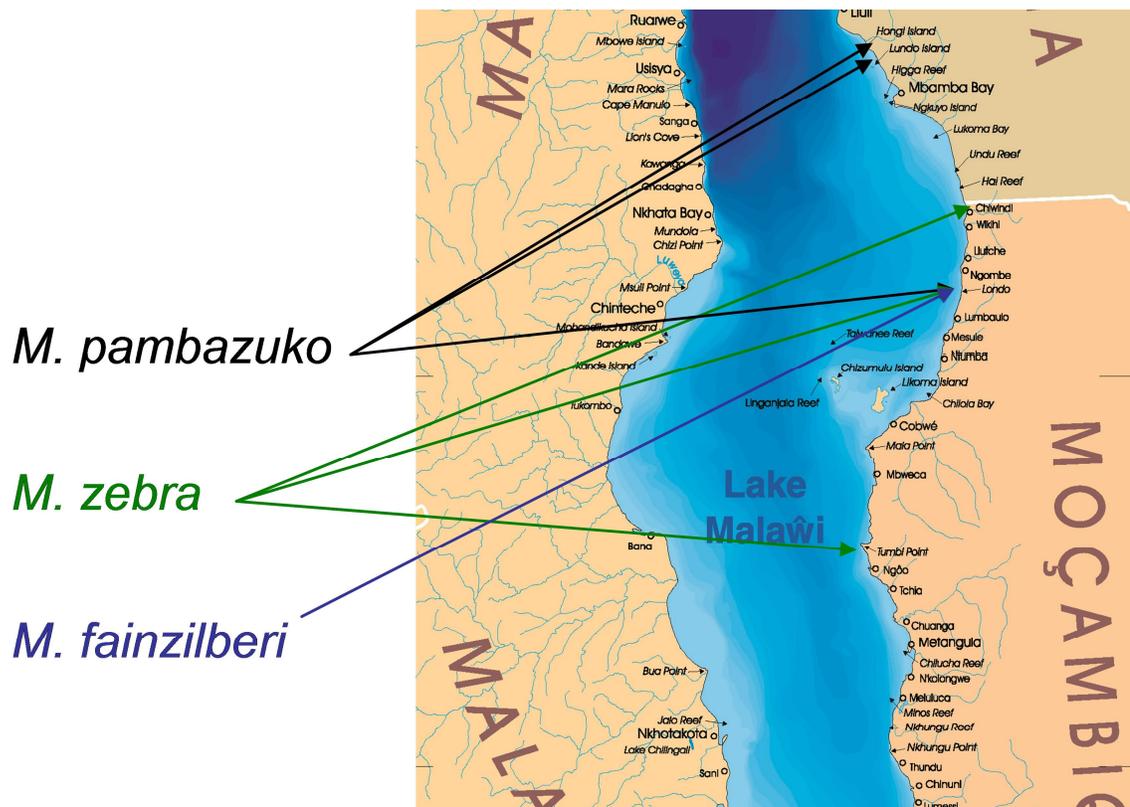


Figure 4.2: Map illustrating collection locations of *M. pambazuko*, *M. zebra*, and *M. fainzilberi* used in the multivariate analysis of morphometric and meristic data for the diagnosis of *M. pambazuko*.

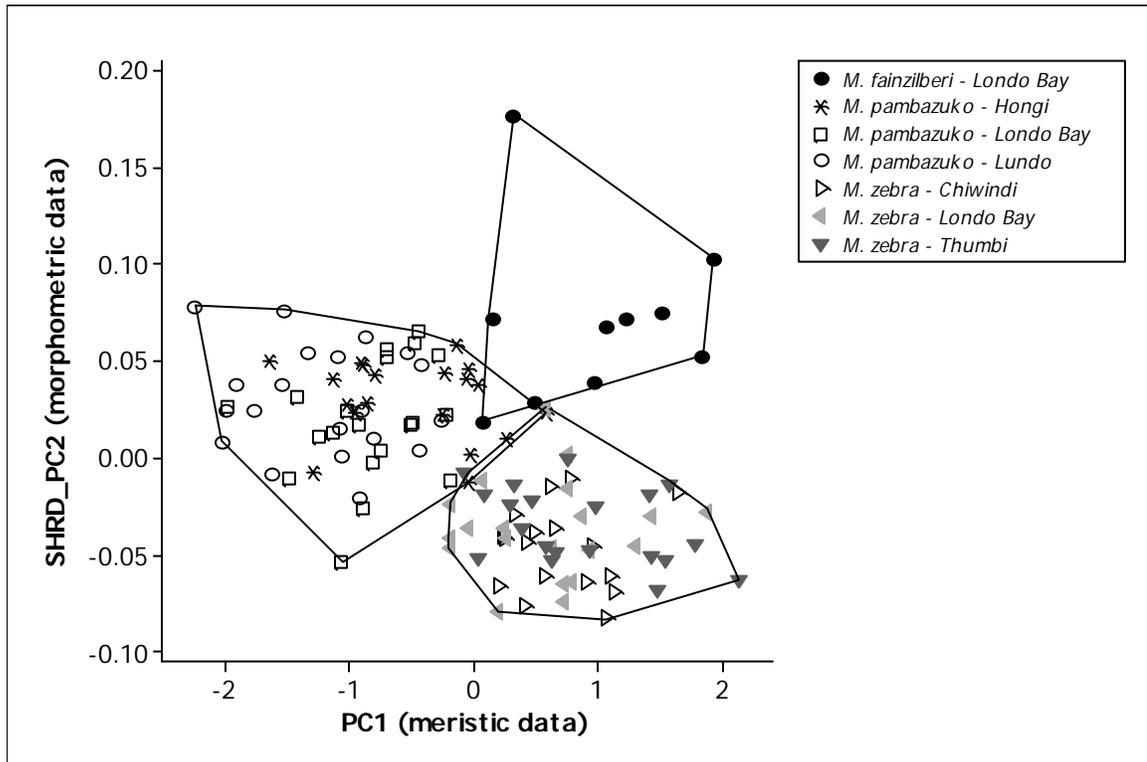


Figure 4.3: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. pambazuko* (N = 59) PSU 4900-4903, *M. zebra* from Thumbi Point, Tanzania (N= 20), *M. zebra* from Chiwindi, Mozambique (N = 17), and *M. zebra* (N=20) and *M. fainzilberi* (N=10) from Londo Bay, Mozambique.

Metriaclima lundoensis n. sp. (Figures 4.4-4.5)

HOLOTYPE.—PSU 4910, adult male, 81.5 mm, S 11°13.438' E 34°44.076', Lundo Island, Lake Malaŵi, Tanzania, Africa, January 2004, Konings and Stauffer (collectors).

PARATYPES. —PSU 4911, 19, (63.2-83.4 mm), same data as holotype.

Diagnosis.— The presence of 1) bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws; 2) moderately sloped ethmo-vomerine block with a swollen rostral tip; 3) lower jaw forming a 45° angle with a line that connects the tip of the snout to the hypural plate; 4) large part of the upper dental arcade is normally exposed when the mouth is closed; 5) tips of the teeth in the premaxilla and dentary are in a V-shaped line with the anterior most in upper and lower jaw furthest apart; and 6) bicuspid teeth in the outer row along the side of the jaws do not follow the contour of the jaw and the lateral teeth are rotated so that the plane of their two-pronged tips runs parallel with those in the anterior part of the jaw place this species in *Metriaclima*. Additionally, this *M. lundoensis* feeds at almost perpendicular angles to the substrate and is capable of aligning the teeth of both the upper and lower jaws by abducting the jaws to a 180°-angle opening in order to collect loose aufwuchs from the substrate.

The presence of a dark submarginal band in the dorsal fin in combination with distinct black lateral bars on a blue ground color in the male distinguish this form from all other member of the genus except for *M. phaeos* and *M. cyneusmarginatus* and some populations of *Metriaclima flavifemina*, *Metriaclima fainzilberi*, and *Metriaclima zebra*. Of the male *M. phaeos*, *M. flavifemina*, *M. cyneusmarginatus* and *M. zebra* having a black band in the dorsal fin, all have lateral bars which extend onto the dorsal fin, a trait not found in *M. lundoensis*. Male *M. lundoensis* are distinguished from *M. fainzilberi* by a black band in the anal fin which lacks in the latter species. Female *M. lundoensis* are distinguished from all other female *Metriaclima* by the presence of a black submarginal band in the dorsal fin.



Figure 4.4: *Metriaclima lundoensis*, male, Lundo Island, Lake Malaŵi, Tanzania. Photo by Ad Konings.



Figure 4.5: *Metriaclima lundoensis*, female, Lundo Island, Lake Malaŵi, Tanzania. Photo by Ad Konings.

Description.—Morphometric and meristic data in Table 4.1. Jaws isognathous; teeth on jaws in 3-4 rows; teeth in outer row bicuspid; those in inner row tricuspid; 14 teeth in outer row of left lower jaw of holotype, 12-20 in paratypes. Dorsal fin with 17 spines in holotype, 17-19 in paratypes; dorsal-fin rays 9 in holotype and 8-10 in paratypes. Pectoral fin with 15 rays in holotype and 14-15 in paratypes; anal fin with 3 spines, 8 rays in holotype and 8-9 rays in paratypes. Scales along side ctenoid; holotype with 31 lateral-line scales and 30-32 in paratypes.

First gill arch with 11-12 rakers on the ceratobranchial, 2-4 on epibranchial, and 1 between epibranchial and ceratobranchial.

Color notes and photos of live breeding adults catalogued under PSU 4927. Males blue/brown flank and 7 narrow, black bars; breast and belly brown; caudal peduncle dark blue. Head dark purple with blue/green highlights; dark blue opercle spot; 2 light blue interorbital bars; brown gular. Dorsal fin proximally blue with black submarginal band and white lappets. Caudal fin with gray rays and orange tips; blue membranes. Anal fin black with white lappets; 2-3 yellow ocelli. Pectoral fin clear. Pelvic fin with blue leading edge; anterior dark brown, posterior light brown.

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

Distribution.—*Metriaclima lundoensis* known only from Lundo Island, Lake Malaŵi, Tanzania.

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

Remarks.— The only other known members of the genus *Metriaclima* possessing a dark submarginal band in the dorsal fin are *Metriaclima phaeos*, *Metriaclima flavifemina*, and some populations of *Metriaclima fainzilberi* and *Metriaclima zebra*. As the populations of *M. fainzilberi* and *M. zebra* possessing the submarginal band are geographically disjunct and the females of both of these species lack a submarginal band in the dorsal fin (a trait of *M. lundoensis*), a morphological analysis of these three species was not conducted.

Table 4.1: Morphometric and meristic values for *Metriaclima lundoensis* from Lundo Island, Tanzania (PSU 4910-4911). Min-Max includes holotype (N=20).

Variable	Holotype	Mean	Std Dev	Min-Max
Standard length, mm	81.5	74.6	5.8	63.2-83.4
Head length, mm	25.6	23.6	1.8	19.5-25.6
Percent head length				
Snout length	39.9	36.8	2.2	33.1-39.9
Postorbital head length	39.2	38.3	1.1	37.1-40.8
Horizontal eye diameter	35.1	36.2	1.5	34.2-40.4
Vertical eye diameter	33.8	35.7	1.4	33.2-38.3
Preorbital depth	21.5	21.1	1.5	19.3-24.8
Cheek depth	24.6	24.4	2.0	20.0-28.1
Lower-jaw length	31.2	33.6	1.6	30.6-35.9
Head depth	79.2	79.2	1.9	75.5-84.2
Percent standard length				
Body depth	31.2	30.1	0.8	28.8-31.6
Snout to dorsal-fin origin	34.8	33.8	0.9	32.4-35.9
Snout to pelvic-fin origin	39.3	40.0	2.1	36.8-44.2
Dorsal-fin base length	59.8	59.7	1.5	57.2-62.2
Anterior dorsal to anterior anal	53.7	50.4	1.4	48.5-53.7
Anterior dorsal to posterior anal	63.8	62.3	1.5	59.6-65.3
Posterior dorsal to anterior anal	28.7	28.1	1.0	25.8-29.8
Posterior dorsal to posterior anal	15.5	15.0	0.7	13.8-16.6
Posterior dorsal to ventral caudal	18.4	17.8	0.5	16.6-18.5
Posterior anal to dorsal caudal	20.3	20.3	1.0	18.5-22.2
Anterior dorsal to pelvic-fin origin	35.5	34.6	1.2	32.6-37.6
Posterior dorsal to pelvic-fin origin	56.7	57.0	1.6	53.1-59.2
Caudal peduncle length	13.2	13.4	0.8	12.2-15.1
Least caudal peduncle depth	11.5	10.9	0.5	9.4-11.6
Counts		Mode	% Frequency	Min-Max
Dorsal-fin spines	17	18	65.0	17-19
Dorsal-fin rays	9	9	75.0	8-10
Anal-fin spines	3	3	100.0	3-3
Anal-fin rays	8	8	90.0	8-9
Pelvic-fin rays	5	5	100.0	5-5
Pectoral-fin rays	15	15	65.0	14-15
Lateral-line scales	31	31	45.0	30-32
Pored scales posterior to lateral line	0	1	55.0	0-1
Scale rows on cheek	4	5	55.0	4-6
Gillrakers on first ceratobranchial	12	11	60.0	11-12
Gillrakers on first epibranchial	2	3	55.0	2-4
Teeth in outer row of left lower jaw	14	14	20.0	12-20
Tooth rows on upper jaw	3	3	95.0	3-4
Tooth rows on lower jaw	3	3	95.0	3-4

In addition to the differentiating color traits mentioned in the above diagnosis section, the heterospecificity of the *M. lundoensis*, *M. phaeos*, and *M. flavifemina* is supported by a multivariate analysis of morphometric and meristic data of these species. The plot of the first principal component of the meristic data versus the sheared second principal component of the morphometric data (Figure 4.6) shows complete separation among the minimum polygon of *M. lundoensis*, *M. phaeos* (type material from Cobwe, Lake Malaŵi) and *M. flavifemina* (type material from Maleri Island, Malaŵi). Size accounts for 76% and the second principal component for 40% of the remaining variation. Variables with the highest loadings on the sheared second principal component in decreasing order are cheek depth (0.41), snout length (0.38), and lower jaw length (0.33). The first principal component of the meristic data accounts for 23% of the total variation. Variables with the highest standardized scoring coefficients on the first principal component of the meristic data in decreasing order are tooth rows lower jaw (0.40), lateral lines scales (-0.39), and anal rays (-0.34).

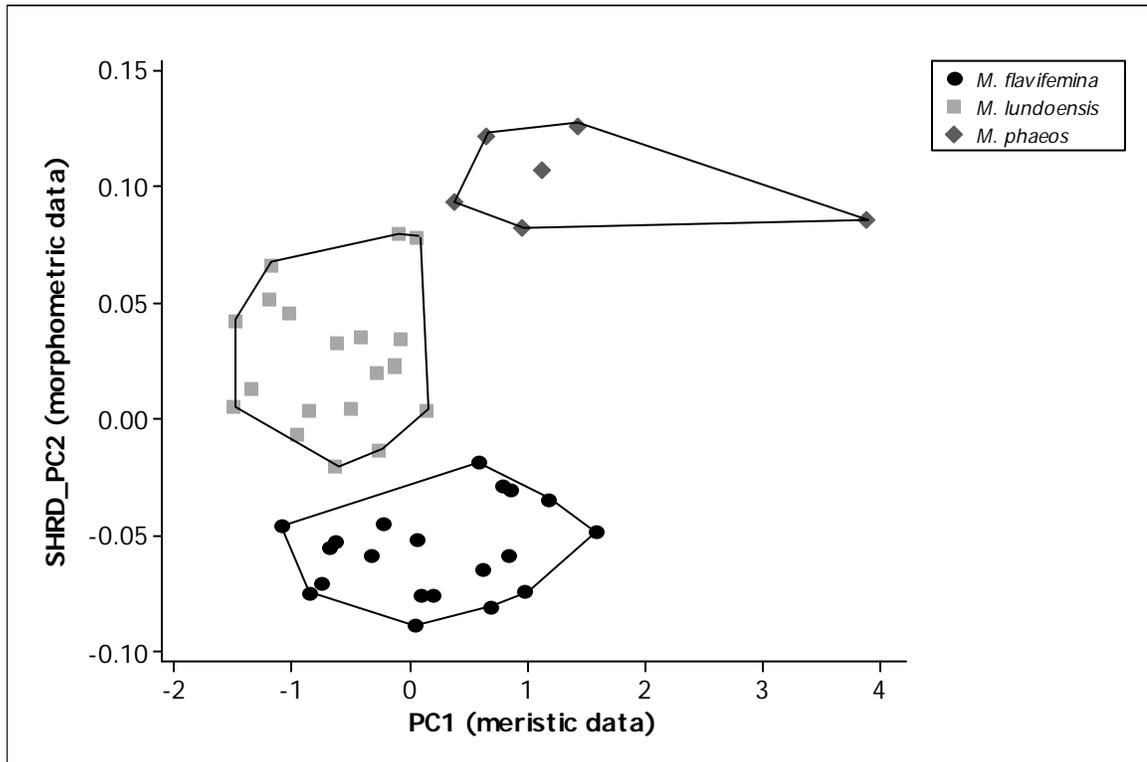


Figure 4.6: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. lundoensis* (N = 20) PSU 4910-4911, *M. phaeos* (N= 6) from Cobwe, Mozambique, and *M. flavifemina* (N=20) from Maleri Island, Malaŵi.

Metriaclima midomo n. sp. (Figures 4.7-4.8)

HOLOTYPE.—PSU 4912, adult male, 69.5 mm, S 11°08.0827' E 34°38.792', Lundo Island, Lake Malaŵi, Tanzania, Africa, January 2004, Konings and Stauffer (collectors).

PARATYPES. —PSU 4913, 18, (66.3-98.3), same data as holotype.

Diagnosis.— The presence of 1) bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws; 2) moderately sloped ethmo-vomerine block with a swollen rostral tip; 3) lower jaw forming a 45° angle with a line that connects the tip of the snout to the hypural plate; 4) large part of the upper dental arcade is exposed when the mouth is closed; 5) tips of the teeth in the premaxilla and dentary are in a V-shaped line with the anterior most in upper and lower jaw furthest apart; and 6) bicuspid teeth in the outer row along the side of the jaws do not follow the contour of the jaw and the lateral teeth are rotated so that the plane of their two-pronged tips runs parallel with those in the anterior part of the jaw place this species in *Metriaclima*. Additionally, this species feeds at almost perpendicular angles to the substrate and is capable of aligning the teeth of both the upper and lower jaws by abducting the jaws to a 180°-angle opening in order to collect loose aufwuchs from the substrate.

The blue ground color with distinct black bars, absence of dark pigmentation on a light blue dorsal fin distinguishes *M. midomo* from all other members of the genus except for *M. xanstomachus*, *M. hajomaylandi*, *M. fainzilberi*, and *M. zebra*. The bright yellow gular of male *M. xanstomachus* and of some *M. fainzilberi*, and the orange/yellow head, throat, and chest of male *M. hajomaylandi* separate these species from *M. midomo*. *Metriaclima midomo* is distinguished from *M. fainzilberi* and *M. zebra* by the number of tooth rows in both the upper and lower jaw – where *M. midomo* has a Min-Max of 6-8 and 7-11 respectively (Table 4.2) versus *M. zebra* with a Min-Max of 2-4 and 3-5 and *M. fainzilberi* with a Min-Max of 3-4 and 3-6 (Table 4.3).

Table 4.2: Morphometric and meristic values for *Metriaclima midomo* from Lundo Island, Tanzania (PSU 4912-4913). Min-Max includes holotype (N=19).

Variable	Holotype	Mean	Std Dev	Min-Max
Standard length, mm	69.5	77.4	9.3	66.3-98.3
Head length, mm	22.6	24.8	2.9	21.9-32.0
Percent head length				
Snout length	34.9	38.0	2.2	34.9-41.3
Postorbital head length	40.1	38.9	1.1	35.6-40.3
Horizontal eye diameter	34.4	34.6	1.1	32.1-36.4
Vertical eye diameter	36.3	35.0	0.9	33.8-36.6
Preorbital depth	22.7	23.4	1.5	20.7-26.0
Cheek depth	29.8	29.6	1.9	27.5-34.3
Lower-jaw length	33.8	36.9	1.5	33.7-39.5
Head depth	88.1	90.6	2.5	86.9-96.0
Percent standard length				
Body depth	36.3	35.4	1.1	34.0-37.7
Snout to dorsal-fin origin	34.2	34.0	1.2	31.8-36.3
Snout to pelvic-fin origin	39.1	40.3	1.4	37.3-41.9
Dorsal-fin base length	61.9	61.1	1.6	57.7-64.4
Anterior dorsal to anterior anal	52.0	52.5	1.4	49.8-55.6
Anterior dorsal to posterior anal	64.8	63.6	1.7	60.3-66.4
Posterior dorsal to anterior anal	29.2	29.2	0.9	27.0-30.7
Posterior dorsal to posterior anal	15.8	15.9	0.5	15.2-16.8
Posterior dorsal to ventral caudal	18.2	18.5	0.8	16.6-19.8
Posterior anal to dorsal caudal	22.8	21.3	1.1	19.5-23.5
Anterior dorsal to pelvic-fin origin	39.3	39.0	1.6	36.0-42.7
Posterior dorsal to pelvic-fin origin	59.0	57.8	1.4	54.7-60.4
Caudal peduncle length	13.6	14.1	1.2	11.2-16.8
Least caudal peduncle depth	11.5	11.1	0.6	10.0-12.2
Counts		Mode	% Frequency	Min-Max
Dorsal-fin spines	17	17	63.2	17-18
Dorsal-fin rays	9	9	68.4	8-10
Anal-fin spines	3	3	100.0	3-3
Anal-fin rays	8	8	94.7	7-8
Pelvic-fin rays	5	5	100.0	5-5
Pectoral-fin rays	15	15	79.0	14-15
Lateral-line scales	31	31	57.9	29-32
Pored scales posterior to lateral line	2	1	57.9	0-2
Scale rows on cheek	4	5	52.6	3-6
Gillrakers on first ceratobranchial	12	11	84.2	10-12
Gillrakers on first epibranchial	2	2	68.4	2-3
Teeth in outer row of left lower jaw	30	26	21.1	23-32
Tooth rows on upper jaw	8	7	47.4	6-8
Tooth rows on lower jaw	10	10	31.6	7-11

Table 4.3: Comparison of morphometric and meristic values for *Metriaclima midomo* from Lundo Island, Tanzania (N=19; PSU 4912-4913), *M. zebra* holotype (BMNH1891.12.17.7) and *M. zebra* from Tanzanian shores (Pombo Rocks, Thumbi Point, Makonde, Sanga Rocks, Manda) (N=100) and Chiwindi, Mozambique (N=17), and *M. fainzilberi* holotype (BMNH1976.6.18.2) and *M. fainzilberi* from Hongi Island, Tanzania (N=20), Lupingu, Tanzania (N=10), Lumbaulo, Mozambique (N=10), and Londo Bay, Mozambique (N=10). Min-Max includes holotype.

Variable	<i>M. midomo</i>		<i>M. zebra</i>		<i>M. fainzilberi</i>	
	Mean	Min-Max	Mean	Min-Max	Mean	Min-Max
Standard length, mm	77.4	66.3-98.3	69.6	57.8-84.6	76.8	63.0-101.5
Head length, mm	24.8	21.9-32.0	21.8	17.7-26.3	23.9	20.0-31.7
Percent head length						
Snout length	38	34.9-41.3	36.6	29.6-43.0	34.9	30.6-43.5
Postorbital head length	38.9	35.6-40.3	38.6	34.3-41.8	38.4	36.0-40.9
Horizontal eye diameter	34.6	32.1-36.4	35.4	31.0-39.1	33.8	29.4-37.4
Vertical eye diameter	35	33.8-36.6	35.7	31.6-39.6	34.9	31.5-37.6
Preorbital depth	23.4	20.7-26.0	23.1	19.6-27.2	22.8	19.6-27.2
Cheek depth	29.6	27.5-34.3	29.3	23.5-33.4	27.7	17.0-32.6
Lower-jaw length	36.9	33.7-39.5	37.2	34.0-41.8	37.7	34.6-40.9
Head depth	90.6	86.9-96.0	88.4	75.5-99.7	91.6	80.0-98.3
Percent standard length						
Body depth	35.4	34.0-37.7	33.2	28.8-36.0	34.4	32.0-36.3
Snout to dorsal-fin origin	34	31.8-36.3	33.5	30.7-35.9	33.6	30.6-35.8
Snout to pelvic-fin origin	40.3	37.3-41.9	38.9	35.8-43.8	38.7	36.0-42.4
Dorsal-fin base length	61.1	57.7-64.4	61.1	55.9-65.4	61.6	59.7-63.8
Anterior dorsal to anterior anal	52.5	49.8-55.6	50.8	48.2-54.4	51.9	50.0-53.6
Anterior dorsal to posterior anal	63.6	60.3-66.4	63	58.7-66.4	64.2	62.2-66.8
Posterior dorsal to anterior anal	29.2	27.0-30.7	29.3	27.1-32.0	29.6	27.7-32.1
Posterior dorsal to posterior anal	15.9	15.2-16.8	15.8	14.0-17.8	16	14.7-17.8
Posterior dorsal to ventral caudal	18.5	16.6-19.8	18.5	16.9-20.5	18.8	17.4-20.5
Posterior anal to dorsal caudal	21.3	19.5-23.5	21.6	19.8-23.8	21.5	19.6-23.3
Anterior dorsal to pelvic-fin origin	39	36.0-42.7	37.3	34.2-40.7	37.9	34.4-40.6
Posterior dorsal to pelvic-fin origin	57.8	54.7-60.4	57.8	53.1-62.1	58	52.1-60.3
Caudal peduncle length	14.1	11.2-16.8	14.7	13.1-17.3	14.8	13.0-16.7
Least caudal peduncle depth	11.1	10.0-12.2	11.1	10.0-12.1	11.6	10.6-12.6
Counts	Mode	Min-Max	Mode	Min-Max	Mode	Min-Max
Dorsal-fin spines	17	17-18	17	16-19	18	16-19
Dorsal-fin rays	9	8-10	9	8-10	9	8-10
Anal-fin spines	3	3-3	3	3-3	3	3-3
Anal-fin rays	8	7-8	8	7-9	8	7-9
Pelvic-fin rays	5	5-5	5	5-5	5	5-5
Pectoral-fin rays	15	14-15	14	14-15	15	14-15
Lateral-line scales	31	29-32	31	29-32	31	29-32
Pored scales posterior to lateral line	1	0-2	1	0-2	1	0-2
Scale rows on cheek	5	3-6	5	3-6	5	4-6
Gillrakers on first ceratobranchial	11	10-12	11	10-13	11	10-13
Gillrakers on first epibranchial	2	2-3	3	2-4	3	2-3
Teeth in outer row of left lower jaw	26	23-32	19	15-26	22	16-26
Tooth rows on upper jaw	7	6-8	3	2-4	3	3-4
Tooth rows on lower jaw	10	7-11	4	3-5	4	3-6



Figure 4.7: *Metriaclima midomo*, male, Lundo Island, Lake Malaŵi, Tanzania. Photo by Ad Konings.



Figure 4.8: *Metriaclima midomo*, female, Lundo Island, Lake Malaŵi, Tanzania. Photo by Ad Konings.

Description.— Morphometric and meristic data in Table 4.2. Jaws isognathous to slightly prognathous; teeth on jaws in 6-11 rows; teeth in outer row bicuspid; those in inner row tricuspid; 30 teeth in outer row of left lower jaw of holotype, 23-32 in paratypes. Dorsal fin with 17 spines in holotype, 17-18 in paratypes; dorsal-fin rays 9 in holotype and 8-10 in paratypes. Pectoral fin with 15 rays in holotype and 14-15 in paratypes; anal fin with 3 spines, 8 rays in holotype and 7-8 rays in paratypes. Scales along side ctenoid; holotype with 31 lateral-line scales

and 29-32 in paratypes. First gill arch with 10-12 rakers on the ceratobranchial, 2-3 on epibranchial, and 1 between epibranchial and ceratobranchial.

Color notes and photos of live breeding adults catalogued under PSU 4928. Males with blue flank, green highlights, and 5-7 black lateral bars. Head with light blue opercle and green highlights; gray opercle spot; cheek, preorbital and preopercle dark blue/gray; gular blue/white; interorbital light blue. Dorsal fin light blue; yellow/orange distal rays sometimes present. Caudal fin proximally dark blue and distally gray. Anal fin blue/white with 0-2 yellow ocelli. Pectoral fin with gray rays and clear membranes. Pelvic fin with blue/white leading edge; first 2 membranes black; remaining membranes clear.

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

Distribution.—*Metriaclima midomo* is known from Lundo Island, Lake Malaŵi, Tanzania.

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

Remarks.— Ad Konings and Jay Stauffer, Jr. (personal communication) originally suspected that *M. midomo* was in fact *M. zebra* as *M. zebra* is not found at Lundo Island and *M. midomo* most closely resembles *M. zebra*. In order to determine if this “thick-lipped” population at Lundo Island was in fact *M. zebra*, a multivariate analysis of morphometric and meristic data from neighboring populations of *M. zebra* (from the 5 localities along the Tanzanian shore and Chiwindi, Mozambique; Figure 4.9) and the holotype of *M. zebra* were compared to *M. midomo*. The results support the heterospecificity of these two species. The plot of the first principal component of the meristic data versus the sheared second principal component of the

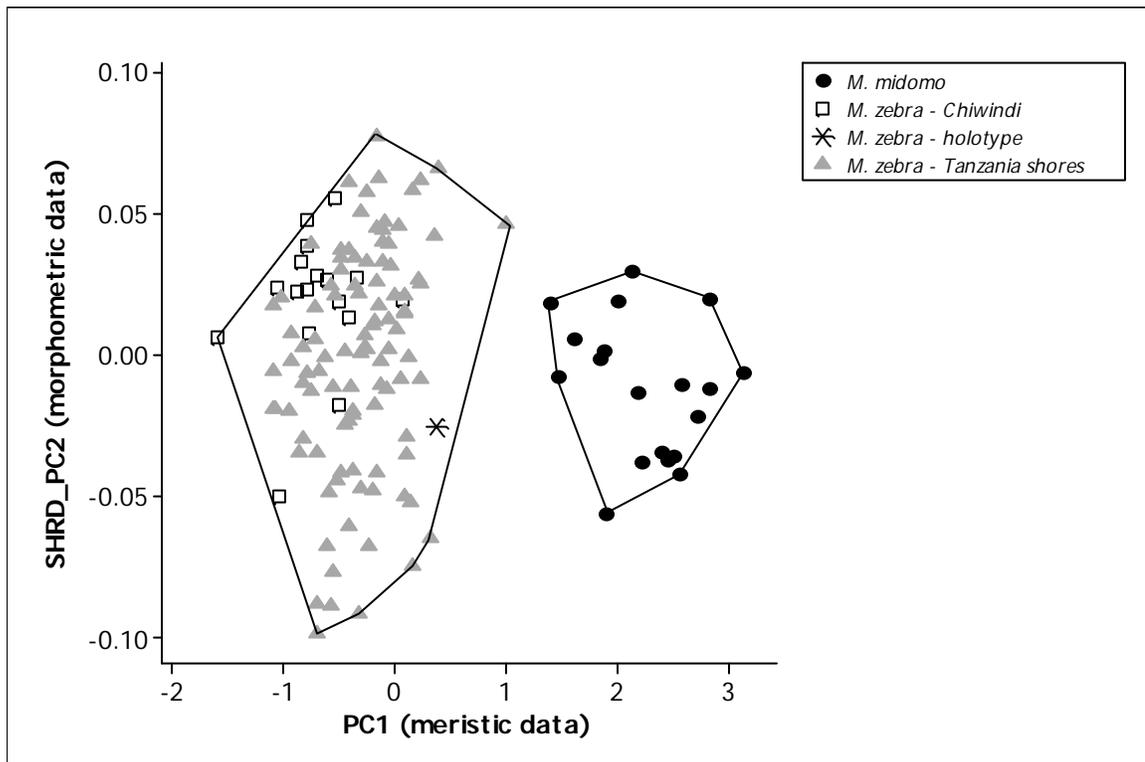


Figure 4.10: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. midomo* (N = 19) PSU 4912-4913, *M. zebra* (N= 100; 20 per locality) from Tanzanian shores (Pombo Rocks, Thumbi Point, Makonde, Sanga Rocks, Manda), *M. zebra* (N=17) from Chiwindi, Mozambique, and *M. zebra* holotype (BMNH1891.12.17.7).

Metriaclima midomo is found at Lundo Island, a location which is inhabited by at least three other members of *Metriaclima* – *M. fainzilberi*, *M. pambazuko*, and *M. lundoensis*. These can be distinguished by male color pattern – where male *M. fainzilberi* and *M. pambazuko* have a red/orange dorsal fin, while those of *M. midomo* and *M. lundoensis* are blue. The dorsal fin of *M. lundoensis* has a black submarginal band, lacking in *M. midomo*, and the anal fin of *M. pambazuko* is black while it is blue in *M. fainzilberi*.

At Lundo Island, Tanzania, three of the newly described *Metriaclima* are sympatric – *M. pambazuko*, *M. lundoensis*, and *M. midomo*. Comparison of these species using principal component analysis revealed distinct clustering when the first principal components of the meristic data are plotted against the sheared second principal components of the morphometric

data (Figure 4.11). Although there is some overlap between *M. pambazuko* and *M. lundoensis*, these species are significantly different along both axes ($P < 0.05$, Duncan's Multiple Range Test). Size accounts for 90% and the second principal component for 22% of the remaining variation. Variables with the highest loadings on the sheared second principal component in decreasing order are cheek depth (0.51), snout length (-0.40) and snout to pelvic fin insertion (-0.34). The first principal component of the meristic data accounts for 30% of the total variation. Variables with the highest standardized scoring coefficients on the first principal component of the meristic data in decreasing order are tooth rows on the upper jaw (0.50), tooth rows on the lower jaw (0.50), and teeth on the outer row of left lower jaw (0.45).

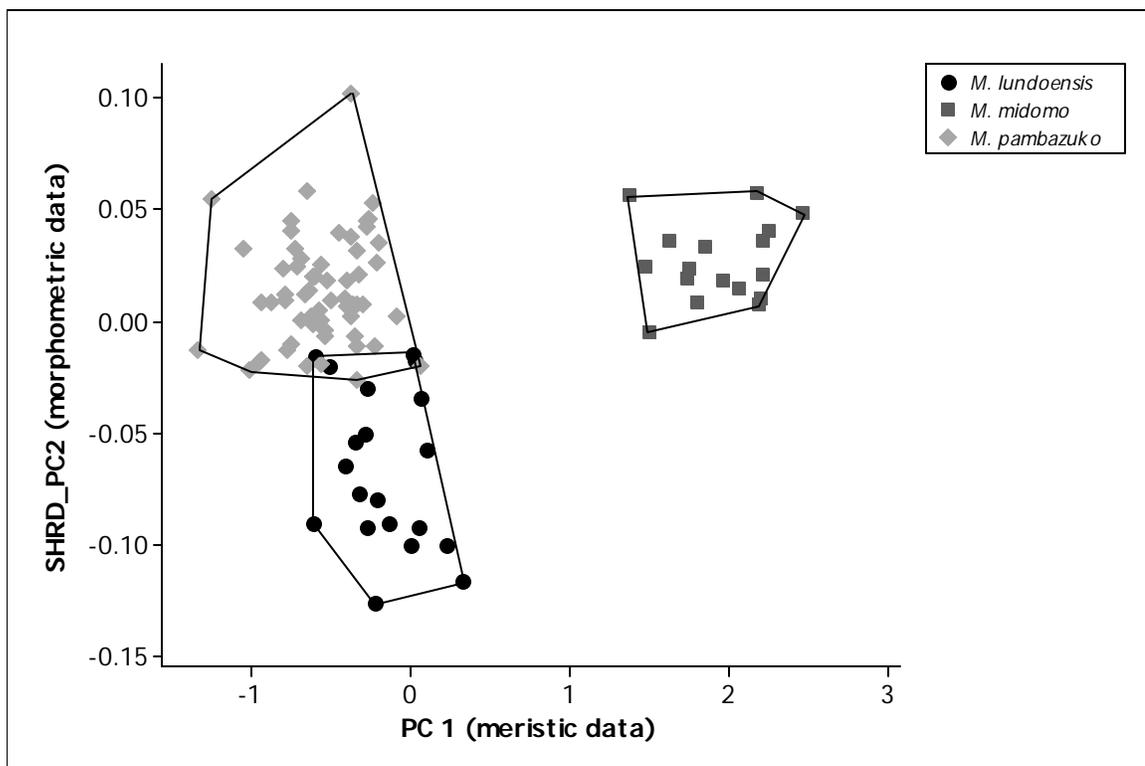


Figure 4.11: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. pambazuko* (N = 59) PSU 4900-4903, *M. lundoensis* (N = 20) PSU 4910-4911, and *M. midomo* (N = 19) PSU 4912-4913.

Metriaclima tarakiki n. sp. (Figures 4.12-4.14)

HOLOTYPE.—PSU 4914, adult male, 115.2 mm, S 11°18.380' E 34°44.791', Higga Reef, Lake Malaŵi, Tanzania, Africa, February 2005, Konings, Stauffer, and Kocher (collectors).

PARATYPES. —PSU 4915, 11, (72.2-119.3 mm), same data as holotype; PSU 4916, 20, (75.9-96.8 mm), Ngkuyo Island, Lake Malaŵi, Tanzania, January 2004.

Diagnosis.— The presence of 1) bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws; 2) moderately sloped ethmo-vomerine block with a swollen rostral tip; 3) lower jaw forming a 45° angle with a line that connects the tip of the snout to the hypural plate; 4) lower jaw is often slightly longer and thicker than the upper jaw; 5) large part of the upper dental arcade is exposed when the mouth is closed; 6) tips of the teeth in the premaxilla and dentary are in a V-shaped line with the anterior most in upper and lower jaw furthest apart; and 7) bicuspid teeth in the outer row along the side of the jaws do not follow the contour of the jaw and the lateral teeth are rotated so that the plane of their two-pronged tips runs parallel with those in the anterior part of the jaw place this species in *Metriaclima*. Additionally, this species feeds at almost perpendicular angles to the substrate and is capable of aligning the teeth of both the upper and lower jaws by abducting the jaws to a 180°-angle opening in order to collect loose aufwuchs from the substrate.

Male *M. tarakiki* are distinguished from those of other members of *Metriaclima* by the blue ground color with distinct black bars, the extension of lateral bars onto the blue dorsal fin, the blue anal fin, and no submarginal band in the dorsal fin or yellow pigment on the body. While some males of *M. zebra* and *M. fainzilberi* exhibit extension of the lateral bars into the dorsal fin, these extensions fuse into a broad submarginal band, which is not observed in males of *M. tarakiki*. Male and female *M. tarakiki* are further distinguished from *M. zebra* by a shallower body where the measurement of anterior of dorsal fin to pelvic-fin origin ranges from 28.1-36.0%SL in *M. tarakiki* (Table 4.4) and 34.2-40.7%SL in *M. zebra* populations from Tanzanian

shores and Chiwindi, Mozambique (Table 4.3). In general *M. tarakiki* has more teeth on the upper and lower jaws (range 4-8, 5-8, respectively) to *M. zebra* (range 2-4, 3-5, respectively).



Figure 4.12: *Metriaclima tarakiki*, male, Ngkuyo Island, Lake Malaŵi, Tanzania. Photo by Ad Konings.



Figure 4.13: *Metriaclima tarakiki*, female, Higga Reef, Lake Malaŵi, Tanzania. Photo by Ad Konings.

Description.—Morphometric and meristic data in Table 4.4. Jaws isognathous to slightly prognathous; teeth on jaws in 4-8 rows; teeth in outer row bicuspid; those in inner row tricuspid; 27 teeth in outer row of left lower jaw of holotype, 20-31 in paratypes. Dorsal fin with 18 spines in holotype, 17-19 in paratypes; dorsal-fin rays 8 in holotype and 8-10 in paratypes. Pectoral fin

with 15 rays in holotype and 14-15 in paratypes; anal fin with 3 spines in holotype and 3-4 in paratypes, 8 rays in holotype and 8-9 rays in paratypes. Scales along side ctenoid; holotype with 31 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 epibranchial and ceratobranchial.

Color notes and photos of live breeding adults catalogued under PSU 4929. Breeding males with blue flank and 7-9 black lateral black bars; caudal peduncle blue/gray; belly gray; breast dark gray. Head blue/black with two blue interorbital bars; gular blue/gray; opercle with light blue and green highlights. Dorsal fin blue to dark blue with some lateral bars extend onto proximal portion of dorsal fin; white marginal band usually present. Proximal 2/3 caudal fin dark gray and distal 1/3 light gray; gray rays; blue membranes. Anal fin blue/gray; distally light gray in some individuals; 2-8 yellow ocelli. Pectoral fin with gray rays and clear membranes. Pelvic fin black/dark gray; white leading edge sometimes present.

Females brown or orange blotch (OB). Non-OB females with brown flank; center of scales blue; belly blue/white or beige; breast brown. Head brown; blue/black opercular spot; light brown gular or white. Dorsal fin dark gray or brown with gray/white/blue marginal band. Proximal 1/2 caudal fin blue/dark brown and distal 1/2 light brown. Pectoral fin with gray rays and clear membranes. Pelvic fin brown or gray; white leading edge sometimes present.

OB females with orange flank with black blotches; belly blue/white with black blotches; breast yellow with black blotches. Head orange with black blotches; gular white with black blotches; opercle with blue/green highlights. Dorsal, caudal and anal fins yellow with black blotches. Pectoral fins with yellow/black rays and clear membranes with black blotches.

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

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

Table 4.4: Morphometric and meristic values for *Metriaclima tarakiki* from Higga Reef, Tanzania (PSU 4914-4915) and Ngkuyo, Tanzania (PSU 4916). Min-Max includes holotype (N=32). Data per collection found in Appendix D.

Variable	Holotype	Mean	Std Dev	Min-Max
Standard length, mm	115.2	90.0	11.1	72.2-119.3
Head length, mm	34.0	26.6	3.2	21.7-35.8
Percent head length				
Snout length	39.8	37.4	2.3	32.9-42.2
Postorbital head length	39.1	38.7	1.1	36.0-40.8
Horizontal eye diameter	27.2	32.5	2.3	27.2-36.3
Vertical eye diameter	28.4	32.6	2.1	28.2-36.5
Preorbital depth	23.5	22.5	1.1	20.5-25.1
Cheek depth	29.9	26.5	2.0	23.3-30.8
Lower-jaw length	35.2	37.0	1.3	34.8-39.7
Head depth	90.6	81.9	6.3	73.3-96.4
Percent standard length				
Body depth	32.9	28.8	1.9	25.8-32.9
Snout to dorsal-fin origin	31.3	30.9	1.1	28.5-33.0
Snout to pelvic-fin origin	36.4	36.5	1.2	34.7-39.3
Dorsal-fin base length	61.7	59.9	1.4	56.7-62.4
Anterior dorsal to anterior anal	51.9	48.4	1.7	45.8-51.9
Anterior dorsal to posterior anal	63.5	61.6	1.3	59.5-63.9
Posterior dorsal to anterior anal	30.4	27.6	1.5	25.3-30.8
Posterior dorsal to posterior anal	17.0	15.3	1.0	13.2-17.0
Posterior dorsal to ventral caudal	20.2	18.8	0.9	16.4-20.5
Posterior anal to dorsal caudal	22.8	21.6	0.6	20.3-22.8
Anterior dorsal to pelvic-fin origin	35.6	31.7	2.2	28.1-36.0
Posterior dorsal to pelvic-fin origin	61.9	58.5	1.6	56.0-62.0
Caudal peduncle length	15.0	15.4	0.8	13.7-17.5
Least caudal peduncle depth	12.3	10.8	0.7	9.7-12.3
Counts				
		Mode	% Frequency	Min-Max
Dorsal-fin spines	18	18	93.8	17-19
Dorsal-fin rays	8	9	84.4	8-10
Anal-fin spines	3	3	96.9	3-4
Anal-fin rays	8	8	93.8	8-9
Pelvic-fin rays	5	5	100.0	5-5
Pectoral-fin rays	15	14	62.5	14-15
Lateral-line scales	31	32	71.9	31-33
Pored scales posterior to lateral line	0	1	87.5	0-2
Scale rows on cheek	5	4	53.1	4-5
Gillrakers on first ceratobranchial	11	11	56.3	10-12
Gillrakers on first epibranchial	2	3	59.4	2-3
Teeth in outer row of left lower jaw	27	26	21.9	20-31
Tooth rows on upper jaw	6	6	50.0	4-8
Tooth rows on lower jaw	8	8	40.6	5-8

Remarks.—*Metriaclima tarakiki* exhibits polychromatism. For example, OB females and males are found at Higga Reef (Konings 2001; Figure 4.14).



Figure 4.14: *Metriaclima tarakiki*, OB female, Ngkuyo Island, Lake Malaŵi, Tanzania. Photo by Ad Konings.

Metriaclima tarakiki most closely resembles *M. zebra* but appears to have a more slender body than *M. zebra*. As *M. zebra* is not documented either Ngkuyo Island or Higga Reef, it was necessary to compare *M. tarakiki* to neighboring populations of *M. zebra* (Figure 4.15) to test their conspecificity or heterospecificity. Results of a multivariate analysis of morphometric and meristic data show that *Metriaclima tarakiki* and *M. zebra* are not conspecific. The plot of the first principal component of the meristic data versus the sheared second principal component of the morphometric data (Figure 4.16) clearly demonstrates that the minimum polygon of *M. tarakiki* and *M. zebra* from nearby Chiwindi, Mozambique and Thumbi Point, do not overlap. The holotype of *M. zebra* falls within the minimum polygon clusters of the nearby *M. zebra*. Size accounts for 92% and the second principal component for 43% of the remaining variation. Variables with the highest loadings on the sheared second principal component in decreasing order are caudal peduncle length (-0.48), cheek depth (-0.43) and anterior of dorsal fin to pelvic-fin insertion (0.41). The first principal component of the meristic data accounted for 26% of the

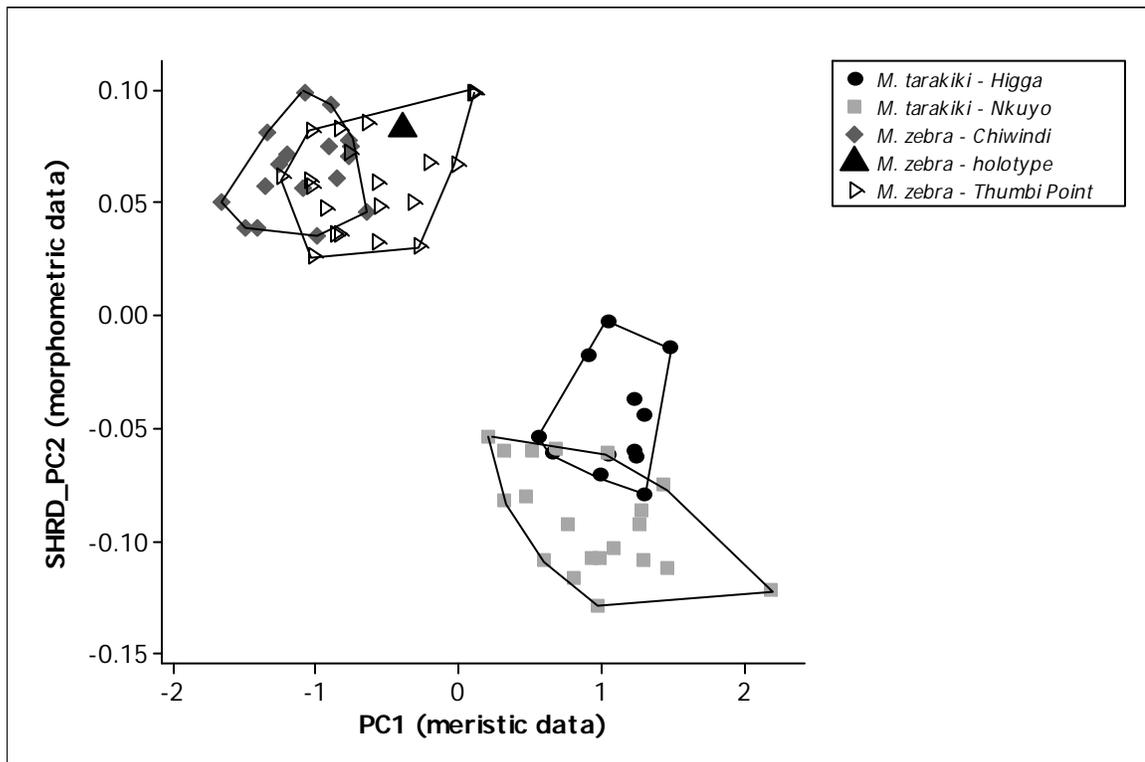


Figure 4.16: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. tarakiki* (N = 32) PSU 4914-4916, *M. zebra* from Thumbi Point, Tanzania (N= 20), *M. zebra* from Chiwindi, Mozambique (N = 17), and *M. zebra* holotype (BMNH1891.12.17.7).

Metriaclima tarakiki occurs within 15 kilometers of Lundo Island, which is inhabited by three newly described species – *M. midomo*, *M. pambazuko*, and *M. lundoensis*. Comparison of these newly described species using principal component analysis revealed distinct clustering when the first principal component of the meristic data is plotted against the sheared second principal component of the morphometric data (Figure 4.17). This comparison revealed distinct clustering of *M. tarakiki*. Size accounts for 91% and the second principal component for 32% of the remaining variation. Variables with the highest loadings on the sheared second principal component in decreasing order are caudal peduncle length (0.57), anterior of dorsal fin to pelvic-fin insertion (-0.32) and posterior of anal fin to dorsal part of hypural plate (-0.32). The first principal component of the meristic data accounts for 30% of the total variation. Variables with

the highest standardized scoring coefficients on the first principal component of the meristic data in decreasing order are tooth rows on the upper jaw (0.47), tooth rows on the lower jaw (0.47), and teeth on the outer row of left lower jaw (0.44).

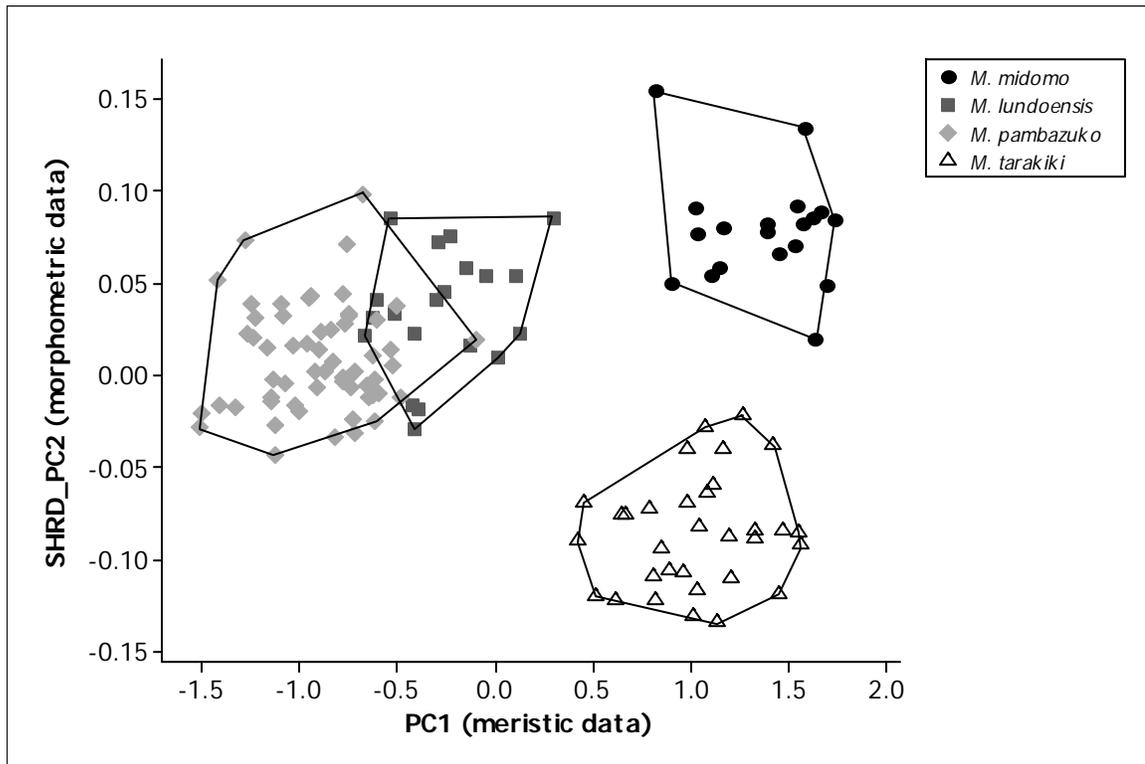


Figure 4.17: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. tarakiki* (N = 32) PSU 4914-4916, *M. pambazuko* (N = 59) PSU 4900-4903, *M. lundoensis* (N = 20) PSU 4910-4911, and *M. midomo* (N = 19) PSU 4912-4913.

Metriaclima nigrodorsalis n. sp. (Figures 4.18-4.21)

HOLOTYPE.—PSU 4904, adult male, 75.83 mm, S 12 °47.671' E 34°47.159', N'kolongwe, Lake Malaŵi, Mozambique, Africa, February 2002, Konings and Stauffer (collectors).

PARATYPES.—PSU 4905, 19, (66.5-78.7 mm), same collection data as for holotype; PSU 4906, 20, (63.8-81.6 mm), Charlie's Bay, Lake Malaŵi, Mozambique, February 2002; PSU 4907, 20, (65.4-83.3 mm), Nkhungu Point, Lake Malaŵi, Mozambique, February 2002; PSU 4908, 20, (55.3-76.1 mm), Thundu, Lake Malaŵi, Mozambique, February 2002; PSU 4909, 8, (60.8-71.7 mm), Chilolo, Lake Malaŵi, Mozambique, March 2006.

Diagnosis.— The presence of the 1) bicuspid teeth in the anterior portion of the outer row on both the upper and lower jaws; 2) moderately sloped ethmo-vomerine block with a swollen rostral tip; 3) lower jaw forming a 45° angle with a line that connects the tip of the snout to the hypural plate; 4) large part of the upper dental arcade is exposed when the mouth is closed; 5) tips of the teeth in the premaxilla and dentary are in a V-shaped line with the anterior most in upper and lower jaw furthest apart; and 6) bicuspid teeth in the outer row along the side of the jaws do not follow the contour of the jaw and the lateral teeth are rotated so that the plane of their two-pronged tips runs parallel with those in the anterior part of the jaw place this species in *Metriaclima*. Additionally, this species feeds at almost perpendicular angles to the substrate and is capable of aligning the teeth of both the upper and lower jaws by abducting the jaws to a 180°-angle opening in order to collect loose aufwuchs from the substrate.

The presence of a black submarginal band in the dorsal fin in combination with distinct black lateral bars on a blue or yellow flank and yellow pigment on the cheek and breast distinguish males of this species from all other member of the genus except from the Maleri Island population of *Metriaclima flavifemina*. *Metriaclima nigrodorsalis* can be separated from the Maleri Island population of *M. flavifemina* on the basis of cheek depth expressed as a

percentage of head depth – whereas *M. nigrodorsalis* has a cheek depth expressed as a percentage of body depth greater than 25% (range 25.3-32.0%BD; Table 4.5) and it is less than 25% for *M. flavifemina* from Maleri Island (range 20.3-24.8%BD; Table 4.5).

Description.— Morphometric and meristic data in Table 4.5. Jaws isognathous to slightly prognathous; teeth on jaws in 3-5 rows; teeth in outer row bicuspid; those in inner row tricuspid; 18 teeth in outer row of left lower jaw of holotype, 14-26 in paratypes. Dorsal fin with 18 spines in holotype, 18-19 in paratypes; dorsal-fin rays 9 in holotype and 8-10 in paratypes. Pectoral fin with 14 rays in holotype and 13-15 in paratypes; anal fin with 3 spines, 8 rays in holotype and 7-9 rays in paratypes. Scales along side ctenoid; holotype with 31 lateral-line scales and 30-32 in paratypes. First gill arch with 10-13 rakers on the ceratobranchial, 2-4 on epibranchial, and 1 between epibranchial and ceratobranchial.

Color notes and photos of live breeding adults catalogued under PSU 4930.

Chiloelo and Charlies Bay (Figure 4.18): Breeding males with dark blue flank and 6-7 lateral bars; belly gray; yellow pigmentation on belly. Interorbital dark gray/blue; blue interorbital bars sometimes present; cheek with blue and yellow markings; gray gular. Dorsal fin proximally black; distally blue/white. Caudal fin with blue membranes and some/all black rays; distally yellow. Anal fin black with gray marginal band in anterior portion and distally yellow; 1 yellow ocelli. Pectoral fin black with clear membranes. Pelvic fin black with blue/gray leading edge and distally yellow.

Females with blue/beige flank and 7 gray lateral bars; brown/orange spot on anterior portion of scales. Head dark gray with 2 light gray interorbital bars; cheek light gray; lower jaw blue; ventral edge of opercle blue; blue opercle spot. Dorsal fin proximally dark gray fading distally to light gray; white lappets sometimes present. Caudal fin gray with distal 1/3 rays black. Anal fin gray fading to yellow with 1-2 yellow ocelli. Pectoral fin with gray rays and clear

membranes. Pelvic fin gray; white leading edge sometimes present.



Figure 4.18: *Metriaclima nigrodorsalis* male (left), female (right) from Chiloele Bay, Lake Malaŵi, Mozambique. Photos by Ad Konings.

N'kolongwe (Figure 4.19): Males with light blue flank and 6-7 black bars; belly yellow; caudal peduncle yellow/brown. Interorbital blue with 1-2 black interorbital bars; cheek and preopercle dark brown; dark blue gray opercle with black opercle spot. Dorsal fin proximally yellow/orange with extension of lateral bars from side; black/gray marginal band; white/blue/brown lappets; 5 posterior rays orange/brown with blue membrane. Caudal fin yellow/brown with some black rays. Anal fin black with 2-3 yellow ocelli. Pectoral fin black on proximate half with remainder gray. Pelvic fin black with white leading edge.

Females with blue/beige flank and 6 brown lateral bars; center of lateral scales brown; caudal peduncle brown. Head brown with faint blue interorbital bar; green/blue highlights on opercle; gular gray/brown. Dorsal fin proximally brown, distally light brown; orange/yellow lappets. Caudal fin proximally dark brown and distally light brown; blue spots on membranes; orange/yellow tips. Anal fin proximate 1/8 dark brown, distal 7/8 orange/yellow; 0-1 ocelli. Pectoral fin clear or with gray rays. Pelvic fin with white leading edge on first ray, remainder rays black; membrane clear.



Figure 4.19: *Metriaclima nigrodorsalis* male (left), female (right) from N'kolongwe, Lake Malaŵi, Mozambique. Photos by Ad Konings.

Thundu (Figure 4.20): Breeding males with blue ground flank and 6-7 black lateral bars; some lateral scales outlined in orange; caudal peduncle rust brown; belly gray/yellow. Interorbital light blue with 1-2 brown/orange interorbital bars; cheek brown with yellow highlights; gular brown/orange; dark green opercle spot. Dorsal-fin with proximally blue with black submarginal band; white marginal band; orange lappets. Caudal rays orange; membranes blue; some rays with black blotches. Anal fin black; spines with white tips; 1-6 orange/yellow ocelli. Pectoral fin clear. Pelvic fin with white leading edge; rays black.

Females with light brown ground colorations and 7 dark brown faint bars; white belly. Head brown/beige with white/light brown gular; black opercle spot sometimes present. Dorsal fin brown with light blue spots in membrane; white lappets with orange/brown tips. Caudal rays proximally brown and distally orange/yellow. Anal fin proximally brown, distally orange/yellow; 0-2 ocelli. Pectoral fin clear. Pelvic fin with clear rays and orange/yellow membranes; white leading edge.

Nkhungu (Figure 4.21): Males with yellow flank and 7-8 black bars; center of many scales blue; belly yellow/blue. Head yellow with 1 pale blue interorbital bar; opercle brown/yellow with dark orange opercle spot; gular orange. Dorsal fin proximally blue; black submarginal band; blue/green marginal band; rust-orange lappets. Caudal fin with blue

membranes and rays proximally blue and distally black; distally orange. Anal fin black with 2- 7 yellow ocelli; white/blue tips on rays. Pectoral fin with gray rays and clear membranes. Pelvic fin with black spines and black/gray membranes; white leading edge sometimes present.

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



Figure 4.20: *Metriaclima nigrodorsalis* male (left), female (right) from Thundu, Lake Malaŵi, Mozambique. Photos by Ad Konings.



Figure 4.21: *Metriaclima nigrodorsalis* male (left), female (right) from Nkhungu, Lake Malaŵi, Mozambique. Photos by Ad Konings.

Table 4.5: Morphometric and meristic values for *Metriaclima flavifemina* from Maleri Island Malaŵi (PSU 3729-3730); N=20 and *Metriaclima nigrodorsalis* from N'kolongwe, Mozambique (PSU 4904-4905); Charlie's Bay, Mozambique (PSU 4906); Nkhungu, Mozambique (PSU 4907); Thundu, Mozambique (PSU 4908); and Chilolo, Mozambique (PSU 4909). Min-Max includes holotype (N=88). Data per collection found in Appendix E.

Variable	<i>M. nigrodorsalis</i>			<i>M. flavifemina</i>	
	Holotype	Mean	Min-Max	Mean	Min-Max
Standard length, mm	75.8	71.6	55.3-83.3	74.8	59.2-80.2
Head length, mm	22.9	22.1	17.7-25.2	23.4	19.1-24.9
Percent head length					
Snout length	35.8	34.1	28.8-38.9	35.1	32.0-37.0
Postorbital head length	37.9	39.6	36.0-42.1	38.5	35.8-40.6
Horizontal eye diameter	35.7	36.8	33.9-40.3	37.4	34.7-42.8
Vertical eye diameter	37.1	36.7	34.0-40.1	36.9	34.0-40.7
Preorbital depth	22.3	21.9	19.1-26.0	21.9	20.2-24.2
Cheek depth	27.2	27.7	23.4-33.7	24.4	22.0-27.4
Lower-jaw length	35.7	34.2	30.3-36.9	33.7	32.3-34.7
Head depth	88.1	84.6	77.9-91.1	82.2	78.4-88.6
Percent standard length					
Body depth	32.6	31.8	29.6-36.0	33.9	32.6-35.5
Snout to dorsal-fin origin	33.4	33.4	30.0-35.5	33.9	33.1-35.0
Snout to pelvic-fin origin	39.1	37.8	35.3-42.8	39.5	37.7-41.0
Dorsal-fin base length	61.1	61.6	57.9-65.6	60.8	58.1-62.7
Anterior dorsal to anterior anal	52.3	51.9	48.6-54.3	53.6	50.5-55.9
Anterior dorsal to posterior anal	63.6	64.4	60.8-68.8	64.5	62.9-66.9
Posterior dorsal to anterior anal	29.0	29.9	27.6-32.2	30.5	29.2-32.0
Posterior dorsal to posterior anal	17.4	16.4	15.1-17.9	16.7	15.5-17.9
Posterior dorsal to ventral caudal	18.9	18.4	16.3-20.6	18	16.8-19.1
Posterior anal to dorsal caudal	21.6	21.5	17.8-23.5	20.8	20.1-21.8
Anterior dorsal to pelvic-fin origin	37.3	36.4	34.6-39.6	38.5	36.4-40.4
Posterior dorsal to pelvic-fin origin	59.3	58.9	55.3-61.7	59.3	56.9-61.7
Caudal peduncle length	14.7	14.4	12.3-16.9	12.9	12.1-13.9
Least caudal peduncle depth	11.7	11.5	10.2-12.8	11.7	10.9-12.6
Counts					
		Mode	Min-Max	Mode	Min-Max
Dorsal-fin spines	18	18	18-19	18	17-19
Dorsal-fin rays	9	9	8-10	9	9-10
Anal-fin spines	3	3	3-3	3	3-3
Anal-fin rays	8	8	7-9	8	8-8
Pelvic-fin rays	5	5	5-5	5	5-5
Pectoral-fin rays	14	14	13-15	15	14-15
Lateral-line scales	31	31	30-32	31	31-32
Pored scales posterior to lateral line	0	1	0-1	1	0-1
Scale rows on cheek	4	5	4-6	4	4-5
Gillrakers on first ceratobranchial	13	12	10-13	11	11-12
Gillrakers on first epibranchial	3	3	2-4	3	3-4
Teeth in outer row of left lower jaw	18	21	14-26	19	16-25
Tooth rows on upper jaw	3	4	3-5	3	3-4
Tooth rows on lower jaw	3	4	3-5	4	3-4

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

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

Remarks.—Ad Konings and Jay Stauffer, Jr. (personal communication) first postulated that the unique color variations in this species may represent several unique species. The results of the multivariate analysis of the morphometric and meristic data show that the five populations *M. nigrodorsalis* included in this investigation are morphologically similar; therefore, the unique color variations in populations represent geographical variation in this species.

The only other members of the genus *Metriaclima* possessing a dark submarginal band in the dorsal fin are *M. phaeos*, *M. lundoensis*, and some populations of *M. flavifemina*, *M. fainzilberi*, and *M. zebra*. The fact that *M. zebra* is sympatric with *M. nigrodorsalis* supports the conclusion that these two taxa are heterospecific. The yellow anal fins of the females and juveniles of *M. nigrodorsalis*, a trait found in neither *M. fainzilberi* nor *M. zebra*, further supports the heterospecificity of these three species.

To prove the heterospecificity of *Metriaclima nigrodorsalis* from the remaining members of *Metriaclima* possessing black submarginal bands (*M. lundoensis*, *M. phaeos*, and the Maleri Island population of *M. flavifemina*) a multivariate analysis of the morphometric and meristic data was completed. *Metriaclima nigrodorsalis* is geographically disjunct from these three species (Figure 4.22).

nigrodorsalis is distinct from *M. phaeos*. Size accounts for 86% and the second principal component for 27% of the remaining variation. Variables with the highest loadings on the sheared second principal component in decreasing order snout length (-0.38), caudal peduncle length (0.35) and cheek depth (-0.34). The first principal component of the meristic data accounts for 15% of the total variation. Variables with the highest standardized scoring coefficients on the first principal component of the meristic data in decreasing order are tooth rows lower jaw (0.58), tooth rows upper jaw (0.49), and teeth on outer row of left lower jaw (0.41).

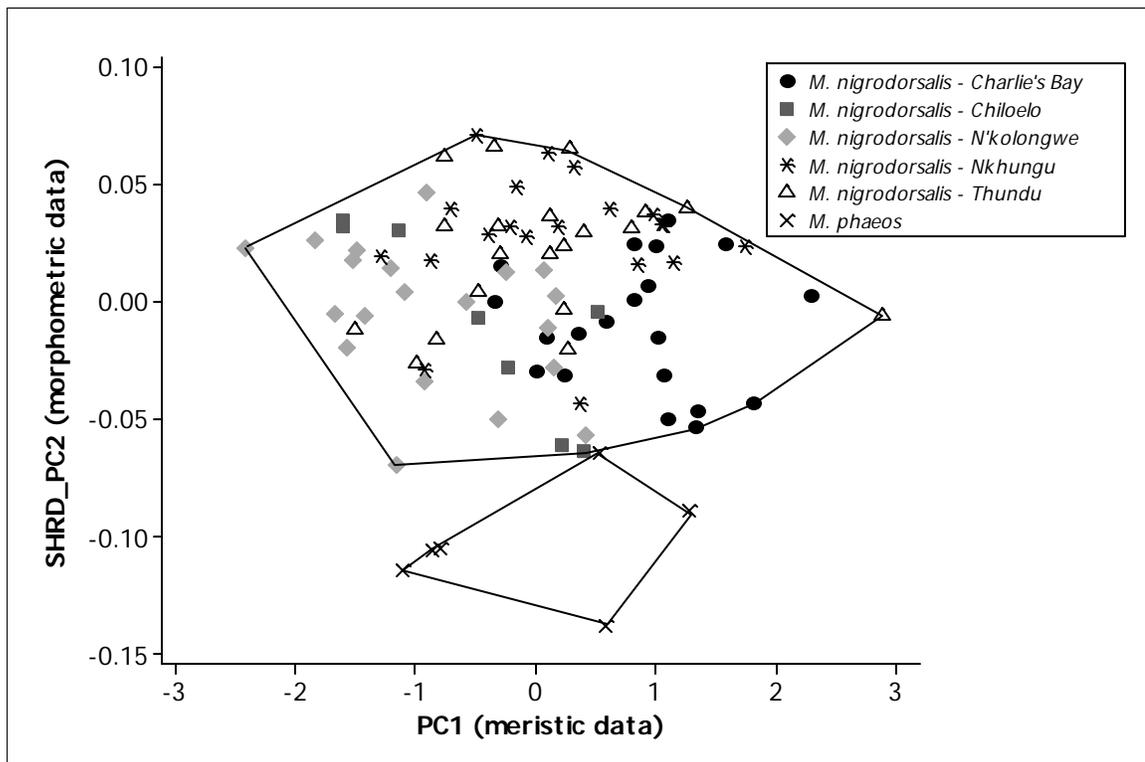


Figure 4.23: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. nigrodorsalis* (N = 88) PSU 4904-4909 and *M. phaeos* (N = 6) PSU 3054-3055 (type specimens).

Although there is some overlap in the minimum polygon clusters formed for *M. nigrodorsalis* and *M. lundoensis* (Figure 4.24), these species are significantly different along both axes ($P < 0.05$, ANOVA). Size accounts for 83% and the second principal component for 32% of

the remaining variation. Variables with the highest loadings on the sheared second principal component in decreasing order snout length (0.59), snout to pelvic fin insertion (0.35) and caudal peduncle length (-0.31). The first principal component of the meristic data accounts for 19% of the total variation. Variables with the highest standardized scoring coefficients on the first principal component of the meristic data in decreasing order are tooth rows on lower jaw (0.54), tooth rows on upper jaw (0.51), and teeth on outer row of left lower jaw (0.44).

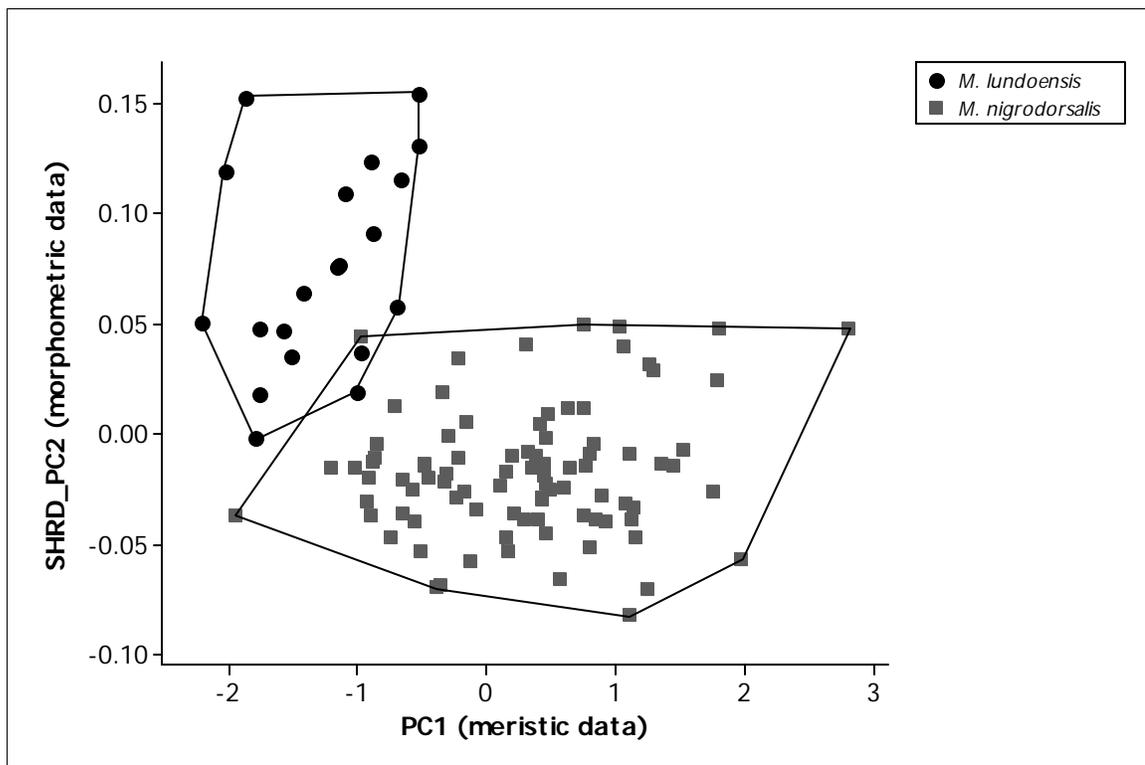


Figure 4.24: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. nigrodorsalis* (N = 88) PSU 4904-4909 and *M. lundoensis* (N = 20) PSU 4910-4911.

Metriaclima nigrodorsalis and *M. flavifemina* are also distinct based on the results of a multivariate analysis of morphometric and meristic data. The plot of the first principal component of the meristic data versus the sheared second principal component of the morphometric data (Figure 4.25) clearly demonstrates that the minimum polygon of the most southerly distributed *M. nigrodorsalis* (Charlie's Bay and Chiloelo, Mozambique) and *M.*

flavifemina from Maleri Island, Malaŵi do not overlap. Size accounts for 80% and the second principal component for 41% of the remaining variation. Variables with the highest loadings on the sheared second principal component in decreasing order are cheek depth (0.69), caudal peduncle length (0.43), and body depth (0.22). The first principal component of the meristic data accounts for 23% of the total variation. Variables with the highest standardized scoring coefficients on the first principal component of the meristic data in decreasing order are tooth rows lower jaw (0.50), tooth rows upper jaw (0.46), and dorsal spines (-0.42).

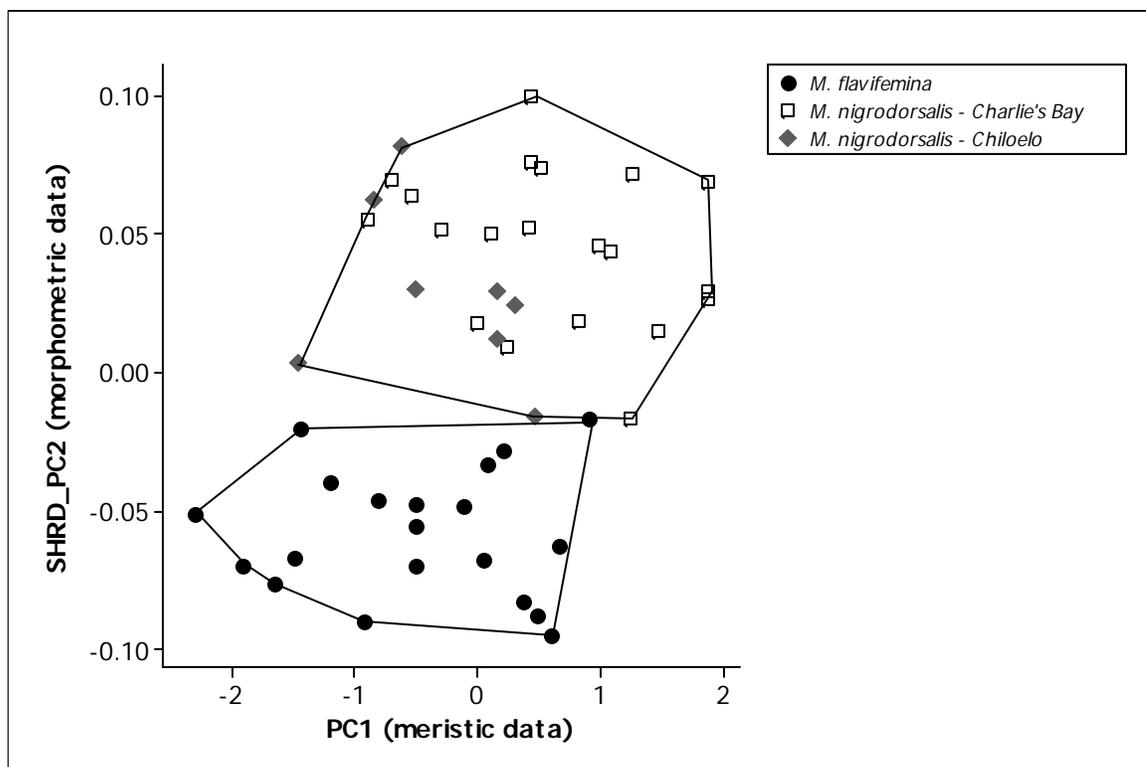


Figure 4.25: Plot of the first principal component of the meristic data (PC1) and the second sheared principal component of the morphometric data (SHRD_PC2) of *M. nigrodorsalis* from Charlie's Bay (N= 20; PSU 4906) and Chiloelo (N=8; PSU 4909) and *M. flavifemina* from Maleri Island, Malaŵi (N = 20).

Chapter 5

Dichotomous Key to the Species of *Metriaclima*

Species of *Metriaclima* are endemic to Lake Malaŵi, Africa. The pigmentation patterns of individuals can vary in all species. To indicate such variations, a slash is placed between the two colors between which the specific pattern varies (e.g., orange/red is used to indicate that the color ranges from orange to red and may include intermediate shades). Pigmentation patterns and coloration based on fresh specimens. This key is not useful for preserved specimens.

1. (a) Females beige to yellow with yellow pigment in anal fin..... 2
(b) Females brown, dark gray or blue without yellow anal fin..... 9
2. (a) Males with black markings in dorsal fin..... 3
(b) Males without black markings in dorsal..... 5
3. (a) Males with yellow pigment on cheek and breast..... 4
(b) Males without yellow pigment on cheek and breast..... *M. phaeos*
4. (a) Cheek depth less than 25% body depth (20.3–24.8 %BD)..... *M. flavifemina*
(b) Cheek depth more than 25% body depth (25.3–32.0 %BD)..... *M. nigrodorsalis*
5. (a) Six or fewer bars below dorsal fin..... *M. aurora*
(b) Seven or more bars below dorsal fin..... 6
6. (a) Males with distinct lateral bars..... *M. hajomaylandi*
(b) Males without distinct lateral bars..... 7
7. (a) Males with yellow nape..... *M. barlowi*
(b) Males with blue nape..... 8
8. (a) Males with distinct interorbital bar..... *M. benetos*
(b) Males without distinct interorbital bar..... *M. chrysomallos*
9. (a) Females light blue or white..... 10
(b) Females brown to blue-gray..... 11
10. (a) Females with distinct bars..... *M. lombardoi*
(b) Females without distinct bars..... *M. callainos*
11. (a) Males without distinct bars..... 12
(b) Males with distinct bars..... 16
12. (a) Males with orange to red pigment in dorsal fin..... 13
(b) Males with blue dorsal..... 14

13. (a) Males with yellow pectoral fin *M. mbenjii*
 (b) Males with clear pectoral fin *M. greshakei*
14. (a) Males with yellow gular *M. xanstomachus*
 (b) Males with white gular 15
15. (a) Females light brown *M. zebra* (part)
 (b) Females dark gray-blue *M. estherae*
16. (a) Five or fewer bars below dorsal fin *M. lanisticola*
 (b) Six or more bars below dorsal fin 17
17. (a) Males with orange to red pigment in dorsal fin 18
 (b) Males with blue dorsal fin 22
18. (a) Anal fin same orange color as dorsal *M. cyneusmarginatus* (part)
 (b) Anal fin blue 19
19. (a) Black submarginal band in anal fin 20
 (b) No black band in anal 21
20. (a) Distance between snout and pelvic-fin origin more than 35 %SL *M. pambazuko*
 (b) Distance between snout and pelvic-fin origin less than 33 %SL *M. emmitos*
21. (a) Base of pectoral fin in males yellow *M. fainzilberi* (part)
 (b) Base of pectoral in males white to blue *M. pyrsonotos*
22. (a) Anal fin black and black streaks in tail fin *M. lundoensis*
 (b) Anal fin blue and no black streaks in tail 23
23. (a) Base of pectoral fin in males yellow *M. fainzilberi* (part)
 (b) Base of pectoral in males white to blue 24
24. (a) Males without black submarginal band in dorsal fin 25
 (b) Males with black submarginal band in dorsal fin 27
25. (a) Males without extension of lateral bars onto dorsal fin 26
 (b) Males with extension of lateral bars onto dorsal fin *M. tarakiki*
26. (a) Fewer than 6 rows of teeth in lower jaw *M. zebra* (part)
 (b) More than 6 rows of teeth in lower jaw *M. midomo*
27. (a) Males with black pigment in anal fin *M. zebra* (part)
 (b) Males without black pigment in anal fin *M. cyneusmarginatus* (part)

Literature Cited

- Albertson, R.C., J.A. Markert, P.D. Danley, and T.D. Kocher. 1999. Phylogeny of a rapidly evolving clade: the cichlid fishes of Lake Malaŵi, East Africa. *Proc. Natl. Acad. Sci.* 96:5107-5110.
- Allender, C.J., O. Seehausen, M.E. Knight, G.F. Tuner and N. Maclean. 2003. Divergent selection during speciation of Lake Malaŵi cichlid fishes inferred from parallel radiations in nuptial coloration. *Proceedings of the National Academy of Sciences.* 100(24):14074-14079.
- Anderson-Morshead, A. E. M. 1897. The history of the Universities' Mission to Central Africa, 1859-1909. Published in 1897, Office of the Universities' Mission to Central Africa (London). 474pp.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, New Jersey. 624pp.
- Arnegard, M.E., J.A. Markert, P.D. Danley, J.R. Stauffer, Jr., A.J. Ambali, and T.D. Kocher. 1999. Population structure and colour variation of the cichlid fish *Labeotropheus fuelleborni* Ahl along a recently formed archipelago of rocky habitat patches in southern Lake Malaŵi. *Proceedings of the Royal Society, London (Series B)*. 266:119-130.
- Barel, C.D.N., M.J. P. van Oijen, F. Witte, and E.L.M. Witte-Maas. 1977. An introduction to the taxonomy and morphology of the haplochromine Cichlidae from Lake Victoria. *Netherlands Journal of Zoology*. 27:333-389.
- Barlow. 1974. Contrast in social behavior between Central American cichlid fishes and coral reef surgeon fishes. *American Zoologist*. 14:9-34.
- Barlow, G.W. 1981. Patterns of parental investment, dispersal and size among coral-reef fishes. *Environmental Biology of Fishes*. 6:65-85.
- Barlow, G.W. 1991. Mating systems among cichlid fishes, p. 173-190. In: *Cichlid Fishes: Behaviour, Ecology and Evolution*. M.H.A. Keenleyside (ed.). Chapman and Hall, New York.
- Barlow, G.W. 2000. *Cichlid Fishes. Nature's Grand Experiment in Evolution*. Perseus Books, Cambridge, 334pp.
- Bookstein, F., B. Chernoff, R. Elder, J. Humphries, G. Smith, and R. Strauss. 1985. *Morphometrics in evolutionary biology: the geometry of size and shape change, with examples from fishes*. The Academy of Natural Sciences of Philadelphia, Philadelphia, 277pp.

- Boulenger, G.A. 1899. A revision of the African and Syrian fishes of the family Cichlidae..-Part II. Proceedings of the Zoological Society of London. 1899:98-143.
- Bowers, N.J. and J.R. Stauffer, Jr. 1993. A new species of rock-dwelling cichlid (Pisces: Cichlidae) from Lake Malaŵi, Africa, with comments on *Melanochromis vermicorus* Trewavas. Copeia. 11993:715-722.
- Crapon de Caprona, M.D. 1986. Are preferences and tolerances in cichlid mate choice important for speciation? Journal of fish biology. 29(a):151-158.
- Danley, P.D., and T.D. Kocher. 2001. Speciation in rapidly diverging systems: Lessons from Lake Malaŵi. Molecular Ecology. 10(5):1075-1086.
- Danley, P.D., J.A. Markert, M.E. Arnegard, and T.D. Kocher. 2000. Divergence with gene flow in the rock-dwelling cichlids of Lake Malaŵi. Evolution. 54(5):1725-1737.
- Dayrat, B. 2005. Towards integrative taxonomy. Biological Journal of the Linnean Society. 85(3):407-415.
- Delvaux, D. 1995. Age of Lake Malaŵi (Nyasa) and water level fluctuations. Musée royal de l'Afrique Centrale (Tervuren), Département de Géologie et Minéralogie, rapport annuel. 1995-1996:99-108.
- Ebinger, C.J, A.L. Deino, A.L. Tesha, T. Becker, and U. Ring. 1993. Tectonic controls on rift basin morphology - evolution of the Northern Malaŵi (Nyasa) Rift. J Geophys Res. 98:17821-17836.
- Fink, W.L., and M. L. Zelditch. 1995. Phylogenetic analysis of ontogenetic shape transformations: a reassessment of the piranha genus *Pygocentrus* (Teleostei). Systematic Biology. 44(3):343-360.
- Frost, D.R. and A.G. Kluge. 1994. A consideration of epistemology in systematic biology, with special reference to species. Cladistics. 10:259-294.
- Fryer, G. 1959. The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with especial reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. Proceedings of the Zoological Society of London. 132:153-281.
- Fryer, G., and T.D. Iles. 1972. The cichlid fishes of the Great Lakes of Africa. Oliver & Boyd, Edinburgh, 64pp.
- Genner, M.J., and G.F. Turner. 2005. The mbuna cichlids of Lake Malaŵi: A model for rapid speciation and adaptive radiation. Fish and Fisheries. 6(1):1-34.
- Genner, M.J., G.F. Turner, and S.J. Hawks. 1999. Niche segregation among Lake Malaŵi cichlid fishes? Evidence from stable isotope signatures. Ecology Letters 2:185-190.

- Genner, M.J., O. Seehausen, D.F.R. Cleary, M.E. Knight, E. Michel, and G.F. Turner. 2004. How does the taxonomic status of allopatric populations influence species richness within African cichlid fish assemblages? *Journal of Biogeography*. 31:93-102.
- Genner, M.J, A. Botha, and G.F. Turner. 2006. Translocations of rocky habitat cichlid fishes to Nkhata Bay, Lake Malaŵi. *Journal of Fish Biology*. 69(2):622-628.
- Ghiselin, M.T. 1969. The evolution of hermaphroditism among animals. *Quarterly Review of Biology*. 44:189-208.
- Ghiselin, M.T. 1974. A radical solution to the species problem. *Systematic Zoology*. 23:536-544.
- Ghiselin, M.T. 2002. Species Concept: the basis for controversy and reconciliation. *Fish and Fisheries* 3:151-160.
- Greenwood, P.H. 1974. The cichlid fishes of Lake Victoria, East Africa: The biology and evolution of a species flock. *Bulletin of the British Museum (Natural History), Zoology*, Supplement 6, 134pp.
- Greenwood, P.H. 1984. African cichlids and evolutionary theories. In: *Evolution of fish species flocks* (eds. A. A. Echelle and I. Kornfield), pp. 141-154. University of Maine at Orono Press, Orono, Maine.
- Hert, E. 1991. Female choice based on egg-spots in *Pseudotropheus aurora* Urgess 1976, a rock-dwelling cichlid of Lake Malaŵi, Africa. *Journal of Fish Biology*. 38:951-953.
- Holzberg, S. 1978. A field and laboratory study of the behaviour and ecology of *Pseudotropheus zebra* (Boulenger), an endemic cichlid of Lake Malaŵi (Pisces: Cichlidae). *Zeitschrift für zoologische Systematik und Evolutionsforschung*. 16:171-187.
- Humphries, J.M., F.L. Bookstein, B. Chernoff, G.R. Smith, R.L. Elder, and S.G. Poss. 1981. Multivariate discrimination by shape in relation to size. *Systematic Zoology*. 30(3):291-308.
- Jordan, R., D. Howe, K. Kellogg, F. Juanes, J.R. Stauffer Jr., and E. Garcia-Vazquez. 2007. *Afr. J. Ecol.* 46: 107-109.
- Kassam, D., S. Mizoiri, and K. Yamaoka. 2004. Interspecific variation of body shape and sexual dimorphism in three coexisting species of the genus *Petrotilapia* (Teleostei: Cichlidae) from Lake Malaŵi. *Ichthyological Research*. 51:195-201.
- Kellogg, K.A., J.R. Stauffer Jr., and K.R. McKaye. 2000. Characteristics that influence male reproductive success on a lek of *Lethrinops c.f. parvidens* (Teleostei: Cichlidae). *Behav. Ecol. Sociobiol.* 47:164-170.
- Kidd, M.R., P.D. Danley, and T. D. Kocher. 2006. A direct assay of female choice in cichlids: all the eggs in one basket. *Journal of Fish Biology* 68:373-384.

- Knight, M.E., and G.F. Turner. 1999. Reproductive isolation among closely related Lake Malaŵi cichlids: Can males recognize conspecific females by visual cues? *Animal Behaviour*. 58:761-768.
- Knight, M.E., and G.F. Turner. 2004. Laboratory mating trials indicate incipient speciation by sexual selection among populations of the cichlid fish *Pseudotropheus zebra* from Lake Malaŵi. *Proceedings of the Royal Society, London (Series B)*. 271(1540):675-680.
- Konings, A. 1995. Malaŵi cichlids in their natural habitat. Second edition. Cichlid Press, El Paso, Texas, 303pp.
- Konings, A. 1999. Comments on the revision of *Pseudotropheus zebra*, *Cichlid News*, vol. 8(1):18-26.
- Konings, A. 2001. Malaŵi cichlids in their natural habitat. Third edition. Cichlid Press, El Paso, Texas, 352pp.
- Konings, A. 2007. Malaŵi cichlids in their natural habitat. Fourth edition. Cichlid Press, El Paso, Texas, 424pp.
- Konings A. and M. Geerts. 1999. Comments on the revision of *Pseudotropheus zebra*. *Cichlid News*, January:18-26.
- Konings, A.F., and J.R. Stauffer, Jr. 2006. Revised diagnosis of *Metriaclima* (Teleostei: Cichlidae) with description of a new species from Lake Malaŵi National Park, Africa. *Ichthyological Exploration of Freshwaters*. 17(3):233-246.
- Kornfield, I.L. 1978. Evidence for rapid speciation in African cichlid fishes. *Experientia*. 34:335-336.
- Kornfield, I. 1984. Descriptive genetics of cichlid fishes. In: *Evolutionary Genetics of Fishes* (ed. B.J. Turner), pp. 591-616. Plenum Publishing Corp., New York.
- Kornfield, I. 1991. Genetics. In: *Cichlid fishes. Behaviour, ecology and evolution* (ed. M.H.A. Keenleyside), pp. 103-128. Chapman & Hall, London.
- Kornfield, I., and A. Parker. 1997. Molecular systematics of a rapidly evolving species flock: the mbuna of Lake Malaŵi and the search for phylogenetic signal. In: *Molecular Systematics of Fishes*. (eds. T. Kocher and C. Stepien), pp. 25-37. Academic Press, San Diego.
- Kornfield, I. and P.F. Smith. 2000. African cichlid fishes: model systems for evolutionary biology. *Annual Reviews in Ecology and Systematics*. 31:163-196.
- Kornfield, I., K.R. McKaye, and T. Kocher. 1985. Evidence for the immigration hypothesis in the endemic cichlid fauna of Lake Tanganyika. *Isozyme Bulletin*. 18:76.
- Lewis, D.S.C. 1982. Problems of species definition in Lake Malaŵi cichlid fishes (Pisces: Cichlidae). *Special Publications of the J.L.B. Smith Institute of Ichthyology*. 23:1-5.

- Lewis, D.S.C., P.N. Reinthal, and J. Trendall. 1986. A guide to the fishes of Lake Malaŵi National Park. Creda Press, for World Wildlife Fund, Gland, Switzerland. 71pp.
- Markert, J.A., M.E. Arnegard, P.D. Danley, and T.D. Kocher. 1999. Biogeography and population genetics of the Lake Malaŵi cichlid *Melanochromis auratus*: habitat transience, philopatry and speciation. *Molecular Ecology*. 8:1013-1026.
- Marsh, A.C. 1983. A taxonomic study of the fish genus *Petrotilapia* (Pisces: Cichlidae) from Lake Malaŵi. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology*, Number 48:1-14.
- Marsh, A.C., A.J. Ribbink, and B.A. Marsh. 1981. Sibling species complexes in sympatric populations of *Petrotilapia trewavas* (Cichlidae, Lake Malaŵi). *Zoological Journal of the Linnean Society*. 71:253-264.
- Mayden, R.L. 1997. A hierarchy of species concepts: the denouement of the species problem. In: *The Units of Biodiversity – Species in Practice*. Special Vol.54. (eds. M.F. Claridge, H.A. Dawah, and M.R. Wilson), pp. 381-424. Systematics Association, Chapman and Hall Ltd, London.
- Mayden, R.L. 2002. On biological species, species concepts and individuation in the natural world. *Fish and Fisheries* 3:171-196.
- Mayr, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York. 334pp.
- Mayr, E. 1986. Uncertainty in science: Is the giant panda a bear or raccoon? *Nature*. 232:769-771
- Mayr, E. and Ashlock, P. 1991. *Principles of systematic zoology*. Second Edition. McGraw –Hill, New York, 475pp.
- McElroy, D.M., and I. Kornfield. 1990. Sexual selection, reproductive behavior, and speciation in the mbuna species flock of Lake Malaŵi (Pisces: Cichlidae). *Environmental Biology of Fishes*. 28: 273-284.
- McKaye, K.R., and J.R. Stauffer, Jr. 1986. Description of a gold cichlid (Teleostei: Cichlidae) from Lake Malaŵi, Africa. *Copeia*. 1986(4):870-875.
- McKaye, K.R., T. Kocher, P. Reinthal, R. Harrison, and I. Kornfield. 1984. Genetic evidence for allopatric and sympatric differentiation among morphs of a Lake Malaŵi cichlid fish. *Evolution*. 38: 215-219.
- Meyer, A. 1993. Phylogenetic relationships and evolutionary processes in East African cichlid fishes. *Trends in Ecology and Evolution*. 8(8):279-284.
- 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 Française d'Aquariologie et de Herpetologie*. 10(4):107-112.

- Meyer, A., T.D. Kocher, P. Basasibwaki, and A.C. Wilson. 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. *Nature*. 347:550-553.
- Moran, P., and I. Kornfield. 1993. Retention of an ancestral polymorphism in the mbuna species flock (Teleostei: Cichlidae) of Lake Malaŵi. *Molecular Biology and Evolution*. 10(5):1015-1029.
- Moran, P., and I. Kornfield. 1995. Were population bottlenecks associated with the radiation of the mbuna species flock (Teleostei: Cichlidae) in Lake Malaŵi? *Molecular Biology and Evolution*. 12(6):1085-1093.
- Moran, P., I. Kornfield, and P. Reinthal. 1994. Molecular systematics and radiation of the haplochromine cichlids (Teleostei: Perciformes) of Lake Malaŵi. *Copeia*. 1994:274-288.
- Nelissen MHJ (1992) Does body size affect the ranking of a cichlid fish in a dominance hierarchy? *J Ethol* 10:153–156.
- Oppen, M.J.H, G.F. Turner, C. Rico, R.L. Robinson, J.C. Deutsch, M.J. Genner, and G.M Hewitt. 1998. Assortative mating among rock-dwelling cichlid fishes supports high estimates of species richness from Lake Malaŵi. *Molecular Ecology* 7:991-1001.
- Owen, R.B., R. Crossley, T.C. Johnson, D. Tweddle, I. Kornfield, S. Davison, D.H. Eccles, and D.E. Engstrom. 1990. Major low levels of Lake Malaŵi and their implications for speciation rates in cichlid fishes. *Proceedings of the Royal Society, London*. 240:519-553.
- Pauers M.J, McKinnon J.S, Ehlinger T.J. 2004. Directional sexual selection on chroma and within-pattern colour contrast in *Labeotropheus fuelleborni*. *Proc. R. Soc. B*. 271(Suppl. 6):S444–S447.
- Pauers, M.J., Kapfer, J.M., Fendos, C.E., Berg, C.S. 2008. Aggressive biases towards similarly coloured males in Lake Malaŵi cichlid fishes. *Biol Lett*. 2008 Apr 23;4(2):156-9.
- Paterson, H.E.H., 1978. More evidence against speciation by reinforcement. *South African Journal of Science*. 74:369-371.
- Peterson, A.T. and A.G. Navarro-Sigüenza. 1999. Alternative species concepts as bases for determining priority conservation areas. *Conservation Biology*. 13(2):427-431.
- Plenderleith, M., C. van Oosterhout, R.L. Robinson, and G.F. Turner. 2005. Female preference for conspecific males based on olfactory cues in a Lake Malaŵi cichlid fish. *Biology Letters*. 1: 411-414.
- Regan, C.T. 1922. The cichlid fishes of Lake Nyasa. *Proceedings of the Zoological Society of London*. 1921:675-727.
- Reinthal, P. 1993. Evaluating biodiversity and conserving Lake Malaŵi cichlid fish fauna. *Conservation Biology* 7(3):712-718.

- Reyment, R.A., R.E. Blackith, and N.A. Campbell. 1984. Multivariate morphometrics. Second Edition. Academic Press, London, 412pp.
- Ribbink, A.J. 1986. The species concept, sibling species and speciation. In: Proceedings of the 3rd European Workshop on Cichlid Biology, Bielefeld, West Germany, 5-8 February 1986 (eds. M.D. Crapon de Caprona and B. Fritzsch), pp. 109-116. Annales de la Musée royal de l'Afrique Centrale, Sciences Zoologiques.
- 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 rocky habitats in Lake Malaŵi. South African Journal of Zoology. 18:149-310.
- Seehausen, O. 1996. Lake Victoria Rock Cichlids – Taxonomy, Ecology and Distribution. Zevenhuizen, Netherlands: Verduijn Cichlids. 304pp.
- Seehausen, O., and J.M. van Alphen. 1999. Can sympatric speciation by disruptive sexual selection explain rapid evolution of cichlid diversity in Lake Victoria? Ecology Letters. 2(4):262-271.
- Seehausen, O., P.J. Mayhew, and J.J.M. van Alphen. 1999. Evolution in colour patterns in East African cichlid fish. Journal of Evolutionary Biology. 12(1999):514-534.
- Simpson, G.G. 1961. Principles of animal taxonomy. Columbia University Press, New York, 247pp.
- Smith, P.F., and I. Kornfield. 2002. Phylogeography of Lake Malaŵi cichlids of the genus *Pseudotropheus*: significance of allopatric colour variation. Proceedings of the Royal Society, London (Series B). 269(1509):2495-2502.
- Smith, P.F., A. Konings, and I. Kornfield. 2003. Hybrid origin of a cichlid population in Lake Malaŵi: Implications for genetic variation and species diversity. Molecular Ecology. 12(9):2497-2504.
- Snoeks, J. 2000. How well known is the ichthyodiversity of the ancient African lakes? In: Ancient lakes: Biodiversity ecology and evolution. Advances in Ecological Research, Volume 31 (eds. Rossiter, A., and H. Kawanabe), pp. 17-38. Academic Press, London.
- Stauffer, J.R., Jr., and J.M. Boltz. 1989. Description of a rock-dwelling cichlid (Teleostei: Cichlidae) from Lake Malaŵi, Africa. Proceedings of the Biological Society of Washington. 102:8-13.
- Stauffer, J.R., Jr., and E. Hert. 1992. *Pseudotropheus callainos*, a new species of mbuna (Cichlidae), with analysis of changes associated with two intra-lacustrine transplantations in Lake Malaŵi, Africa. Ichthyological Exploration of Freshwaters. 3(3):253-264.
- Stauffer, J.R. Jr., and K.R. McKaye. 2001. The naming of cichlids. Journal of aquaculture and Aquatic Sciences: Cichlid Research: State of the Art. 9: 1-16.

- Stauffer, J.R., Jr. and K.A. Kellogg. 2002. Description of a new species in the *Pseudotropheus williamsi* complex (Teleostei: Cichlidae), from Lake Malaŵi, Africa. *Copeia*. 2002(1):146-151.
- Stauffer, J.R., Jr. and Isa Posner. 2006. An Investigation of the Utility of Feeding Angles Among Lake Malaŵi Rock-dwelling Cichlids (Teleostei: Cichlidae). *Copeia*. 2006(2):289-292.
- Stauffer, J.R., Jr., T.J. LoVullo, and K.R. McKaye. 1993. Three new sand-dwelling cichlids from Lake Malaŵi, Africa, with a discussion on the status of the genus *Copadichromis* (Teleostei: Cichlidae). *Copeia*. 1993(4):1017-1027.
- Stauffer, J.R., Jr., N.J. Bowers, K.R. McKaye, and T.D. Kocher. 1995. Evolutionary significant units among cichlid fishes: The role of behavior in studies. *American Fisheries Society Symposium*. 17:227-244.
- Stauffer, J.R., Jr., N.J. Bowers, K.A. Kellogg, and K.R. McKaye. 1997. 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. *Proceedings of the Academy of Natural Sciences of Philadelphia*. 148:189-230.
- Stauffer, J.R. Jr, P.M. Kocovsky, and R.A. Ruffing. 2002a. Species concepts and speciation of fishes: concluding remarks. *Fish and Fisheries* 3:230-232.
- Stauffer, J.R., Jr., K.R. McKaye, A.F. Konings. 2002b. Behaviour: an important diagnostic tool for Lake Malaŵi cichlids. *Fish and Fisheries*. 3(3):213-224.
- Stauffer, J.R., K.A. Kellogg, and K.R. McKaye. 2005. Experimental evidence of female choice in Lake Malaŵi cichlids. *Copeia*: 657-660.
- Stauffer, J.R., Jr., K.E. Black, M. Geert, A.F. Konings, and K.R. McKaye. 2006. Cichlid Fish Diversity and Speciation. In: *Reconstructing the Tree of Life: Taxonomy and Systematics of Species Rich Taxa*. (eds. T.R. Hodgkinson and J.A.N. Parnell), pp. 213-226. CRC Press, New York.
- Stiassny, M.L.J. 1991. Phylogenetic intrarelationships of the family Cichlidae: and overview. In: *Cichlid Fishes: Behavior, Ecology, and Evolution* (ed. M.H.A. Keenleyside), pp. 1-35. Chapman & Hall, New York.
- Stiassny, M.L. 1996. An Overview of Freshwater Biodiversity: With Some Lessons from African Fishes. *Fisheries*. 21(9):7-13.
- Sturmbauer, C., S. Baric, W. Salzburger, L. Rüber, and E. Verheyen. 2001. Lake level fluctuations synchronize genetic divergences of cichlid fishes in African Lakes. *Molecular Biology and Evolution*. 18:144-154.
- Takahashi, K., M. Nishida, M. Yuma, and N. Okada. 2001. Retroposition of the AFC family of SINEs (short interspersed repetitive elements) before and during the adaptive radiation of cichlid fishes in Lake Malaŵi and related inferences about phylogeny. *Journal of Molecular Evolution*. 53(4-5):496-507.

- Trewavas, E. 1935. A synopsis of the cichlid fishes of Lake Nyasa. *Annals and Magazine of Natural History*. (10)16:65-118.
- Trewavas, E. 1984. Nouvel examen des genres et sous-genres du complexe *Pseudotropheus-Melanochromis* du lac Malaŵi (Pisces, Perciformes, Cichlidae). *Revue Française d'Aquariologie et de Herpetologie*. 10(4)1983:97-106.
- Turner, G. F. 1996. Offshore cichlids of Lake Malaŵi. Cichlid Press, Lauenau, Germany; 240pp.
- Turner, G.F. 2000. The nature of species in ancient lakes: Perspectives from the fishes of Lake Malaŵi. In: *Ancient lakes: Biodiversity, ecology and evolution. Advances in Ecological Research*, volume 31 (eds. A. Rossiter and H. Kawanabe), pp. 39-60. Academic Press, London.
- Turner, G.F., and M.T. Burrows. 1995. A model of sympatric speciation by sexual selection. *Proceedings of the Royal Society, London (Series B)*. 260(1359):287-292.
- Turner, G.F., O. Seehausen, M.E. Knight, C.J. Allender, and R.L. Robinson. 2001. How many species of cichlid fishes are there in African lakes? *Molecular Ecology*. 10(3):793-806.
- van Doorn, G. S., A. J. Noest, and P. Hogeweg. 1998. Sympatric speciation and extinction driven by environment dependent sexual selection. *Proceedings of the Royal Society of London B*. 265:1915-1919.
- van Oppen, M.J.H., C. Rico, J.C. Deutsch, G.F. Turner, and G.M. Hewitt. 1997. Isolation and characterization of microsatellite loci in the cichlid fish *Pseudotropheus zebra*. *Molecular Ecology*. 6(4):387-388.
- van Oppen, M.J.H., G.F. Turner, C. Rico, R.L. Robinson, J.C. Deutsch, M.J. Genner, and G.M. Hewitt. 1998. Assortative mating among rock-dwelling cichlid fishes supports high estimates of species richness from Lake Malaŵi. *Molecular Ecology*. 7:991-1001.
- Wickler, W. 1962. 'Egg-dummies' as natural releasers in mouth-breeding cichlids. *Nature*. 194:1092-1094.
- Wiley, E.O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology*. 27(1):17-26.
- Wiley, E.O. 2002. On species and speciation with reference to the fishes. *Fish and Fisheries* 3:161-170.
- Zink, R.M., and M.C. McKittrick. 1995. The debate over species concepts and its implications for ornithology. *Auk*. 112:701-719.

Appendix A: Collections Examined. Accession number refers to the location of the collection housed in The Pennsylvania State University Fish Museum (PSUFM). Three collections are on loan from the Natural History Museum (London; BMNH).

Accession	Genus	species	Location	Date	Collectors	Lat Long	# Examined
170	<i>Metriaclima</i>	<i>zebra</i>	Pombo Rocks, Tanzania				20
171	<i>Metriaclima</i>	<i>fainzilberi</i>	Hongi Island, Tanzania	January 28, 2004	Konings & Stauffer	S 10°39.720' E 34°38.380'	20
172	<i>Metriaclima</i>	<i>pambazuko</i>	Hongi Island, Tanzania	January 18, 2004	Konings & Stauffer	S 11°08.0827' E 34°38.792'	19
173	<i>Metriaclima</i>	<i>pambazuko</i>	Lundo Island, Tanzania	January 29, 2004	Konings & Stauffer	S 11°13.438' E 34°44.076'	20
176	<i>Metriaclima</i>	<i>zebra</i>	Thumbi, Tanzania	January 27, 2004	Konings & Stauffer	S 11°01.702' E 34°36.700'	20
177	<i>Metriaclima</i>	<i>lundoensis</i>	Lundo Island, Tanzania	January 29, 2004	Konings & Stauffer	S 11°13.438' E 34°44.076'	20
189	<i>Cynotilapia</i>	<i>afra</i>	Ngkuyo Island, Tanzania	January 29, 2004	Konings & Stauffer	S 11°19.184' E 34°46.074'	9
203	<i>Metriaclima</i>	<i>zebra</i>	Hongi Island, Tanzania	January 28, 2004	Konings & Stauffer	S 11°08.0827' E 34°38.792'	3
219	<i>Metriaclima</i>	<i>zebra</i>	Chiwindi, Mozambique	January 30, 2004	Konings & Stauffer	S 11°35.007' E 34°57.882'	17
261	<i>Metriaclima</i>	<i>zebra</i>	Taiwane Reef, Malawi	January 31, 2004	Konings & Stauffer	S 11°57.459' E 34°35.272'	20
271	<i>Metriaclima</i>	<i>tarakiki</i>	Ngkuyo Island, Tanzania	January 29, 2004	Konings & Stauffer	S 11°19.184' E 34°46.074'	20
288	<i>Metriaclima</i>	<i>tarakiki</i>	Higga Reef, Tanzania	February 13, 2005	Konings, Stauffer & Kocher	S 11°18.380' E 34°44.791'	12
293	<i>Metriaclima</i>	<i>fainzilberi</i>	south of Lupingu, Tanzania	February 9, 2005	Konings, Stauffer & Kocher	S 10°05.668' E 34°32.161'	10
429	<i>Metriaclima</i>	<i>zebra</i>	Mainango Island off Likoma Is., Malawi	February 14, 2005	Konings, Stauffer & Kocher	S 12°02.621' E 34°45.366'	3
432	<i>Metriaclima</i>	"zebra blaze"	Makonde, Tanzania	February 24, 2005	Konings, Stauffer & Kocher	S 9°56.882' E 34°27.297'	20
458	<i>Metriaclima</i>	<i>zebra</i>	Nkhata Bay, Malawi	February 1, 1994	Stauffer	S 11°36.465' E 34°17.999'	10
517	<i>Metriaclima</i>	<i>zebra</i>	Mbembe Point, Likoma Is., Malawi	February 3, 2005	Konings, Stauffer & Kocher	S 12°03.514' E 34°45.148'	5
527	<i>Metriaclima</i>	<i>zebra</i>	Membe Island off Chizumulu Is., Malawi	February 3, 2005	Konings, Stauffer & Kocher	S 12°02.964' E 34°36.764'	20
529	<i>Metriaclima</i>	<i>zebra</i>	Sanga Rocks, Tanzania	February 5, 2005	Konings, Stauffer & Kocher	S 9°30.456' E 34°03.148'	20
631	<i>Metriaclima</i>	<i>zebra</i>	Chiwi Rocks off Chizumulu Is., Malawi	February 3, 2005	Konings, Stauffer & Kocher	S 12°02.327' E 34°36.607'	20
670	<i>Metriaclima</i>	<i>fainzilberi</i>	Lumbaulo, Mozambique	February 19, 2002	Konings & Stauffer	S 11°54.024' E 34°54.307'	10
672	<i>Metriaclima</i>	<i>zebra</i>	Tumbi Point, Mozambique	February 17, 2002	Konings & Stauffer	S 12°20.297' E 34°41.853'	20
677	<i>Metriaclima</i>	<i>zebra</i>	N'kolongwe, Mozambique	February 16, 2002	Konings & Stauffer	S 12°47.671' E 34°47.159'	16
678	<i>Metriaclima</i>	<i>zebra</i>	Mkanila Bay, Chizumulu Is., Malawi	February 20, 2002	Konings & Stauffer	S 12°00.566' E 34°36.828'	20
679	<i>Metriaclima</i>	"zebra bevous"	Mkanila Bay, Chizumulu Is., Malawi	February 20, 2002	Konings & Stauffer	S 12°00.566' E 34°36.828'	10
684	<i>Metriaclima</i>	<i>zebra</i>	Mala Point, Mozambique	February 17, 2002	Konings & Stauffer	S 12°11.254' E 34°41.968'	19
685	<i>Metriaclima</i>	<i>zebra</i>	Lumessi, Mozambique	February 12, 2002	Konings & Stauffer	S 13 08.196' E 34°47.844'	20
686	<i>Metriaclima</i>	<i>zebra</i>	Gome Rock, Malawi	February 12, 2002	Konings & Stauffer	S 13 30.744' E 34°52.021'	20
691	<i>Metriaclima</i>	<i>zebra</i>	Lumbaulo, Mozambique	February 19, 2002	Konings & Stauffer	S 11°54.024' E 34°54.307'	20
693	<i>Metriaclima</i>	<i>zebra</i>	Membe Island off Chizumulu Is., Malawi	February 20, 2002	Konings & Stauffer	S 12°02.947' E 34°36.930'	20
695	<i>Metriaclima</i>	<i>zebra</i>	Cobwe, Mozambique	February 18, 2002	Konings & Stauffer	S 12°08.243' E 34°45.391'	20
698	<i>Metriaclima</i>	<i>nigrodorsalis</i>	Charlie's Bay, Mozambique	February 13, 2002	Konings & Stauffer	S 13 22.262' E 34°50.075'	20
699	<i>Metriaclima</i>	<i>zebra</i>	Nkhungu Point, Mozambique	February 15, 2002	Konings & Stauffer	S 12°58.801' E 34°45.807'	20
700	<i>Metriaclima</i>	<i>hajomaylandi</i>	Mkanila Bay, Chizumulu Is., Malawi	February 20, 2002	Konings & Stauffer	S 12°00.566' E 34°36.828'	10
711	<i>Metriaclima</i>	<i>nigrodorsalis</i>	Nkhungu Point, Mozambique	February 15, 2002	Konings & Stauffer	S 12°58.801' E 34°45.807'	20
824	<i>Metriaclima</i>	"zebra Chilumba"	Mpanga Rocks, Chilumba, Malawi	May 1, 1991	Stauffer	S 10°25.895' E 34°16.723'	14
843	<i>Metriaclima</i>	<i>zebra</i>	Nkhata Bay, Malawi	May 1, 1991	Stauffer	S 11°36.465' E 34°17.999'	4
870	<i>Metriaclima</i>	<i>zebra</i>	Mainango Island off Likoma Is., Malawi	October 15, 2004	Konings & Stauffer	S 12°02.818' E 34°45.457'	13
939	<i>Metriaclima</i>	<i>zebra</i>	Nkhata Bay, Malawi	February 15, 1993	Stauffer & Amos	S 11°36.465' E 34°17.999'	6
942	<i>Metriaclima</i>	<i>zebra</i>	Mbaka Beach, Likoma Is., Malawi	February 17, 1993	Barnabus	S 12°02.356' E 34°44.867'	12
972	<i>Metriaclima</i>	"zebra greberi"	Chizumulu Island, Malawi	March 1, 1991	Stauffer	S 12°01.388' E 34°37.793'	10
1090	<i>Metriaclima</i>	<i>zebra</i>	Jala Reef, Lake Malawi	January 19, 2003	Konings & Stauffer	S 12°51.893' E 34°20.219'	20
1097	<i>Metriaclima</i>	<i>nigrodorsalis</i>	Thundu, Mozambique	February 15, 2002	Konings & Stauffer	S 13 00.685' E 34°46.554'	20
1102	<i>Metriaclima</i>	"aggressive red fin"	Same Bay, Chizumulu Is., Malawi	February 20, 2002	Konings & Stauffer	S 12°01.388' E 34°37.793'	10
1115	<i>Metriaclima</i>	<i>nigrodorsalis</i>	N'kolongwe, Mozambique	February 16, 2002	Konings & Stauffer	S 12°47.671' E 34°47.159'	20
1301	<i>Metriaclima</i>	"aggressive yellow fin"	Machili Island off Chizumulu Is., Malawi	October 23, 2005	Konings	S 12°00.842' E 34°36.642'	6

Appendix A: Collections Examined (continued). Accession number refers to the location of the collection housed in The Pennsylvania State University Fish Museum (PSUFM). Three collections are on loan from the Natural History Museum (London; BMNH).

Accession	Genus	species	Location	Date	Collectors	Lat Long	# Examined
1551	<i>Metriaclima</i>	"zebra blaze"	Manda, Tanzania	February 12, 2004	Konings, Stauffer & Kocher	S 10°27.617' E 34°34.357'	20
1751	<i>Metriaclima</i>	<i>nigrodorsalis</i>	Chiloelo, Mozambique	March 1, 2006	Konings & Stauffer	S 13 14.046' E 34°48.718'	8
1753	<i>Cynotilapia</i>	<i>afra</i>	Londo Bay, Mozambique	February 23, 2006	Konings & Stauffer	S 11°49.552' E 34°56.292'	10
1779	<i>Metriaclima</i>	<i>zebra</i>	Mara Point, Mozambique	February 26, 2006	Konings & Stauffer	S 12°11.565' E 34°41.802'	6
1785	<i>Metriaclima</i>	<i>pambazuko</i>	Londo Bay, Mozambique	February 23, 2006	Konings & Stauffer	S 11°49.552' E 34°56.292'	20
1797	<i>Metriaclima</i>	<i>zebra</i>	Londo Bay, Mozambique	February 23, 2006	Konings & Stauffer	S 11°49.552' E 34°56.292'	20
1798	<i>Metriaclima</i>	<i>fainzilberi</i>	Londo Bay, Mozambique	February 23, 2006	Konings & Stauffer	S 11°49.552' E 34°56.292'	10
1867	<i>Metriaclima</i>	<i>midomo</i>	Lundo Island, Tanzania	January 29, 2004	Konings & Stauffer	S 11°08.0827' E 34°38.792'	19
BMNH1976	<i>Metriaclima</i>	<i>fainzilberi</i>	near Makonde, Tanzania	May 29, 1905	Staeck		1
BMNH1891	<i>Metriaclima</i>	<i>zebra</i>	Lake Malawi	1891	M. Woodward		1
BMNH1971	<i>Metriaclima</i>	<i>zebra</i>	Likoma Island, Malawi	May 24, 1905	G. Fryer		1
2060	<i>Metriaclima</i>	<i>zebra</i>	Linganjala Reef, Chizumulu Is., Malawi	August 7, 2006	Konings & Stauffer	S 12°00.386' E 34°35.533'	20
2061	<i>Metriaclima</i>	<i>zebra</i>	Same Bay, Chizumulu Is., Malawi	August 7, 2006	Konings & Stauffer	S 12°01.388 E 3437.793'	11
2073	<i>Metriaclima</i>	"aggressive zebra"	Ndumbi Rocks, Likoma Is., Malawi	November 16, 2006	Konings	S 12°01.614' E 34°44.149'	8
2122	<i>Metriaclima</i>	<i>zebra</i>	Machili Island off Chizumulu Is., Malawi	January 24, 2007	Konings & Stauffer	S 12°00.786' E 34°36.353'	20
2137	<i>Metriaclima</i>	<i>zebra</i>	Nkhata Bay, Malawi	January 23, 2007	Konings & Stauffer	S 11°36.465' E 34°17.999'	20
2143	<i>Metriaclima</i>	"zebra long pelvic"	Mdoka Reef, Malawi	January 18, 2007	Konings & Stauffer	S 10°16.387' E 34°10.756'	20
2144	<i>Metriaclima</i>	"zebra Chilumba"	Luwino Reef, Malawi	January 19, 2007	Konings & Stauffer	S 10°26.873' E 34°16.963'	14
2145	<i>Metriaclima</i>	"zebra Chilumba"	Chitande Island, Malawi	January 12, 2007	Konings & Stauffer	S 10°23.77' E 34°15.250'	20
2146	<i>Metriaclima</i>	"zebra Chilumba"	Mdoka Reef, Malawi	January 18, 2007	Konings & Stauffer	S 10°16.387' E 34°10.756'	20
PSU 3054	<i>Metriaclima</i>	<i>phaeos</i>	Cobwe, Mozambique	March 1, 1996	Grant	S 12°08.243' E 34°45.391'	1
PSU 3055	<i>Metriaclima</i>	<i>phaeos</i>	Cobwe, Mozambique	March 1, 1996	Grant	S 12°08.243' E 34°45.391'	5
PSU 3729	<i>Metriaclima</i>	<i>flavifemina</i>	Maleri Island, Malawi	February 2, 2004	Konings	S 13 53.910' E 34°38.020'	1
PSU 3730	<i>Metriaclima</i>	<i>flavifemina</i>	Maleri Island, Malawi	February 2, 2004	Konings	S 13 53.910' E 34°38.020'	19
3732	<i>Metriaclima</i>	"varicdorsalis"	Thumbi West Island, Malawi	February 6, 2004	Konings & Stauffer	S 14 00.967' E 34°48.641'	3
<i>Total</i>							1006

Appendix B: Collections Described.

PSU #	Coll. ID	Genus	species	Location	Date	Collectors	Lat Long	n
4900	JRS 06-32	<i>Metriaclima</i>	<i>pambazuko</i>	Londo Bay, Mozambique	February 23, 2006	Konings & Stauffer	S 11°49.552' E 34°56.292'	1
4901	JRS 06-32	<i>Metriaclima</i>	<i>pambazuko</i>	Londo Bay, Mozambique	February 23, 2006	Konings & Stauffer	S 11°49.552' E 34°56.292'	19
4902	JRS 04.14	<i>Metriaclima</i>	<i>pambazuko</i>	Hongi Island, Tanzania	January 18, 2004	Konings & Stauffer	S 11°08.0827' E 34°38.792'	20
4903	JRS 04-15	<i>Metriaclima</i>	<i>pambazuko</i>	Lundo Island, Tanzania	January 29, 2004	Konings & Stauffer	S 11°13.438' E 34°44.076'	20
4904	JRS 02-12	<i>Metriaclima</i>	<i>nigrodorsalis</i>	N'kolongwe, Mozambique	February 16, 2002	Konings & Stauffer	S 12°47.671' E 34°47.159'	1
4905	JRS 02-12	<i>Metriaclima</i>	<i>nigrodorsalis</i>	N'kolongwe, Mozambique	February 16, 2002	Konings & Stauffer	S 12°47.671' E 34°47.159'	19
4906	JRS 02-03	<i>Metriaclima</i>	<i>nigrodorsalis</i>	Charlie's Bay, Mozambique	February 13, 2002	Konings & Stauffer	S 13°22.262' E 34°50.075'	20
4907	JRS 02-09	<i>Metriaclima</i>	<i>nigrodorsalis</i>	Nkhungu Point, Mozambique	February 15, 2002	Konings & Stauffer	S 12°58.801' E 34°45.807'	20
4908	JRS 02-08	<i>Metriaclima</i>	<i>nigrodorsalis</i>	Thundu, Mozambique	February 15, 2002	Konings & Stauffer	S 13°00.685' E 34°46.554'	20
4909	JRS 06-45	<i>Metriaclima</i>	<i>nigrodorsalis</i>	Chiloelo, Mozambique	March 1, 2006	Konings & Stauffer	S 13°14.046' E 34°48.718'	8
4910	JRS 04-15	<i>Metriaclima</i>	<i>lundoensis</i>	Lundo Island, Tanzania	January 29, 2004	Konings & Stauffer	S 11°13.438' E 34°44.076'	1
4911	JRS 04-15	<i>Metriaclima</i>	<i>lundoensis</i>	Lundo Island, Tanzania	January 29, 2004	Konings & Stauffer	S 11°13.438' E 34°44.076'	19
4912	JRS 04-15	<i>Metriaclima</i>	<i>midomo</i>	Lundo Island, Tanzania	January 29, 2004	Konings & Stauffer	S 11°08.0827' E 34°38.792'	1
4913	JRS 04-15	<i>Metriaclima</i>	<i>midomo</i>	Lundo Island, Tanzania	January 29, 2004	Konings & Stauffer	S 11°08.0827' E 34°38.792'	18
4914	JRS 05-18	<i>Metriaclima</i>	<i>tarakiki</i>	Higga Reef, Tanzania	February 13, 2005	Konings, Stauffer & Kocher	S 11°18.380' E 34°44.791'	1
4915	JRS 05-18	<i>Metriaclima</i>	<i>tarakiki</i>	Higga Reef, Tanzania	February 13, 2005	Konings, Stauffer & Kocher	S 11°18.380' E 34°44.791'	11
4916	JRS 04-16	<i>Metriaclima</i>	<i>tarakiki</i>	Ngkuyo Island, Tanzania	January 29, 2004	Konings & Stauffer	S 11°19.184' E 34°46.074'	20
<i>Total</i>								219

Appendix C: Morphometric and meristic values for *Metriaclima pambazuko* from Londo Bay, Mozambique (PSU 4900-4901); Lundo Island, Tanzania (PSU 4903); and Hongi, Tanzania (PSU 4902). Min-Max includes holotype (N=59).

Variable	PSU 4900		PSU 4901 Londo Bay		PSU 4902 Hongi			PSU 4903 Lundo		
	Holotype	Mean	Std Dev	Min-Max	Mean	Std Dev	Min-Max	Mean	Std Dev	Min-Max
Standard length, mm	61.3	60.2	5.0	51.9-73.2	65.3	4.7	59.3-75.9	67.3	3.4	61.8-74.7
Head length, mm	19.5	19.0	1.6	16.8-23.2	20.9	1.6	18.6-24.0	21.2	1.1	19.6-23.8
Percent head length										
Snout length	31.4	33.0	1.4	30.1-36.0	33.6	1.1	31.8-35.8	35.1	1.8	30.8-37.9
Postorbital head length	39.3	40.6	1.4	38.4-43.3	40.3	0.9	38.3-42.1	39.3	1.2	37.3-41.7
Horizontal eye diameter	37.0	38.2	1.5	35.3-40.8	36.1	1.7	33.0-39.9	35.7	1.5	31.2-37.9
Vertical eye diameter	35.4	37.2	1.6	35.0-41.3	35.0	1.7	32.4-38.3	35.5	1.4	32.1-37.8
Preorbital depth	22.1	20.9	1.0	18.9-22.7	20.7	0.9	18.6-22.2	20.6	1.2	18.5-22.7
Cheek depth	24.3	25.5	1.9	22.5-30.8	24.6	1.3	22.3-26.4	25.9	1.9	22.8-29.3
Lower-jaw length	36.9	36.6	1.6	34.4-40.2	37.2	1.4	35.4-40.0	37.8	1.0	36.1-40.1
Head depth	81.4	84.3	3.2	78.2-88.5	81.3	3.6	76.2-90.1	87.1	3.4	81.7-92.4
Percent standard length										
Body depth	31.2	32.2	0.9	30.5-33.5	31.3	1.1	28.9-33.0	32.8	1.1	30.6-35.6
Snout to dorsal-fin origin	33.3	33.6	1.2	31.5-35.7	33.6	0.8	32.2-35.1	33.4	1.5	30.4-36.2
Snout to pelvic-fin origin	38.3	36.9	1.1	35.3-39.1	37.3	1.0	35.9-39.8	39.7	2.2	36.1-44.2
Dorsal-fin base length	59.4	60.7	1.1	58.8-62.7	60.1	1.3	58.3-62.6	59.8	2.1	56.8-63.7
Anterior dorsal to anterior anal	50.1	49.3	1.3	46.9-52.4	49.1	1.4	46.6-52.7	49.8	1.3	47.3-52.3
Anterior dorsal to posterior anal	62.3	63.1	0.8	61.8-64.7	62.8	1.2	61.2-65.3	62.3	1.6	59.4-66.6
Posterior dorsal to anterior anal	29.1	30.4	0.9	28.7-32.3	29.2	1.1	27.0-30.4	29.7	1.0	27.7-31.1
Posterior dorsal to posterior anal	15.9	16.4	0.6	15.4-17.3	16.0	0.5	14.9-17.0	16.3	0.8	15.0-17.9
Posterior dorsal to ventral caudal	18.4	18.5	0.6	17.4-19.6	18.2	0.6	16.5-19.0	18.2	0.9	16.8-20.9
Posterior anal to dorsal caudal	22.4	22.3	0.7	21.0-23.7	22.2	0.5	21.2-23.1	21.9	0.8	20.0-23.3
Anterior dorsal to pelvic-fin origin	36.3	35.8	1.2	33.6-37.9	34.6	1.3	32.1-37.2	36.3	1.4	32.4-38.6
Posterior dorsal to pelvic-fin origin	57.7	57.9	1.2	55.8-59.6	57.1	1.4	55.3-60.3	55.8	1.7	52.4-58.4
Caudal peduncle length	14.6	15.1	0.8	14.2-17.4	15.0	0.9	13.0-16.3	15.1	1.0	12.8-17.2
Least caudal peduncle depth	10.9	11.3	0.4	10.5-12.0	11.1	0.4	10.2-11.5	11.1	0.6	10.3-12.4

	PSU 4900			PSU 4901			PSU 4902			PSU 4903		
				Londo Bay			Hongi			Lundo		
Counts		Mode	% Frequency	Min-Max	Mode	% Frequency	Min-Max	Mode	% Frequency	Min-Max		
Dorsal-fin spines	16	17	80.0	16-17	17	68.4	16-18	17	80.0	16-18		
Dorsal-fin rays	10	9	80.0	8-10	9	79.0	8-10	9	80.0	8-10		
Anal-fin spines	3	3	100.0	3-3	3	100.0	3-3	3	100.0	3-3		
Anal-fin rays	8	8	95.0	7-8	8	94.7	7-8	8	95.0	7-8		
Pelvic-fin rays	5	5	100.0	5-5	5	100.0	5-5	5	100.0	5-5		
Pectoral-fin rays	14	14	90.0	13-14	14	94.7	14-15	14	90.0	14-15		
Lateral-line scales	31	30	50.0	30-32	31	57.9	29-32	31	45.0	29-32		
Pored scales posterior to lateral line	1	1	70.0	0-1	1	73.7	0-1	1	60.0	0-1		
Scale rows on cheek	4	4	85.0	4-6	4	73.7	3-5	4	65.0	3-5		
Gillrakers on first ceratobranchial	12	12	60.0	11-14	13	47.4	11-18	12	60.0	11-13		
Gillrakers on first epibranchial	3	3	55.0	2-3	3	52.6	2-4	3	70.0	2-4		
Teeth in outer row of left lower jaw	20	17	25.0	16-22	17	26.3	17-23	16	30.0	12-22		
Tooth rows on upper jaw	3	3	100.0	3-3	3	89.5	3-4	3	60.0	2-4		
Tooth rows on lower jaw	3	3	95.0	3-4	3	84.2	3-4	3	65.0	2-3		

Appendix D: Morphometric and meristic values for *Metriaclima tarakiki* from Higga Reef, Tanzania (PSU 4914-4915) and Ngkuyo, Tanzania (PSU 4916). Min-Max includes holotype (N=32).

Variable	PSU 4914		all tarakiki (n=32)			PSU 4915 Higga Reef			PSU 4916 Ngkuyo		
	Holotype	Mean	Std Dev	Min-Max	Mean	Std Dev	Min-Max	Mean	Std Dev	Min-Max	
Standard length, mm	115.2	90.0	11.1	72.2-119.3	95.9	13.8	72.2-119.3	86.5	7.3	75.9-96.8	
Head length, mm	34.0	26.6	3.2	21.7-35.8	28.4	3.8	21.9-35.8	25.5	2.1	21.7-28.1	
Percent head length											
Snout length	39.8	37.4	2.3	32.9-42.2	39.2	1.6	37.1-42.2	36.4	2.0	32.9-39.9	
Postorbital head length	39.1	38.7	1.1	36.0-40.8	39.1	0.9	37.7-40.6	38.4	1.2	36.0-40.8	
Horizontal eye diameter	27.2	32.5	2.3	27.2-36.3	31.1	2.3	27.2-35.0	33.4	1.9	30.6-36.3	
Vertical eye diameter	28.4	32.6	2.1	28.2-36.5	31.1	1.8	28.2-33.5	33.5	1.7	30.2-36.5	
Preorbital depth	23.5	22.5	1.1	20.5-25.1	22.8	1.6	20.5-25.1	22.3	0.7	20.8-23.2	
Cheek depth	29.9	26.5	2.0	23.3-30.8	27.4	2.1	23.7-30.8	26.0	1.7	23.3-29.2	
Lower-jaw length	35.2	37.0	1.3	34.8-39.7	36.5	1.4	35.0-39.7	37.4	1.2	34.8-38.9	
Head depth	90.6	81.9	6.3	73.3-96.4	88.0	5.7	77.4-96.4	78.3	3.0	73.3-85.1	
Percent standard length											
Body depth	32.9	28.8	1.9	25.8-32.9	30.8	1.4	28.2-32.9	27.6	0.8	25.8-29.1	
Snout to dorsal-fin origin	31.3	30.9	1.1	28.5-33.0	30.8	1.2	28.5-32.7	30.9	1.0	29.4-33.0	
Snout to pelvic-fin origin	36.4	36.5	1.2	34.7-39.3	36.9	1.1	35.3-39.3	36.3	1.1	34.7-39.0	
Dorsal-fin base length	61.7	59.9	1.4	56.7-62.4	60.8	0.9	59.4-61.8	59.4	1.4	56.7-62.4	
Anterior dorsal to anterior anal	51.9	48.4	1.7	45.8-51.9	50.0	1.5	47.6-51.9	47.5	1.0	45.8-50.0	
Anterior dorsal to posterior anal	63.5	61.6	1.3	59.5-63.9	62.5	1.0	60.9-63.9	61.1	1.2	59.5-63.7	
Posterior dorsal to anterior anal	30.4	27.6	1.5	25.3-30.8	28.9	1.2	26.6-30.8	26.9	1.1	25.3-29.0	
Posterior dorsal to posterior anal	17.0	15.3	1.0	13.2-17.0	16.2	0.5	15.4-17.0	14.7	0.6	13.2-15.5	
Posterior dorsal to ventral caudal	20.2	18.8	0.9	16.4-20.5	19.4	0.6	18.5-20.2	18.4	0.8	16.4-20.5	
Posterior anal to dorsal caudal	22.8	21.6	0.6	20.3-22.8	21.7	0.6	20.6-22.8	21.6	0.7	20.3-22.6	
Anterior dorsal to pelvic-fin origin	35.6	31.7	2.2	28.1-36.0	33.9	1.2	31.9-36.0	30.3	1.3	28.1-33.1	
Posterior dorsal to pelvic-fin origin	61.9	58.5	1.6	56.0-62.0	60.0	1.5	56.9-62.0	57.6	0.9	56.0-59.5	
Caudal peduncle length	15.0	15.4	0.8	13.7-17.5	14.8	0.6	13.7-15.5	15.8	0.7	14.7-17.5	
Least caudal peduncle depth	12.3	10.8	0.7	9.7-12.3	11.4	0.5	10.7-12.3	10.4	0.5	9.7-11.5	

Counts	PSU 4914	all tarakiki (n=32)			PSU 4915			PSU 4916		
					Higga Reef			Ngkuyo		
		Mode	% Frequency	Min-Max	Mode	% Frequency	Min-Max	Mode	% Frequency	Min-Max
Dorsal-fin spines	18	18	93.8	17-19	18	100.0	18-18	18	90.0	17-19
Dorsal-fin rays	8	9	84.4	8-10	9	91.7	8-9	9	80.0	8-10
Anal-fin spines	3	3	96.9	3-4	3	91.7	3-4	3	100.0	3-3
Anal-fin rays	8	8	93.8	8-9	8	100.0	8-8	8	90.0	8-9
Pelvic-fin rays	5	5	100.0	5-5	5	100.0	5-5	5	100.0	5-5
Pectoral-fin rays	15	14	62.5	14-15	14	50.0	14-15	14	70.0	14-15
Lateral-line scales	31	32	71.9	31-33	31	50.0	31-32	32	85.0	32-33
Pored scales posterior to lateral line	0	1	87.5	0-2	1	83.3	0-2	1	90.0	1-2
Scale rows on cheek	5	4	53.1	4-5	5	75.0	4-5	4	70.0	4-5
Gillrakers on first ceratobranchial	11	11	56.3	10-12	11	58.3	11-12	11	55.0	10-12
Gillrakers on first epibranchial	2	3	59.4	2-3	2	58.3	2-3	3	70.0	2-3
Teeth in outer row of left lower jaw	27	26	21.9	20-31	27	33.3	24-31	23	25.0	20-28
Tooth rows on upper jaw	6	6	50.0	4-8	6	50.0	5-7	6	50.0	4-8
Tooth rows on lower jaw	8	8	40.6	5-8	8	58.3	7-8	7	35.0	5-8

Appendix E: Morphometric and meristic values for *Metriaclima nigrodorsalis* from N'kolongwe, Mozambique (PSU 4904-4905); Charlie's Bay, Mozambique (PSU 4906); Nkhungu, Mozambique (PSU 4907); Thundu, Mozambique (PSU 4908); and Chiloele, Mozambique (PSU 4909). Min-Max includes holotype (N=88).

Variable	PSU 4904		PSU 4905		PSU 4906			PSU 4907			PSU 4908			PSU 4909		
	Holotype	Mean	Std Dev	Min-Max	Mean	Std Dev	Min-Max	Mean	Std Dev	Min-Max	Mean	Std Dev	Min-Max	Mean	Std Dev	Min-Max
Standard length, mm	78.7	74.2	3.7	66.5-78.7	73.1	4.8	63.8-81.6	75.5	5.0	65.4-83.3	66.0	5.7	55.3-76.1	65.8	3.7	60.8-71.7
Head length, mm	24.0	22.8	1.3	20.1-25.2	22.8	1.5	19.8-25.0	22.8	1.5	19.6-25.2	20.2	1.5	17.7-23.3	21.0	1.3	19.0-22.9
Percent head length																
Snout length	36.1	34.2	1.4	31.0-36.1	33.8	1.9	30.0-37.2	34.9	1.5	32.3-38.9	34.2	2.0	29.9-37.3	32.2	2.7	28.8-37.1
Postorbital head length	38.8	38.6	1.0	36.9-41.2	39.8	1.5	36.0-41.9	40.2	0.8	38.5-41.4	39.5	1.2	36.9-41.8	39.8	1.5	37.9-42.1
Horizontal eye diameter	34.9	37.4	1.4	34.9-40.3	36.5	1.0	34.8-38.1	35.6	0.8	33.9-37.0	37.2	1.3	34.6-39.3	37.5	1.7	34.5-39.2
Vertical eye diameter	35.5	37.8	1.2	35.5-40.1	36.2	1.0	34.0-37.7	35.4	0.8	34.0-36.9	36.9	1.3	35.3-39.5	37.4	1.4	35.4-39.2
Preorbital depth	22.7	22.6	1.1	21.1-26.0	22.4	1.1	20.6-24.4	21.9	1.0	20.2-24.4	21.0	1.2	19.1-23.4	20.9	0.9	19.5-22.6
Cheek depth	82.7	28.9	2.0	26.0-32.9	29.0	2.0	25.3-33.7	27.3	1.6	25.4-31.8	26.2	1.7	23.4-28.6	26.7	1.6	24.4-29.2
Lower-jaw length	33.8	34.4	0.8	33.2-35.8	33.9	1.4	30.3-36.3	34.4	0.9	33.0-36.5	34.5	1.1	33.3-36.9	33.6	1.3	31.2-35.5
Head depth	88.0	84.5	3.1	78.4-89.4	84.8	2.5	79.9-89.2	86.0	3.2	77.9-91.1	83.8	3.8	77.9-90.5	83.2	3.3	79.7-90.1
Percent standard length																
Body depth	31.4	32.6	1.1	31.3-36.0	31.7	0.9	29.6-34.4	31.4	0.9	30.1-33.4	31.6	0.9	30.0-33.4	32.2	0.9	30.6-33.5
Snout to dorsal-fin origin	33.2	34.0	0.8	32.5-35.5	32.8	1.0	30.0-34.2	33.3	1.0	31.5-35.5	33.3	0.7	32.5-35.2	34.0	1.0	32.2-35.3
Snout to pelvic-fin origin	36.7	38.1	1.2	35.7-40.1	38.2	1.7	35.3-42.8	36.8	0.8	35.3-38.3	37.6	0.9	36.1-39.3	38.9	2.1	36.6-42.1
Dorsal-fin base length	60.7	61.0	1.6	59.0-64.7	62.0	1.7	58.4-65.6	62.4	1.3	60.2-64.8	61.1	1.5	57.9-63.9	61.1	2.1	57.9-64.4
Anterior dorsal to anterior anal	54.3	52.6	1.2	50.1-54.3	51.4	1.3	49.1-53.4	52.0	1.0	49.9-53.8	51.6	1.1	48.6-53.2	51.4	1.2	50.0-53.0
Anterior dorsal to posterior anal	65.7	64.6	1.5	61.7-68.8	64.6	1.4	61.4-66.6	64.9	1.0	63.0-66.7	63.8	1.3	61.3-66.3	63.7	1.8	60.8-65.7
Posterior dorsal to anterior anal	30.9	29.8	1.0	27.9-32.2	30.2	0.9	28.7-31.4	30.0	1.0	28.4-31.7	29.4	1.0	27.6-31.0	30.3	1.0	28.5-31.3
Posterior dorsal to posterior anal	15.6	16.6	0.6	15.6-17.7	16.4	0.4	15.7-17.3	16.4	0.7	15.2-17.9	16.4	0.7	15.1-17.3	16.2	0.6	15.1-16.8
Posterior dorsal to ventral caudal	18.8	18.4	0.6	17.4-19.4	18.6	0.7	17.2-20.6	18.2	0.6	16.3-19.6	18.2	0.4	17.4-19.2	19.1	0.9	18.0-20.0
Posterior anal to dorsal caudal	21.7	21.5	0.9	20.0-22.9	21.4	1.0	17.8-22.6	21.5	0.9	19.8-23.4	21.7	0.8	20.1-23.0	21.6	1.1	20.4-23.5

	N'kolongwe				Charlie's Bay			Nkhungu				Thundu		Chiloelo		
	PSU 4904	PSU 4905	PSU 4906	PSU 4907	PSU 4908	PSU 4909	PSU 4904	PSU 4905	PSU 4906	PSU 4907	PSU 4908	PSU 4909	PSU 4904	PSU 4905		
Anterior dorsal to pelvic-fin origin	34.8	36.8	1.2	34.8-39.6	36.5	0.8	35.1-37.9	36.2	0.8	34.7-37.9	36.2	1.1	34.6-38.4	36.4	1.0	34.9-38.0
Posterior dorsal to pelvic-fin origin	59.4	58.9	1.0	56.8-60.7	58.7	1.2	55.8-61.7	58.9	1.4	55.3-61.7	59.5	1.1	57.4-61.7	58.0	1.0	56.5-59.1
Caudal peduncle length	13.9	14.1	0.6	13.2-15.2	14.2	0.7	13.2-15.3	14.7	0.9	13.1-16.3	14.5	0.8	13.2-16.1	14.3	1.6	12.3-16.9
Least caudal peduncle depth	12.0	11.7	0.6	10.5-12.8	11.4	0.5	10.4-12.4	11.4	0.5	10.2-12.2	11.4	0.6	10.5-12.4	11.6	0.4	10.7-12.0
Counts	Mode	% Frequency	Min-Max													
Dorsal-fin spines	18	18	70.0	17-19	18	80.0	17-19	18	75.0	17-19	18	85.0	17-19	18	75.0	18-19
Dorsal-fin rays	9	9	70.0	8-9	9	75.0	8-9	9	70.0	8-10	9	85.0	8-10	8	100.0	8-8
Anal-fin spines	3	3	100.0	3-3	3	100.0	3-3	3	100.0	3-3	3	100.0	3-3	3	100.0	3-3
Anal-fin rays	9	8	60.0	7-9	8	85.0	7-9	8	70.0	7-9	8	90.0	7-9	8	87.5	7-8
Pelvic-fin rays	5	5	100.0	5-5	5	100.0	5-5	5	100.0	5-5	5	100.0	5-5	5	100.0	5-5
Pectoral-fin rays	15	15	60.0	14-15	14	75.0	14-15	14	55.0	14-15	14	60.0	13-15	14	75.0	14-15
Lateral-line scales	31	31	80.0	30-32	31	65.0	30-32	31	60.0	31-32	31	85.0	30-32	31	87.5	30-31
Pored scales posterior to lateral line	1	1	55.0	0-1	1	65.0	0-1	1	65.0	0-1	1	85.0	0-1	1	87.5	0-1
Scale rows on cheek	5	5	65.0	4-5	5	55.0	4-6	5	50.0	4-6	5	50.0	4-6	5	75.0	4-6
Gillrakers on first ceratobranchial	12	12	60.0	11-13	11	55.0	11-12	11	45.0	10-12	11	45.0	10-13	12	87.5	11-12
Gillrakers on first epibranchial	2	3	80.0	2-4	3	75.0	2-4	3	65.0	2-4	3	85.0	3-4	3	87.5	2-3
Teeth in outer row of left lower jaw	22	21	25.0	14-24	21	25.0	20-24	21	30.0	17-26	20	20.0	16-24	22	37.5	18-23
Tooth rows on upper jaw	4	3	95.0	3-4	4	80.0	3-5	4	60.0	3-4	4	60.0	3-5	4	62.5	3-4
Tooth rows on lower jaw	4	3	50.0	3-4	4	70.0	4-5	4	85.0	3-5	4	65.0	3-5	4	62.5	3-4

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PROFESSIONAL EXPERIENCE

Endangered Species Review Biologist (September 2008 – Present)

Natural Heritage and Endangered Species Program, Div. Fisheries & Wildlife, Westborough, MA

- Provide guidance to project proponents, consultants, and attorneys on the legal requirements of the MESA and negotiate terms of permits
- Prepare written analyses of the environmental impacts of proposed projects on species protected under the MESA and the Wetlands Protection Act
- Review Environmental Notification Forms and Environmental Impact Reports submitted to MEPA for impacts on protected rare species
- Extract relevant information from the NHESP's rare species databases
- Consult and coordinate with Natural Heritage staff, state and federal agencies, and private organizations on potential rare species impacts
- Inspect selected project sites to evaluate potential impacts of projects on rare species habitats

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Vertebrate Biology Laboratory (Sept. 2002 – Dec. 2006)

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