

# The naming of cichlids

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## ABSTRACT

The explosive radiation, recent origin, and high degree of endemism of cichlids have posed serious challenges for taxonomists to delimit species. We advocate that species are not simply categories constructed by systematists for information retrieval purposes, but that they do form distinct entities. Furthermore, we believe that the evolutionary species concept (ESC) is the only species concept that provides taxonomists with the theoretical basis of circumscribing all species. Because the ESC is nonoperational, practicing taxonomists must use surrogate species concepts (e.g., biological species concept, phylogenetic species concept) to discern different taxa. We recognize that the ranking of allopatric populations is problematic, and we propose that if two or more allopatric populations show the same phenotypic, behavioral, and genetic differences present in sympatric species, that they be described as separate species.

## EXPLOSIVE RADIATION OF CICHLIDS: A PROBLEM FOR TAXONOMISTS

*"What's the use of their having names," the Gnat said, "if they won't answer to them?"*

*"No use to them," said Alice, "but it's useful to the people that name them, I suppose. If not, why do things have names at all?"*

— Through the Looking Glass by Lewis Carroll

Cichlidae are found primarily in Africa and South and Central America, where they are the most species rich of all freshwater percoid fishes. The cichlids of the Great Lakes of Africa represent the most spectacular examples of speciation and adaptive radiation within a single vertebrate family, and many undescribed species are being discovered and described from newly explored areas (Keenleyside, 1991). In Lake Malawi alone, there may be as many as 1500 species of cichlids (Stauffer et al., 1997). The radiation of cichlids in Central America, since the late Pliocene, has also been impressive and has yielded close to 100 species (Barlow, 1974). We are currently discovering new species in Nicaragua from many of the crater lakes.

Cichlid fishes have been the focus of considerable ecological, evolutionary, and behavioral research

(Fryer, 1959; Jackson et al., 1963; Holzberg, 1978; Ribbink et al., 1983; Marsh et al., 1981; Sato and Gashagaza, 1997; Kawanabe et al., 1997). Undoubtedly, the cichlids' explosive speciation, unique feeding specializations, diverse mating systems, and great importance as a protein source in tropical countries have all been factors stimulating research interest in this group (Fryer and Iles, 1972; McKaye, 1984; Keenleyside, 1991). Unfortunately, many of these research efforts have been slowed and results often are confused as a result of the uncertain systematic status of some of the cichlids being examined. Many species from Lake Victoria became extinct before they were formally described. The vast majority of Lake Malawi's fauna is undescribed. Furthermore, the nomenclature in Central America is in a state of controversy, since Kullander (1983) revised the genus *Cichlasoma*. The high diversity and localized

nature of cichlids, in conjunction with the taxonomic uncertainty, makes it extremely difficult to identify reproductive units – a task which must be completed if this valuable resource is to be managed effectively.

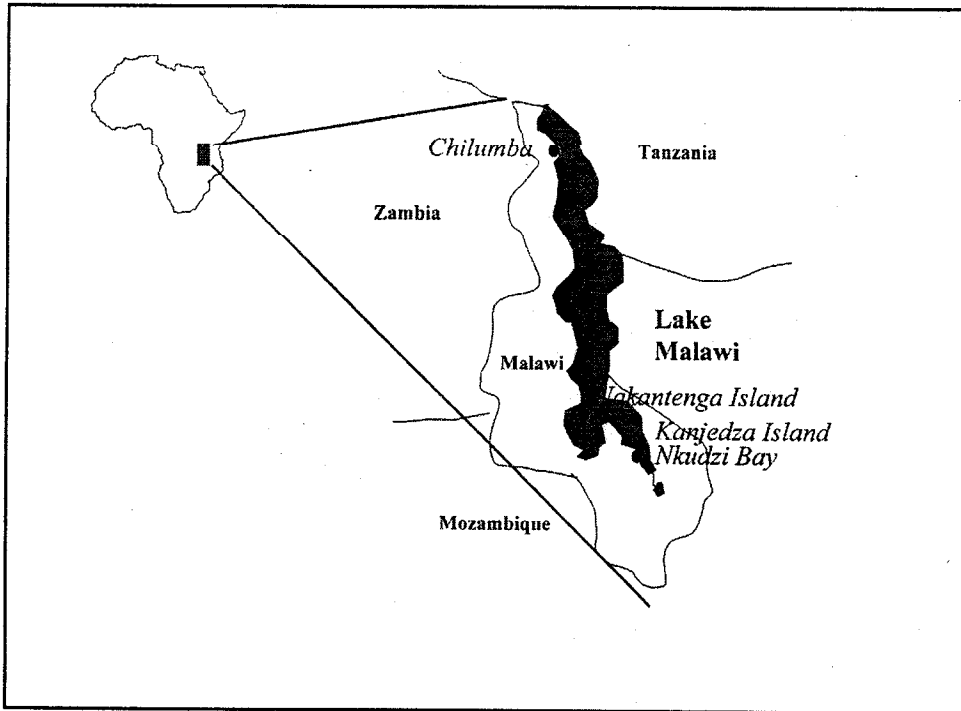
The extremely recent origin of these species flocks also poses serious challenges for systematists attempting to delimit species. As noted by Ghiselin (1997), it is usually presumed that post-mating isolating mechanisms evolved first, followed by pre-mating isolating mechanisms. It is recognized, however, that post-mating mechanisms do on occasion evolve subsequent to pre-mating ones (Ghiselin, 1997), and, in fact, in many of the cichlids inhabiting the Great Lakes of Africa, this is the norm. This acquisition of reproductive isolation with minimal morphological change (Lewis, 1982) and parallel evolution (Kocher et al., 1993) probably constitute the greatest problems to the taxonomist attempting to distinguish species. This problem is compounded by the fact that many of these cichlids are endemic to particular localities and are represented by allopatric populations. For example, the localities of four populations of redtop zebras are depicted in Figure 1. Stauffer et al. (1997) described the population from Chilumba as *Metriaclima emmiltos* Stauffer, Bowers, Kellogg, and McKaye, the population from Nakantenga Island as *Metriaclima prysonotos* Stauffer, Bowers, Kellogg, and McKaye, and the two populations from Kanjedza Island and Nkudzi Bay as *Metriaclima sandaracinos*.

Morphology has always played an important role in the study of the systematics and evolution of organisms. Historically, fishes were delimited by meristic and univariate morphometric analysis, and many species were described from one or two specimens. Recently, attempts have been made to qualify and quantify the shapes of organisms (Atchley, 1971; Humphries et al., 1981; Reymont et al., 1984; Bookstein et al., 1985). Such data are needed from many organisms from each population in order to determine the variation within and between populations and species. For example, Stauffer and Boltz (1989) used multivariate analysis of both morphometric and meristic data to distinguish between two sympatric species of rock-dwelling fishes from Lake Malawi, and

Stauffer (1991) used this technique to delimit populations of *Metriaclima pursus* Stauffer from *Metriaclima livingstonii* (Boulenger) and *Metriaclima lanisticola* (Burgess and Axelrod). The use of multivariate analysis of shape requires adequate sample sizes and that the fishes be pinned before preservation. In many cases, however, distinct species within the Lake Malawi cichlid species flock are morphologically similar.

The rapid radiation of the Cichlidae also poses serious challenges for the use of genetic techniques in determining phylogenetic relationships among species. Initial studies using allozymes have supported the notion of a recent origin for these species flocks (Sage et al., 1984) and have confirmed the separateness of gene pools for closely related taxa (McKaye et al., 1982; 1984; Kornfield, 1978). Attempts to use allozymes to resolve phylogenetic relationships have been limited (Kornfield et al., 1985). There may be too little variation within the flocks to resolve the phylogeny of many of the cichlid species flocks with allozymes. Preliminary data, however, indicate that mtDNA haplotype frequencies have been useful in distinguishing Lake Malawi sand-dwelling species. Stauffer et al. (1995) showed that haplotype frequencies of three new species of *Copadichromis* were significantly different. Kocher et al. (1998) have discovered a large number of simple sequence length polymorphisms in the tilapia genome, and Arnegard et al. (1999) and Markert et al. (1999) have used microsatellites to study population structure on several Lake Malawi rock-dwelling cichlids. A new method using amplified fragment length polymorphisms (AFLP) may be promising both for the identification of species and determination of supraspecific relationships among closely related taxa (Albertson et al., 1999).

Nevertheless, the lack of morphological differentiation, the absence of sympatry, and the inability of allozyme data to delimit species do not diminish the validity of the species status of many of these populations. For example, observations have demonstrated that behavioral diversity of the Lake Malawi sand-dwelling fishes is extremely high. Furthermore, after approximately five hundred hours of SCUBA diving and behavioral observations, it has been determined that different genera can be distinguished by bower (spawning platform) shape. Stauffer et al. (1993) used these bower-shape differences as manifesta-



**Figure 1.** Map of Lake Malawi showing the location sites of the “redtop” zebras.

tions of a behavioral characteristic to distinguish among three species of the sand-dwelling *Copadichromis*. Moreover, preliminary evidence has indicated that members of different genera exhibit different courtship dances (Stauffer et al., 1995). Thus, it is our contention that in order to effectively delimit many of the recently radiated cichlid species, it is necessary to use a combination of genetic, morphological, and behavioral data.

Based on the above discussion, it follows that cichlids have posed several problems for the practicing taxonomist attempting to delineate the taxa. In some cases, biologists identify unique populations before formally describing selected taxa as species (Murry et al., this volume, Vivas and McKaye, this volume). Therefore, the purposes of this paper are to discuss the theoretical basis for naming cichlid fishes and the role of the *International Code of Zoological Nomenclature* in stabilizing scientific names. The properties or constraints will first be discussed, followed by a brief summary of portions of the *International Code of Zoological Nomenclature* that apply to assigning specific and generic epithets.

#### ATTEMPTS AT A SPECIES DEFINITION

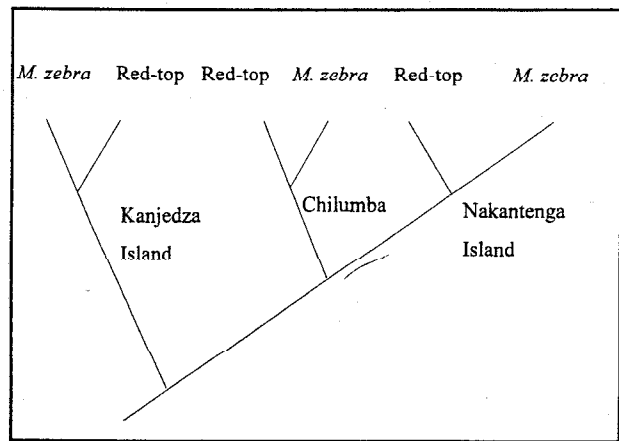
The attempt to define species has provoked more discussions and arguments than perhaps any other topic in comparative or evolutionary biology (Eldridge, 1995). Wilson (1992) characterized the search for a species concept that accurately represents the diversity of life as the “Holy Grail” of the natural sciences. Darwin (1859:49) recognized the difficulty in circumscribing species when he wrote, “It must be admitted that many forms, considered by highly competent judges as varieties, have so perfectly the character of species that they are ranked by other highly competent judges as good and true species.” In practice, the taxonomist recognizes populations of organisms that exist in nature, and such populations can range from the local deme, the sympatric community of potentially interbreeding organisms, to the species taxon (Mayr, 1996). In order for the biologist to assign various populations to one or more species, he/she must

complete two tasks: 1) select a species concept within the Linnaean hierarchy and 2) apply this concept when designating a population specific status or joining two or more populations into the species taxon (Mayr, 1996).

Mayden (1997) currently lists 22 different species concepts. The proliferation of so many concepts is a function of semantic confusion, verbal conventions, logical mistakes, and one's philosophical outlook (Ghiselin, 1969). At one extreme, nominalists would argue that individuals exist as separate entities, but taxonomic categories (e.g. class, family, genus, and species) are constructs of human minds. According to this viewpoint, species do not exist other than for our convenience (Ghiselin, 1997). Such scholars as Gilmour (1940), Ehrlich and Holm (1963), and Haldane (1956) espoused this opinion. At the other extreme, Simpson (1961), Mayr (1949; 1963; 1996), Hennig (1966), Ghiselin (1969), Dobzhansky (1970), Grant (1971), Hull (1976), and White (1978) advocate that species are not merely categories for the taxonomists' convenience, but individuals, and as such exist in nature. Mayr (1996) further elucidated the fact that species exist in nature, by referring to species as concrete describable objects in nature. Ghiselin (1969) reasons that species are social individuals, not merely an abstraction or group of similar things. He further states that it is necessary to think of such groups of individuals in terms of social interactions and not as a category only defined by taxonomic characters. Before one can employ one of the 22 different concepts, he/she must first decide whether species do, in fact, exist as separate entities (Kellogg and Stauffer, 1998).

### SPECIES AS INDIVIDUALS

The premise that species are individuals as conceived by Ghiselin (1997) is essential to the processes that we propose to recognize and delimit cichlid species. Traditionally, the term "individual" is synonymous with "organism," but the ontological (e.g., how things exist or the nature of being) term is much broader. Ghiselin (1997) further emphasizes that while all biological individuals are individuals in the ontological sense, not all ontological individuals are organisms. Parts of an

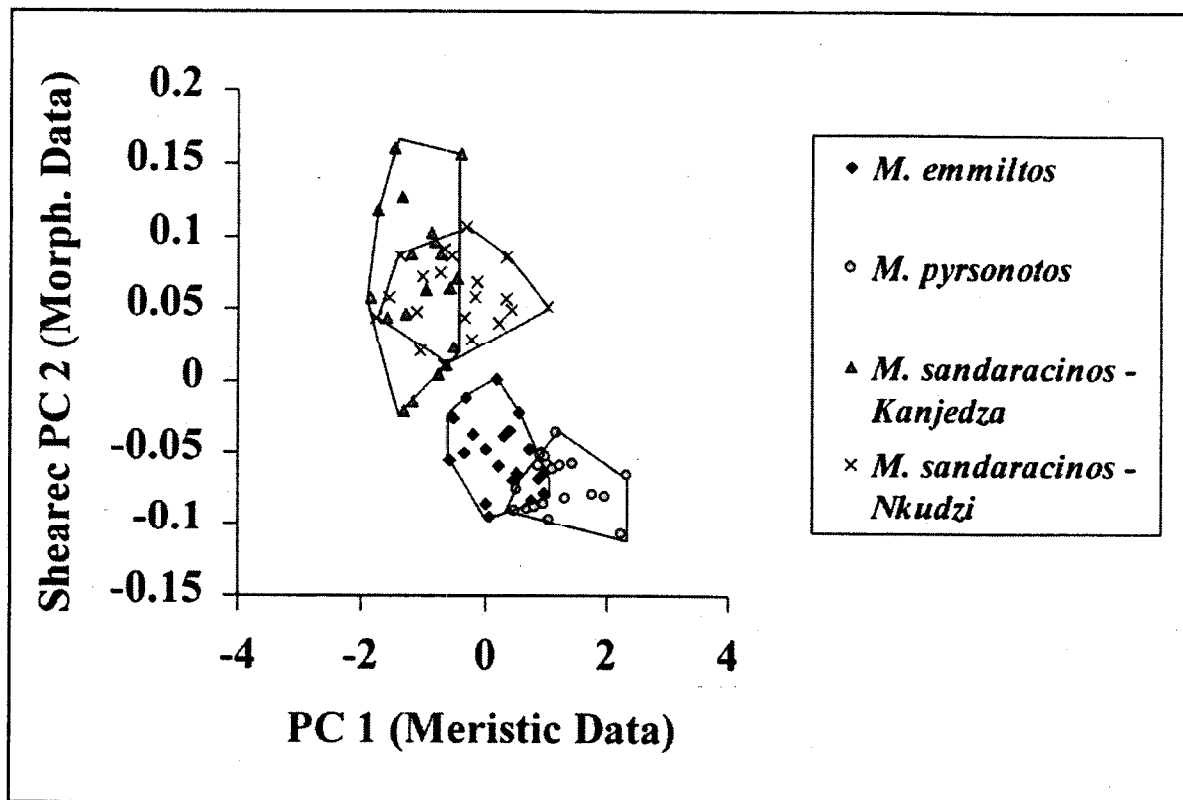


**Figure 2.** Hypothetical tree depicting the evolutionary lineage, if three redtop species arose independently from three populations of *Metriaclima zebra*.

organism or individual (e.g., organs, cells, molecules) can be individuals, *sensu* Ghiselin, and larger groups (e.g., an individual nation or state) can also be individuals, *sensu* Ghiselin. An individual is not by definition a nongroup (Ghiselin, 1997). There are at least six criteria used by Ghiselin (1997) to identify individuals in the ontological sense: 1) non-instantiability, 2) spatio-temporal restriction, 3) concreteness, 4) not functioning in laws, 5) lack of defining properties, and 6) ontological autonomy.

Gracia (1988) postulated that the only criterion for individuality, *sensu* Ghiselin, was non-instantiability. For example, a single specimen of the blue-black zebra, *Metriaclima zebra* Boulenger (Teleostei: Cichlidae), from Lake Malawi is an instance of an organism and, in fact, is an organism; thus "organism," as a category, would not be an individual, *sensu* Ghiselin. What would be the instance of *M. zebra*? Certainly it is not a single organism of the species, because it would not represent males, females, juveniles, sub-adults, etc. Even the population of *M. zebra* that inhabits a particular rock reef or island in Lake Malawi is not an instance of the species *M. zebra*. The population is a sample of the species, it is not an example.

The second criterion of individuals stated by Ghiselin (1997) is that they are spatio-temporally restricted. An individual has a beginning and an end, and once it is gone, it is gone forever. Species are individuals, *sensu* Ghiselin, because they originate through a speciation event, evolve over time, and they



**Figure 3.** Plot of the sheared second principal components (morphometric data) and the first principal component (meristic data) for *Metriaclima pyrsonotos*, *Metriaclima sandaracinos*, and *Metriaclima emmitos*.

cease to exist when they become extinct (Mayden 1999). In this sense, taxa higher than the species (e.g. genera, family, order, and classes) are also individuals. Categories, which are constructs of the human mind, such as “organism”, as defined above can not evolve or become extinct.

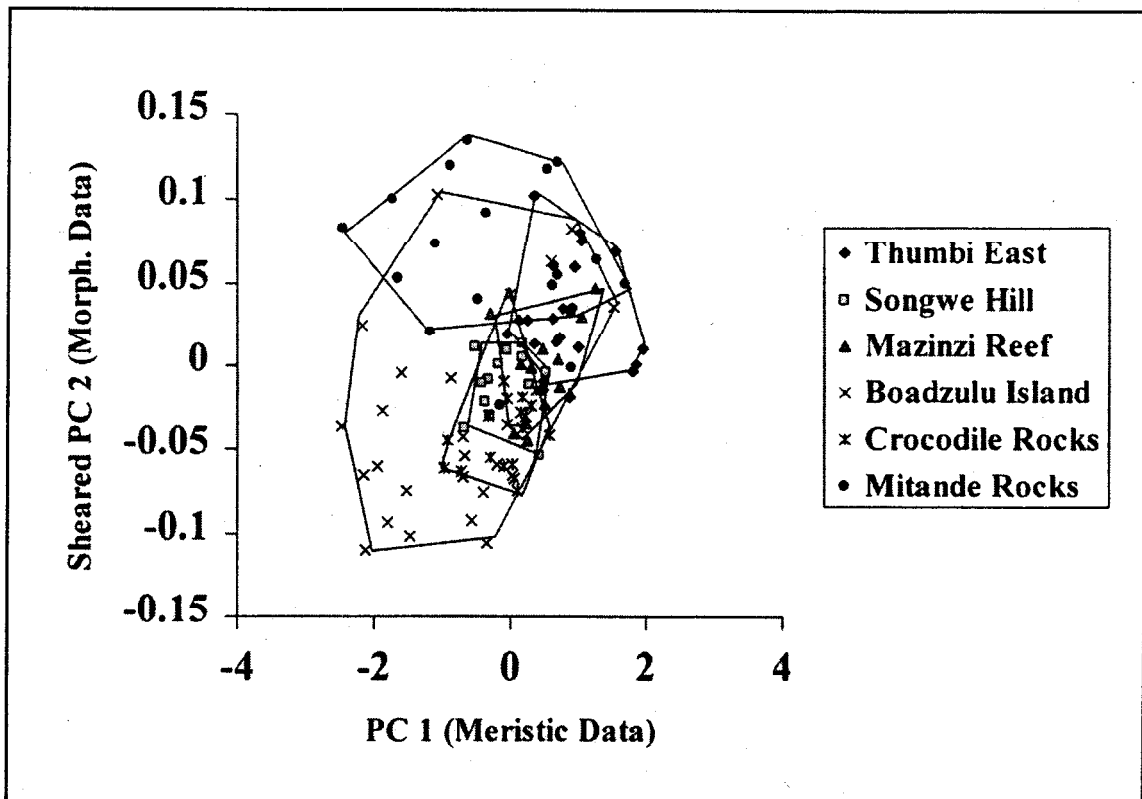
We refer you to Ghiselin (1997), who further discusses the other four criteria that are used to identify individuals, and illustrates why species satisfy all of these criteria. We agree with Ghiselin (1997), and propose that the two criteria, non-instantiability and spatio-temporally restricted, suffice to show that a particular entity is in fact an individual.

### SPECIES CONCEPTS

While an all encompassing operational definition of a species would be wonderful, as indicated above, it would be difficult at best and, in reality, perhaps impossible (Ghiselin, 1997). Hull (1997) concluded that all species concepts would have flaws; they will either be only narrowly applicable or will be nonoperational. Endler (1989) suggested that differ-

ent species concepts are necessary to study different evolutionary processes. Early definitions or concepts (Linnaeus, 1758; Ramsbottom, 1938) stated that species were distinct and monotypic, immutable and created as such, and bred true. Although Mayden (1997) compiles a list of 22 species concepts, Graybeal (1995), stated that modern species concepts can be placed into two categories: 1) those that give primary emphasis to a process such as mate choice or species recognition and 2) those that focus on the correct representation of evolutionary patterns.

The evolutionary species concept (ESC) was proposed by Simpson (1951) and defined by Wiley (1978) as “...a single lineage of ancestor-descendant populations, which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate.” Subsequently, Mayden

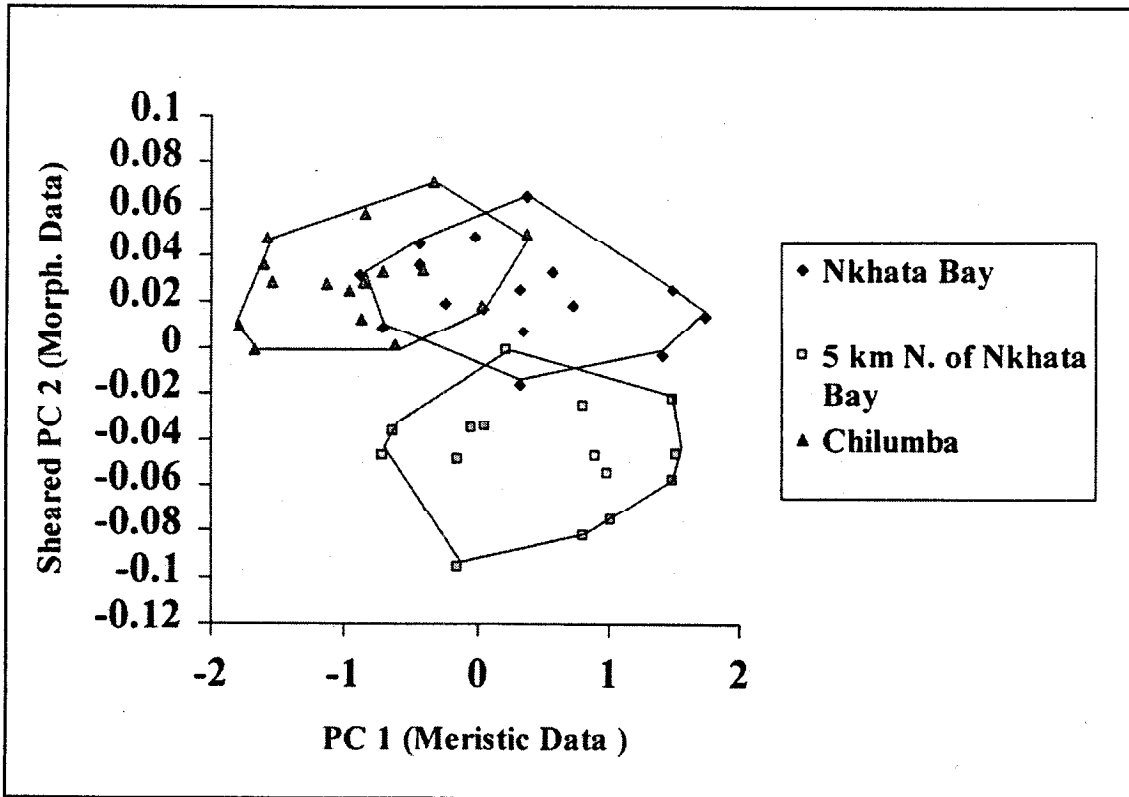


**Figure 4a.** Plot of the sheared second principal components (morphometric data) and the first principal components (meristic data) for *Metriaclima zebra* populations from the southern end of Lake Malawi.

(1997) argued that the evolutionary species concept was the only concept that was apropos to all taxa. The evolutionary species concept is premised on descent with modification; thus, taxa are delimited irrespective of whether they reproduce asexually or sexually, or are allopatric or sympatric. Although the evolutionary species concept provides taxonomists with the theoretical basis of circumscribing species, it is not operational in that it can not be observed (Mayden and Wood, 1995; Mayden, 1997). For example, if three populations of redtop zebra arose independently from three disjunct populations of *M. zebra* from Chilumba, Nakantenga Island, and Kanjedza Island they would have an evolutionary lineage as shown in Fig. 2. Although the evolutionary species concept would correctly recognize the three populations of redtops as separate species, it would provide no methodology,

other than the use of a time machine to detect these hypothetical historical lineages. Therefore, taxonomists have used phenotypic criteria, such as derived characteristics, to infer evolutionary relationships, although direct observations of changes in evolutionary lineages are not possible.

Given that the evolutionary species concept is nonoperational, the practicing taxonomist must use surrogate species concepts (e.g. biological species concept) to distinguish species taxa. With the advent of the evolutionary synthesis (Eldridge, 1995; Mayr and Provine, 1998), the biological species concept probably had the biggest impact on the way in which taxonomists delimited species. Without a doubt, Mayr (1963) was the biggest proponent of the importance of recognizing a process with his biological species concept, when he defined species as groups that are reproductively isolated. In essence, Mayr (1969:316) was defining the biological species as "The segregation of the total genetic variability of nature into discrete packages, so called species, which are separated from each other by reproductive barriers."



**Figure 4b.** Plot of the sheared second principal components (morphometric data) and the first principal component (meristic data) for *Metriaclima zebra* populations from the northern end of Lake Malawi.

ers, ..." Mayr (1996) further emphasized that the mechanisms by which reproductive isolation is achieved are properties of the individual organisms; thus geographic isolation of allopatric populations does not qualify as an isolating mechanism. Authors both before (Dobzhansky, 1935; 1937; 1940) and after (Patterson, 1985; Buerton, 1995) the articulation of the biological species concept recognized the importance of reproductive isolation. Finally, Mayr (1969) emphasized that the sorting of genetic variability of nature into discrete packages, which he termed species, prohibited the creation of too many disharmonious incompatible gene combinations. Certainly, within vertebrate zoology, the groups that are studied as the units of evolution are biological species (Cracraft, 1992). Closely related to the biological species concept is Patterson's (1985) recognition concept, which recognizes species as groups of organisms with coincident fertilization systems and important specific mate recognition systems.

The two major historical problems with the biological species concept are the definition of asexually

reproducing entities (Hull, 1997), and the need to speculate as to whether allopatric populations are reproductively isolated (Thompson, 1991; Zink, 1997). Many allopatric populations, assumed to be potentially capable of interbreeding, are in effect a combination of several geographical variants of the same species (i.e. polytypic species), which are often designated subspecies (Cracraft, 1992). In fact, these groups of putative subspecies (Kleinschmidt, 1900; Stresemann, 1936; Mayr, 1942) were often recognized by taxonomists to facilitate the comprehension of taxonomic differentiation and to solve classification problems. More emphasis is now being placed on representation of evolutionary patterns as the biological species concept is being criticized. Sympatric populations that assortatively mate represent distinct species (McKittrick and Zink, 1988).

Awise and Ball (1990) further argue that the correct representation of phylogenetic history will produce taxa that are best, although not perfect representatives of the majority of biological units. These discussions resulted in the 22 species concepts enumerated by Mayden (1997). Many of these theories, however, allude to reproductive isolation or genetic continuity; although, the primary emphasis centers on the correct representation of evolutionary patterns rather than on a process such as mate choice (Zink, 1997). In effect, a species that consists of two or more groups that are not nearest relatives is no longer acceptable to systematists (Zink, 1997). Furthermore, it is now realized that processes, such as reproductive isolation or mate selection, do not evolve concomitantly with characters that diagnose evolutionary species (Zink, 1997). Therefore, most history-based concepts (e.g., evolutionary species concept, phylogenetic species concept), because they reject that reproductive compatibility is the primary criterion of conspecific status, recognize that species can hybridize because of the retention of the ancestral ability to do so (Zink, 1997). Because all hybrids that occur are not sterile, it is recognized that there is a certain leakage of genes among species (Mayr, 1996). The fact that isolating mechanisms are not absolute compelled Mayr (1970; 1996) to revise his biological species definition to "biological properties of individuals, which prevent the interbreeding [fusion] of populations." (Mayr, 1970:56 in Mayr, 1996).

Cichlids, of course pose some special problems relating to reproductive isolation. It is widely known from aquarists that many cichlids hybridize under laboratory or aquarium conditions and produce fertile offspring. If two captive putative species hybridize and their offspring die or are sterile, then that is excellent evidence that these two forms are separate species. If, however, the offspring are fertile that is not evidence that the two forms are conspecific. The investigator probably altered any pre-reproductive isolating mechanisms that would favor assortative mating in the wild.

For the most part, history-based concepts use character analysis to reveal groups of individuals that

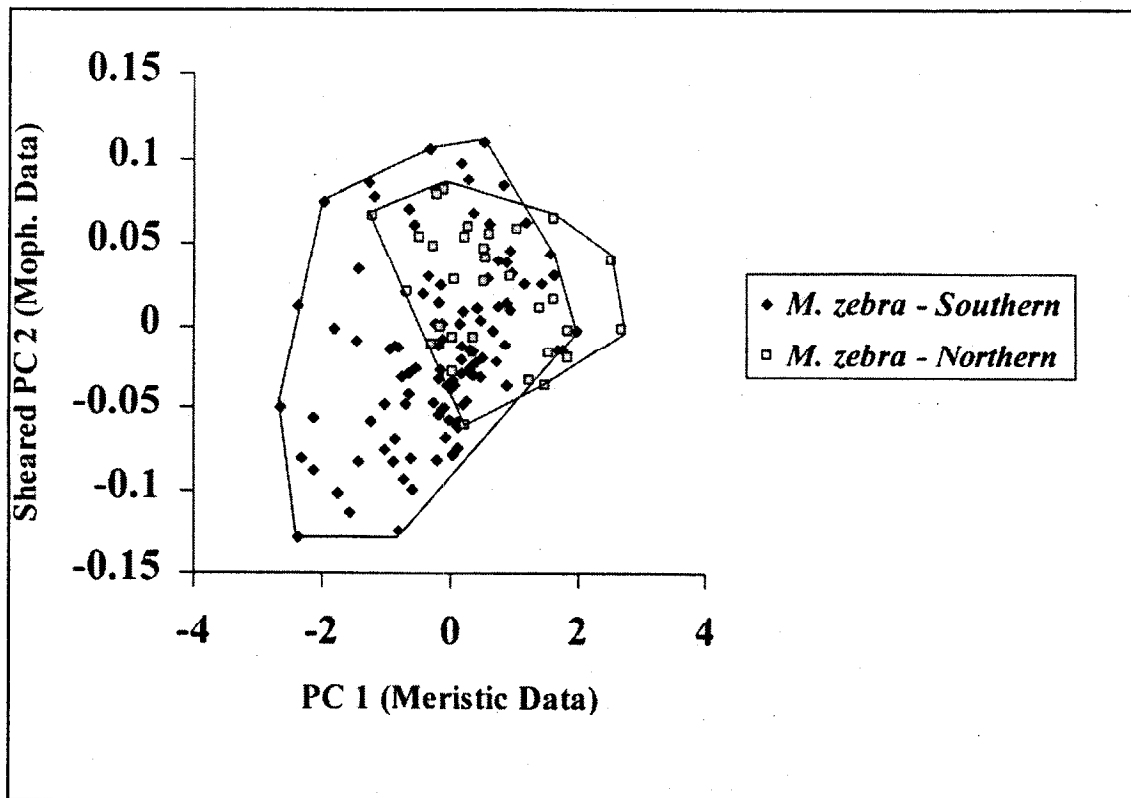
qualify as basal evolutionary units or species (Cracraft, 1983; 1989; 1992). It is the existence of unique phenotypes, not observations of reproductive isolation, that is the primary criterion upon which taxonomists recognize species (Platnick, 1977; Rosen, 1978; 1979). Therefore, if allopatric populations have evolved one or more derived characters, then the evolutionary modification of primitive characters has been satisfied and the population should be given species status (Cracraft, 1992). Such criteria were used when Stauffer et al. (1997) described 10 new species of *Metriaclima* from Lake Malawi.

If reproductive isolation were the sole criterion upon which populations were given species status, then it is conceivable that a biological species would be commensurate with: 1) a single taxonomic unit, or 2) a collection of taxonomic units that do not comprise a monophyletic unit. The latter situation is not coincident with the concept of a species envisioned by most evolutionary biologists. These unique phenotypes can be diagnosed based on morphological, genetic, biological, or behavioral characters. Although the description of unique phenotypes appears to be straightforward, problems arise in determining the degree to which two populations must differ in order to be regarded as distinct species (Claridge et al., 1997).

If in the judgement of the taxonomist, two allopatric populations are deemed not to be sufficiently distinct to be diagnosed as separate species, then they are considered to be the same polytypic species (Cracraft, 1992) and the populations may be designated as subspecies. Mayr (1942) argued that allopatric speciation is only plausible if the aforementioned subspecies are incipient species. Thus, while not every subspecies will develop into so called good species, all species that develop through allopatric speciation must pass through the subspecies state.

In the descriptions of many Lake Malawi cichlids, Stauffer et al. (1993; 1997) embraced the evolutionary species concept, but used morphological and behavioral traits to delimit species. When sympatric forms assortatively mated, they concluded that the populations had achieved independent evolutionary lineages and regarded them as separate species. In reality, they compared morphological and behavioral differences among sympatric populations and used these differences as a yardstick. Thus, if allopatric populations exhibited the same differentiation displayed among sympatric species, they described the allopatric popu-





**Figure 4c.** Plot of the sheared second principal components (morphometric data) and the first principal components (meristic data) for *Metriaclima zebra* populations from the northern and southern end of Lake Malawi.

lations as separate species. In so doing, they (Stauffer et al., 1997) used morphological traits to determine that sufficient morphological differences existed to indicate that the populations formed different evolutionary lineages (Kellogg and Stauffer, 1998). The concept that phenotypic similarity in a particular character present in geographically disjunct forms denoted that these forms were conspecific was rejected; especially if these populations could be delimited using other morphological character states. Thus, three geographically isolated populations of what were historically recognized as redtop zebras were described as three separate species. All three species have the typical blue/black barring, which is found in many of the Lake Malawi rock-dwelling cichlids, and these three species all possess a red dorsal fin. Stauffer et al. (1997) illustrated that the minimum polygons formed when the second sheared principal components (morphometric data) were plotted against the first principal components of the meristic data were not

significantly different ( $p > 0.05$ ) from the two populations (*M. sandaracinos*) at Kanjedza Island and Nkudzi Bay (Fig. 3). The minimum polygon clusters of *M. emmitos* from Chilumba and *M. prysonotos* from Nakantenga Island were significantly different ( $p < 0.05$ ) from each other and from both the *M. sandaracinos* populations (Fig. 3).

If a single species that encompassed all three forms had been defined as those blue-black forms that possess a red dorsal fin, it would have been treating species as a category, rather than an individual *sensu* Ghiselin. In this case, the three forms that phenotypically resembled one another, would have had different evolutionary lineages and as such would not represent a single species.

Conversely, nine populations of *Metriaclima zebra* were considered conspecific because they demonstrated morphological gradation among the isolated populations. For example the minimum polygon clusters formed by the populations occurring south of Nakantenga Island (Fig. 1), depict a great deal of overlap, although some populations are distinct (i.e. Songwe Hill versus Mitande Rocks; Fig 4a). When the three populations that are found north of Nakantenga Island are compared, there is less overlap (Fig. 4b). When the populations from the northern portion of Lake Malawi are compared with those from the southern portion, however, there is almost complete overlap in the minimum polygon clusters (Fig. 4c). Thus all the populations were considered as a single individual and regarded as conspecific (Stauffer et al., 1997).

It is important to realize that speciation is not a phenomenon that occurred  $10^6$ ,  $10^3$ , or even 100 years ago and then stopped. It is a dynamic event that continues to occur. Thus, it is conceivable that populations designated as subspecies may have, in fact, achieved species status. Similarly, those populations that are designated as species may be incipient or semi species *sensu* Mayr (1969). Finally, when using differences among sympatric species as a yardstick for evaluating allopatric populations, the taxonomist must be cognizant of the potential influence of character displacement or ecological shift.

#### **BRIEF SUMMARY OF THE INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE**

The *International Code of Zoological Nomenclature* was adopted by the XV International Congress of Zoology, published in 1961, revised and published again in 1964 following changes adopted by the XVI International Congress of Zoology, and subsequently revised and published in 1985 (International Trust for Zoological Nomenclature, 1985). A revised edition of the Code has recently been published and went into effect on 1 January 2000 (<http://www.iczn.org/code.htm>). The Code has two primary functions: to promote stability in the scientific names of animals and to ensure that the binomial name of each animal

taxon is unique. The International Commission of Zoological Nomenclature has five primary functions: 1) submit recommendations for amendments, 2) provide opinions of individual name status, 3) compile official lists (e.g. generic names), 4) interpret the rules, and 5) use its plenary powers to suspend the rules.

A brief summary of the rules follows. According to the rules in effect until 1 January, 2000, the oldest name after 1758, the date of publication of Linnaeus' 10<sup>th</sup> edition of *Systema Naturae*, had priority. After 1 January, 2000, if a name has been used as valid by a minimum of 10 authors in 25 publications during the last 50 years, it can not be displaced by an earlier name (<http://www.iczn.org/code.htm>). The scientific name of an organism normally consists of its genus and species, although sometimes a third epithet denoting subspecies is included. When a new species is described, reference must be made to the holotype, which is often referred to as the type specimen. The name of the family must have a type genus designated, and the name of a genus must have a type species denoted. The name of either the family or genus must be changed if the type genus or type species is changed, respectively. Finally, the Commission can use its plenary powers to suspend the rules and render decisions about specific topics. Following are two examples that may demonstrate the necessity of the Code.

Oliver and Loiselle (1972) described the genus *Iodotropheus* for a small group of rock-dwelling cichlids from Lake Malawi. In the same paper, they described *Iodotropheus sprengerae* Oliver and Loiselle and designated it as the type species of the genus. Oliver and Loiselle (1972) listed Boadzulu Island in Lake Malawi as the type locality for *I. sprengerae*. Subsequently, Stauffer (1994) discovered what he thought was a new species from Chinyankwazi and Chinyamwezi islands in Lake Malawi. Morphological analysis of the new specimens indicated that it more closely resembled the type specimens of *I. sprengerae*. *Iodotropheus sprengerae* was described based on aquaria specimens and not from wild-caught fishes from Boadzulu Island. One option available to Stauffer (1994) was to declare the name *Iodotropheus sprengerae* as invalid, as it was described from aquaria-raised specimens that could have been a product of hybridization between the two forms. In any case, the locality of the type specimens was unknown as the primary exporter

of these fishes was collecting at Boadzulu, Chinyankwazi, and Chinyamwezi islands. If this option were pursued, the generic name *Iodotropheus* would become invalid. The name *Iodotropheus* had been used commonly in both the scientific and popular literature (Stauffer, 1995); thus, in order to preserve the name *Iodotropheus*, Stauffer (1994) petitioned the International Commission of Zoological Nomenclature to use its plenary powers to set aside the type specimen for *Iodotropheus sprengerae*, designate a neotype from Chinyankwazi Island, place *Iodotropheus* on the Official List of Generic Names in Zoology, and place *Iodotropheus sprengerae* on the Official List of Specific Names in Zoology. The Commission accepted Stauffer's (1995) petition, thus the name *Iodotropheus* was preserved. Stauffer (1994) described the distinct forms from Boadzulu Island as *Iodotropheus declivitas* Stauffer.

The second example of the utility of the code occurred when Stauffer et al. (1997) proposed the name *Metriaclima* as the generic name for what was previously recognized as the *Pseudotropheus zebra* (Boulenger) complex. Certainly, before Stauffer et al.'s (1997) revision, *Pseudotropheus* was the most diverse and widespread genus of rock-dwelling forms endemic to Lake Malawi. Within *Pseudotropheus*, the *M. zebra* complex was the most widely distributed species group. *Pseudotropheus williamsi* (Gunther 1893) was originally placed in the genus *Chromis*. When Regan (1921) described the genus *Pseudotropheus*, he designated the type species of the genus to be *P. williamsi*. Thus, when Stauffer et al. (1997) recognized the *M. zebra* complex as a distinct genus, *Pseudotropheus* was unavailable for the generic name, because *P. williamsi* was designated as the type species of *Pseudotropheus*. The choice of a new generic name was further complicated because Meyer and Foerster (1984) proposed the name *Maylandia* as a subgenus of *Pseudotropheus*, with *Pseudotropheus [Metriaclima] greshakei* as the type species. In the description of *Metriaclima*, *Maylandia* was available for use because it was proposed at the subgeneric level. Stauffer et al. (1997) thought that the description was not adequate to include all of the proposed members of *Metriaclima*; thus, *Metriaclima* was proposed as a new generic name complete with a full description, it has priority and is the currently accepted name.

## CONCLUSION

Cichlids have undergone the most explosive radiation of any single vertebrate group throughout Africa and Central and South America. The diversity, which resulted from this rapid rate of speciation, gave rise to numerous ecological, evolutionary, and behavioral research studies (Fryer, 1959; Jackson et al., 1963; Holzberg, 1978; McKaye, 1984; McKaye et al., 1982; 1984). Unfortunately, many of these research efforts have been hindered because of the uncertain systematic status of the fishes being examined. The extremely recent origin and high degree of endemism of cichlid species flocks have posed serious challenges for taxonomists to delimit species. Nevertheless, the inability of taxonomists to discern distinct species does not diminish the validity of the species-status of many of these populations.

We advocate that species are not simply categories constructed by systematists for information retrieval purposes, but that they do form a distinct entity and can be regarded as individuals *sensu* Ghiselin (1997). Moreover, we believe that the evolutionary species concept, as proposed by Simpson (1951), is the only concept that provides taxonomists with the theoretical basis of circumscribing all species; however, we recognize that this concept is in effect not operational (Mayden and Wood, 1995; Mayden 1997). Thus, we propose that practicing taxonomists must use surrogate species concepts (e.g. biological species concept, phylogenetic species concept) to discern different taxa. Because of the recent origin of many cichlids, we espouse the use of unique phenotypes that delimit evolutionary lineages to recognize species and not one of the group of species concepts that employ processes (e.g., recognition concept). We would agree, however, that for sexually reproducing sympatric species, the biological species concept is valid. Finally, we recognize that the ranking of allopatric populations is problematic, and we propose that if two or more allopatric populations show the same phenotypic, behavioral, and genetic differences that are present in sympatric species, that they be described as separate species.

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