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Testing Conjectures about Morphological Diversity in Cichlids of Lakes Malawi and Tanganyika

PROSANTA CHAKRABARTY

The morphological diversity of Malawi and Tanganyika cichlids has often been qualitatively described, but rarely have hypotheses based on these descriptions been tested empirically. Using landmark based geometric morphometrics, shapes are analyzed independent of other aspects of the body form (e.g., size). The estimation of shape disparity, the quantitative measure of the variance of these raw shapes, can then be applied in order to objectively test hypotheses about morphological diversity. The shape disparity within and between different groups is explored as well as how it is partitioned within the cichlid body. Tanganyika cichlids are found to have significantly greater shape disparity than Malawi cichlids. Ectodini is found to have significantly greater shape disparity than other Great Lake tribes. Piscivorous cichlids are significantly more disparate in shape than cichlids with other diets, and the shape disparity of the cranial region was significantly greater than that of the post-cranial region.

“We begin by describing the shape of an object in the simple words of common speech: we end by defining it in the precise language of mathematics; and the one method tends to follow the other in strict scientific order and historical continuity.”—D’Arcy Thompson, 1917 (On Growth and Form)

THE cichlids of the Great Lakes of East Africa are favorite textbook examples of several notable elements of natural history and evolutionary theory, including: shape and diet convergence, sympatric and allopatric speciation, adaptive radiations, species flocks, and Fisherian runaway sexual selection (Carroll, 1997; Futuyma, 1998; Strickberger, 2000). The foundations for some of these ideas are the subjective impressions of workers about the morphological diversity of these cichlids. Such inferences are not empirically repeatable or quantifiable. Likewise, disagreements over the magnitude of morphological diversity in different groups are left unresolved. This study tests conjectures about morphological diversity from an estimation of the total variance among shapes (i.e., shape disparity, defined mathematically in Materials and Methods).

Contrasting levels of morphological diversity has been difficult because of a lack of metrics that can be compared statistically. Recently a variety of metrics have been devised for quantifying morphological diversity (= morphological disparity; Foote, 1993; Fortey et al., 1996; Eble, 2000), including those suited to the analyses of geometric shape (Zelditch et al., 2003, 2004). Correlation in external geometric shape and trophic morphology of small groups of Great

Lake cichlids have been described (Bouton et al., 2002a; Wautier et al., 2002; Kassam et al., 2003a) including evidence of convergence of these elements between lakes (Rüber and Adams, 2001; Kassam et al., 2003b); however, those studies dealt only with patterns of morphological diversity rather than with its magnitude. A broad analysis of the morphological diversity of Great Lakes cichlids has yet to be done despite its relevance. The analyses presented here attempt to objectively explore the morphological diversity of a large and taxonomically diverse sampling (≈ 100 spp.) of Great Lake cichlids.

The Great Lakes of East Africa, comprised of Lakes Tanganyika, Malawi, and Victoria, each have a cichlid fauna of several hundred described endemic species; however, the final inventory will most probably exceed a total of 1,000 species (Kullander, 1998; Kornfield and Smith, 2000). Lake Victoria has recently undergone a significant loss of its cichlids due to a number of anthropogenic factors (Meyer, 1993; Seehausen et al., 1997; Stiassny and Meyer, 1999) and is not studied here.

Lakes Malawi and Tanganyika, the focal points of this study, are among the ten largest lakes in the world by area and depth and contain more fish species than any other lakes (Fryer and Iles, 1972). These two lakes hold the majority of cichlid species diversity; cichlids are also found in other parts of Africa, the Middle East, the Neotropics, Madagascar, and the Indian sub-continent (Kullander, 1998; Murray, 2001). Lake Tanganyika has been recognized as a harbor for the lineages that gave rise to the cichlids of Malawi and Victoria (Nishida, 1991; Meyer et al., 1994). Both Lake Tanganyika and

the cichlid lineages it contains are recognized as several million years older than Lake Malawi and its cichlids (Meyer, 1993). The many hundreds of cichlid species these lakes contain are proposed to have evolved over the course of less than five million years (Meyer, 1993).

Testing hypotheses about broader mechanisms associated with the rapid speciation of these cichlids is beyond the scope of this paper. However, measuring the magnitude of morphological diversity that is the basis of those hypotheses is a necessary first step. Four conjectures are composed to reflect general observations that have been made about Great Lake cichlid morphological diversity. These are listed below and abbreviated as C1–C4 for the remainder of this paper.

Morphological diversity of Lake Tanganyika cichlids is greater than that of Lake Malawi cichlids (Conjecture 1). Several mechanisms have been proposed to explain the observation that the cichlids of Lake Tanganyika have greater morphological diversity than Malawi cichlids, despite having half to a third of the species richness of Lake Malawi (Greenwood, 1984a; Meyer, 1993; Salzburger et al., 2002). Included among these is the notion that natural selection has had sufficient time to remove intermediate morphologies only from Lake Tanganyika (2–4 million years old) and not Malawi (1–2 million years old; Greenwood, 1984a; Mayr, 1984; Meyer, 1993). Other possibilities raised are that the greater abundance of disjunct rocky habitats in Malawi allowed for higher occurrences of micro-allopatric speciation (Fryer and Iles, 1972; Genner et al., 1999) or that sexual selection has occurred without much corresponding morphological change in Lake Malawi while other processes have occurred in Lake Tanganyika (Meyer, 1993; Parker and Kornfield, 1997; Albertson et al., 1999). Some have even proposed that the noted difference in morphological diversity is due to the artifact of Tanganyika being better studied than Malawi (Kassam et al., 2003b). Until now, the foundational assumption of these hypotheses—whether there is in fact a difference in the morphological diversity between lakes—has never been tested.

Lamprologini or Ectodini have the greatest morphological diversity of the Great Lake tribes (Conjecture 2). Morphological diversity of Great Lake cichlid clades has been a subject of debate (Sturmbauer and Meyer, 1993; Stiassny, 1997; Barlow, 2000), particularly with respect to the 12 tribes into which these cichlids have been divided. This conjecture has been rationalized by propositions that morphological diversity in certain clades is correlated with the range of

trophic levels and habitats occupied by members of those clades. Lamprologini and Ectodini have both been proposed as occupying the greatest amount of morphological, trophic, and habitat diversity of any Great Lake tribes (Sturmbauer and Meyer, 1993; Stiassny, 1997; Barlow, 2000). It is predicted that these two tribes will be more disparate than other groups.

Piscivorous cichlids have less morphological diversity than cichlids with other diets (Conjecture 3). Piscivorous cichlids are often demonstrated as having similar morphologies and/or convergent shapes (Kocher et al., 1993; Meyer, 1993; Martin and Bermingham, 1998). It has been proposed that this constraint may be due to the relatively minor morphological modifications necessary for variation in this diet class (Greenwood, 1974; Liem, 1978; Stiassny, 1981). As Fryer and Iles (1972) noted, “In general, the piscivorous cichlids exhibit the adaptations common to many piscivorous fishes—streamlined, and not infrequently slender bodies. . . large eyes; mouths with a very wide gape.” One would thus expect the piscivorous cichlids to have low shape diversity relative to cichlids in other diet classes because of these commonly shared features. This is because the convergence to the same or similar form reduced the amount of variance in shape of the group.

The majority of differences between the shapes of cichlids lie within the shape of the head region (Conjecture 4). Several authors have hypothesized that most of the differences between haplochromine cichlid species lie in the head (Greenwood, 1974, 1984b; Barel, 1983). Studies that correlate head shape with environmental variables or trophic level, without considering the rest of the body, exemplify the acceptance of this assumption (Strauss, 1984; Bouton et al., 2002a and references within). Conjecture 4 was tested for all the cichlid species sampled here from Lake Malawi and Lake Tanganyika. Greenwood (1991) suggested that the trophic plasticity provided by the dual oral and pharyngeal-feeding systems of cichlids might explain much of the corresponding morphological diversity of the group. Potentially, those modifications of the cranial elements, reflected externally, explain more of the shape diversity than do post-cranial modifications.

All four of these conjectures predict a pattern other than the default explanation that morphological diversity increases with the number of species sampled. Others have shown persuasively that there is not a simple relationship between the numbers of groups sampled and morphological diversity (Foote, 1997 and citations within).

These four conjectures were derived from subjective impressions about morphological diversity proposed by various researchers. These conjectures must be objectively evaluated before any process explanations based upon them can be judged. To test these conjectures, and to describe how shapes are distributed within different groups, mathematical estimates of morphological diversity are used to quantitatively examine the shapes of Great Lake cichlids.

MATERIALS AND METHODS

Ninety-eight species and 953 specimens were used in these analyses. All specimens were obtained from collections at the University of Michigan Museum of Zoology (UMMZ) and from the American Museum of Natural History (AMNH). Species were selected with the goal of sampling as many Malawi and Tanganyika cichlids as possible. The criterion used to select species from the available lots was indiscriminate in respect to habitat, diet, or phylogenetic position. This information was not known before or during the sampling process. Species were initially selected if a minimum of 10 adults were available. It was determined that 10 or more individuals must be measured to give the most reliable estimate of the variability within a species. After these were exhausted (61 of 98 species have at least 10 specimens), the remaining species were selected in an attempt to get an adequate sampling of the remaining shape diversity in the collections. This includes species that would fall near the mean shape as well as outliers. In the case of size dimorphic species, the sex with the largest adults was selected. In the two cases of species with dimorphic shape (the hump-headed males of *Cyrtocara moorii* and *Cyphotilapia frontosa*) the sex with the most distinctive shape was selected (i.e., the males) *a priori*. The effects of intraspecific allometry were also minimized mathematically as described below.

Lists of Tanganyika and Malawi species used and their group designations are in Appendix 1. The sampled species are found in a wide range of habitats and diet classes and should represent a fair sampling of the trophic and ecological diversity of these cichlids (see Appendix 1). However, the original collecting method (e.g., seining) may bias the selection of cichlids available at these museums. Habitat and diet designations and definitions were obtained from Konings (1998, 2001).

Digital images were taken from the left side of all specimens, and landmarks (discrete points on anatomical structures that could be found on every specimen) were digitized. Landmarks

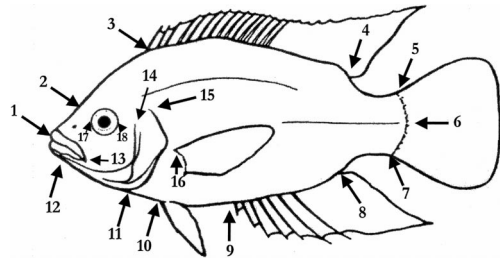


Fig. 1. Landmarks (1) rostral tip of premaxilla (2) dorsal tip of premaxillary pedicel (3) anterior insertion of dorsal fin (4) posterior insertion of dorsal fin (5) dorsal insertion of caudal fin (6) caudal border of hypural plate aligned with lower lateral line (7) ventral insertion of caudal fin (8) posterior insertion of anal fin (9) anterior insertion of anal fin (10) dorsal base of pelvic fin (11) end of opercular membrane ventrally (12) inner aspect of dentary symphysis (13) caudal end of maxilla (14) dorsal end of preopercle ventral to pterotic (15) caudal end of opercle (16) pectoral fin origin (17) anterior margin of midline through eye (18) posterior margin of midline through eye. The base figure is redrawn from Nelson (1994).

were chosen in order to best represent the external shape around the body (Fig. 1). Fin shapes were not included (except for their placement on the body) because of the difficulty of preserving fins intact and because of the challenge of determining homologous positions. Several landmarks were selected based on their prior use in other landmark based geometric morphometric studies of fishes (Fink and Zelditch, 1995; Rüber and Adams, 2001). TPSDIG (F. J. Rohlf, 1998, State University of New York, Buffalo, New York. <http://life.bio.sunysb.edu/ee/rohlf/software.html>) was used to digitize the landmarks on the images.

In order to study shape, information unrelated to shape, including size, orientation, and position, was removed from the configuration of landmarks by rescaling, rotation, and translation. Specimens at fixed centroid size of one were superimposed using Generalized Least Squared (GLS) Procrustes superimposition. In that optimal superimposition the distance minimized is called the Procrustes distance, calculated as the square root of the summed squared distances between homologous landmarks (Rohlf and Slice, 1990; Bookstein 1991; Goodall, 1991). This distance can be used to measure shape disparity (D) following Foote (1993): $D = \sum (d_i^2) / (N-1)$, where d_i^2 is the squared Procrustes distance between the mean shape of a species and the mean shape over all species in the sample (i.e., the grand mean shape), divided by the number of species (N) minus one; this

was then summed over all the species in the sample. N-1 is used because this study deals with a sampling of species rather than an exhaustive analysis of the population as a whole.

Intraspecific shape variation related to size was statistically removed by regression. Specifically, the expected shape at a given size was estimated by multivariate regression of the full set of shape variables on log-transformed centroid size. The residuals from the regression were then added to the expected shape for the mean size. This standardization, to remove the effects of intraspecific allometry, was done using Standard6 (Sheets, unpubl., <http://www2.canisius.edu/~sheets/moremorph.html>).

Statistical significance of the observed differences in shape disparity was determined by carrying out a bootstrap (resampling of specimens with replacement; see Efron and Tibshirani, 1993) test of the range in variation of the shape disparities. The null hypothesis used in the bootstrap test was that the observed difference in disparity could have arisen by random fluctuations in the sampling of specimens, which would lead to incorrect estimates of species mean shapes and thus shape disparity. Rejecting this hypothesis implies that the difference in shape disparity is known with a high enough level of certainty to reject the hypothesis that the observed difference is a sampling artifact. The test permutes the departures from the within group mean (i.e., the multivariate measures of difference from the means). One thousand bootstraps (or 10,000 for C3) were done for each pairwise comparison. The percentage of bootstraps with as large or larger disparity than the original value was reported. This observed percentage provides an estimate of the probability that the observed difference in disparity between two groups could appear by chance. The level of significance was adjusted to be significant across all comparisons at a 5% significance level (a Bonferoni adjustment) by dividing this desired significance level ($p = 0.05$) by the number of total pairwise comparisons in the analysis (for example $p < 0.0018$ for the 28 comparisons in C2). Calculations of disparity, Procrustes superimposition, and bootstrap tests of statistical significance were carried out in PairDisparity6 (Sheets, unpubl., <http://www2.canisius.edu/~sheets/moremorph.html>).

In order to compare the disparity of the head region to the disparity of the post-cranial body, landmarks were partitioned into two groups. Landmarks were divided cranially (10 landmarks: 1, 2, 3, 11, 12, 13, 14, 15, 17, 18) and post-cranially (10 landmarks: 3, 4, 5, 6, 7, 8, 9, 10, 15, 16). Points 3 and 15 are both part of the

posterior portion of the head region and the anterior of the post-cranial body (Fig. 1), and were therefore included in both partitions.

Only tribes that form natural groups (clades) were studied. Monophyly of nine of the 12 tribes originally established by Poll (1986) has been demonstrated (Salzburger et al., 2002; Takahashi, 2003, 2004). Seven of these were sampled here: Ectodini, Lamprologini, Cyprichromini, Tropheini, Limnochromini, Bathybatini, and Perrissodini. Tilapiini is not monophyletic (Klett and Meyer, 2002) and therefore was not included in this comparison of natural groups. Poll's (1986) tribe Trematocarini has been synonymized with Bathybatini (Takahashi, 2003). Unfortunately members of the Eretmodini (4 endemic spp.) and Tylochromini (5 endemic spp.), two of Poll's (1986) original tribes, were unavailable for sampling. All endemic Malawi cichlids sampled here are members of the tribe Haplochromini; all but five endemic cichlids of Lake Malawi are haplochromines (Sturmbauer, 1998). Six haplochromines are endemic to Lake Tanganyika and were also unavailable for sampling.

RESULTS

The conjecture that Tanganyika cichlids have greater morphological diversity than Lake Malawi cichlids (C1) is corroborated by estimates of shape disparity. The absolute difference in disparity values for the two lakes show that Tanganyika ($D = 0.00524$) has a value twice that of Lake Malawi ($D = 0.00260$). The difference in shape disparity of the cichlids of the two lakes is statistically significant ($p < 0.05$).

The conjecture that Ectodini or Lamprologini have the greatest morphological diversity of the Great Lake tribes (C2) finds that only the Ectodini ($D = 0.00467$) has significantly greater shape disparity than the other sampled tribes (Fig. 2, Table 1). The Lamprologini is the second most disparate clade ($D = 0.00313$) and are significantly more disparate than the remaining groups except the Limnochromini ($D = 0.00266$) and Bathybatini ($D = 0.00255$). Five species of lamprologines are found in the Congo River system outside of Lake Tanganyika (Salzburger et al., 2002). The disparity level for Lamprologini did not change significantly by including one riverine species, *Lamprologus mocquardi* (AMNH 5828, 10 specimens, 61–50 mm SL). The Cyprichromini ($D = 0.00071$) had significantly lower disparity than all other sampled groups.

The conjecture that piscivores have less morphological diversity than other diet classes (C3)

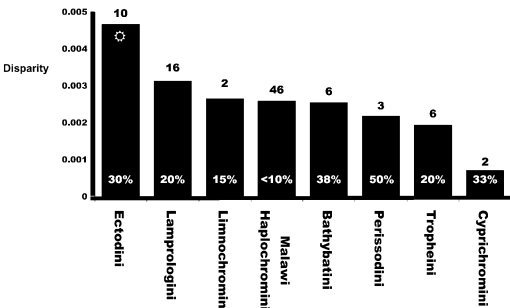


Fig. 2. Tribes shown in descending order of shape disparity. Star indicates a significant difference in shape disparity from all other groups. Numbers above bars indicate the number of species sampled and the number below each bar represents the percentage of species sampled from each clade, calculated using the total number of species found in each tribe as reported by Salzburger et al. (2002) and Takahashi (2003).

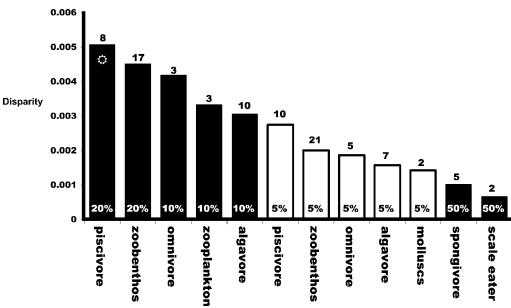


Fig. 3. Cichlid diet classes shown in descending order of shape disparity. Malawi groups are represented by white bars and Tanganyika groups are indicated by black bars. A star indicates a significant difference in disparity from all other groups. The number above each bar is the number of species sampled in this analysis; the percent sampled from each diet class is given below each bar. A rough estimate of the number of species in each group was obtained from Konings (1998, 2001).

is rejected by the analysis of shape disparity (Fig. 3, Table 2). Contrary to any notion that piscivores will be constrained to particular shapes because of their specialized diet, piscivores are the most disparate diet group from each lake. In Lake Malawi, piscivores ($D = 0.00275$) have significantly higher disparity than all other Malawi diet groups except molluscivores ($D = 0.00143$). Tanganyika piscivores ($D = 0.00508$) have significantly higher disparity than any other diet group from either lake. Zoobenthos feeders and omnivores are respectively the second and third most disparate diet class in both lakes. Malawi cichlids group together with intermediate disparity between the more disparate Tanganyika diet guilds (piscivores, zoobenthivores, omnivores, zooplanktivores, algavores) and the least disparate Tanganyika diet guilds (sponge eaters, scale eaters).

The conjecture that the majority of the differences between the shapes of cichlids lie within the shape of the head region (C4) was supported. For the cichlids from both lakes the disparity of the cranial region was significantly higher than that of the post-cranial region. The partitioned disparity values for Tanganyika cichlids were cranially 0.04545 and post-cranially 0.00643. The partitioned disparity values for Malawi cichlids were cranially 0.05174 and post-cranially 0.00255. In all six pairwise comparisons possible between these four partitioned regions, disparity values were significantly different from each other ($p < 0.05$).

DISCUSSION

Two of the four conjectures tested were supported. The shape disparity of Tanganyika cich-

TABLE 1. BOOTSTRAP TEST RESULTS FOR PAIRWISE COMPARISONS OF SHAPE DISPARITY BETWEEN TRIBES. With a Bonferoni adjustment for 28 pairwise comparisons the 5% significance level is reached when $p < 0.0018$. The tribe listed in the left column of each row is significantly more disparate than the tribes listed on the right column of each row.

Tribes	Significantly less disparate tribes
Ectodini	significantly greater shape disparity than all other tribes
Lamprologini	Malawi Haplochromini, Perissodini, Tropheini, Cyprichromini
Limnochromini	Cyprichromini
Malawi Haplochromini	Cyprichromini
Bathybatini	Cyprichromini
Perissodini	Cyprichromini
Tropheini	Cyprichromini
Cyprichromini	significantly lower shape disparity than all other tribes

TABLE 2. BOOTSTRAP TEST RESULTS FOR PAIRWISE COMPARISONS OF SHAPE DISPARITY BETWEEN DIET CLASSES. With a Bonferoni adjustment for 66 pairwise comparisons the 5% significance level is reached when $p < 0.00075$. The diet class listed in the left column of each row is significantly more disparate than the diet classes listed on the right column of each row.

Diet Class	Significantly Less Disparate Diet Classes
Tanganyika piscivores	significantly greater shape disparity than all other diet classes
Tanganyika zoobenthivores	Tanganyika zooplanktivores, Tanganyika algavores, Malawi piscivores, Malawi zoobenthivores, Malawi omnivores, Malawi algavores, Malawi molluscivores, Tanganyika spongivores, Tanganyika scale-eaters
Tanganyika omnivores	same as above group
Tanganyika zooplanktivores	Malawi zoobenthivores, Malawi omnivores, Malawi algavores, Malawi molluscivores, Tanganyika spongivores, Tanganyika scale-eaters
Tanganyika algavores	same as above group
Malawi piscivores	Malawi zoobenthivores, Malawi omnivores, Malawi algavores, Tanganyika spongivores, Tanganyika scale-eaters
Malawi zoobenthivores	Malawi algavores, Tanganyika spongivores, Tanganyika scale-eaters
Malawi omnivores	Tanganyika scale-eaters
Malawi algavores	no diet classes significantly less disparate
Malawi molluscivores	no diet classes significantly less disparate
Tanganyika spongivores	no diet classes significantly less disparate
Tanganyika scale-eaters	no diet classes significantly less disparate

lids was found to be significantly greater than that of Malawi cichlids (C1) and the cranial regions of cichlids were found to be significantly more disparate than the post-cranial regions (C4). Contrary to C3, piscivores were not less disparate than cichlids in other diet classes and contrary to C2 the Lamprologini was not found to be the most disparate of Great Lake tribes.

It has been claimed that ecological diversity is correlated with morphological diversity in cichlids (Liem, 1973; Liem and Osse, 1975; Klingenberg et al., 2003). Given the results of C2 this claim may require further study. Ectodini and Lamprologini had the highest values of shape disparity of any clades in this study and are arguably the two most ecologically diverse clades of Tanganyika cichlids (Sturmbauer and Meyer, 1993; Stiassny, 1997). However, the Limnochromini (which did not differ statistically in disparity from the Lamprologini) are mainly zoobenthivores (Salzburger et al., 2002). The least morphologically disparate clade, the Cyprichromini, have a relatively wide diet range that includes both plankton and crustaceans (Konings, 1998; Salzburger et al., 2002).

Conjecture 4 is an attempt to explain which portion of the cichlid body is responsible for the difference in morphological diversity between the species of these two lakes. The results for C4 show that there are greater differences within the cranial region than in post-cranial comparisons. It appears that this result alone cannot explain where the difference in shape disparity of the cichlids of these two lakes is de-

rived. Cranial disparity of Malawi cichlids is significantly greater than cranial disparity of Tanganyika cichlids; notably, this is the opposite of the result found in the comparison of the entire body (C1). Post-cranially, Tanganyika cichlids have significantly greater disparity than Malawi cichlids; this is consistent with what was found with the total body comparison. Therefore, within a lake, differences in head shape contribute most to differences in the total body shape among species. However, in the comparison of species across the two lakes, it is differences in the post-cranial body that contributes to the greater disparity measured for Lake Tanganyika cichlids over those of Lake Malawi. It is unclear why there is such a high degree of post-cranial diversity in Lake Tanganyika cichlids relative to those of Malawi. Post-cranial diversity has been little discussed in the cichlid literature as the focus has been on the conspicuous differences of the head.

In their subjective estimates of the morphological diversity of piscivorous cichlids (C3), researchers perhaps focused too narrowly on the many large streamlined species while failing to account for the variety of less conspicuous forms. This bias led to the false prediction of conjecture 3, that piscivorous cichlids would be the least disparate diet group. Different kinds of piscivorous cichlids (e.g., ambush hunting, pursuit hunters) have different specialized shapes, leading to the high disparity of this diet class.

A discord between species richness and morphological diversity has been demonstrated

twice in this study, and it is well-known that the two aspects of diversity are unrelated (Foote, 1993). Lake Malawi has two to three times as many species (600–900 spp.) as Lake Tanganyika (200–300 spp.) which has a more disparate cichlid fauna. Ectodines have less than half of the number of described species (30 spp.) of the less disparate lamprologines (79 spp.). The greater disparity in Lake Tanganyika and in the ectodines must represent the effects of processes other than speciation alone. Having found that species richness and disparity are discordant, we can consider other explanations for disparity in these lakes, a subject of much debate (Bouton et al., 2002b; Smith et al., 2003; Terai et al., 2003).

It is important to note that while some of these conjectures were statistically supported, a relatively small percentage of Great Lake cichlids were sampled. The results of any of these conjectures could be problematic if my sampling methods were flawed. Species were selected in order to best test Conjecture 1. An attempt was made to exhaustively sample as many Malawi and Tanganyika species as were available at the UMMZ and AMNH. The number of adults present in these collections limited sampling. Obtaining an accurate measure of within-species variation was initially given priority over the sampling of additional species. Over- or under-estimates of disparity may have resulted from using this criterion. For example, if all selected members of a group are deep bodied and there were no shallow bodied forms with an adequate sample available, disparity of that group will be underrepresented. In an attempt to remedy this I sampled an additional 30 species that had between five and nine adults. These were selected in order to obtain a sample of nearly 50 species from each lake and also to better represent the disparity of the cichlids of Lake Tanganyika and Malawi. Sampling was not purposefully biased in favor of any particular ecology, habitat, clade, or diet. However, it is important to remember that this deals only with the sampling from these museums (UMMZ, AMNH). The disparity of a group, as it is found in nature, may be misrepresented by the collections available. Undoubtedly, some readers may know of species not sampled that could have changed disparity values for the groups studied. Despite the large numbers of species sampled many more could have been included. Selective sampling of particular species or groups would have compromised the unbiased procedure used here. In future studies more focused sampling of different groups could be important.

My results should be viewed as exploratory

rather than complete. Any study on Great Lake cichlids that spans all major clades, diets, and habitats would require a greater number of species than analyzed here. Nevertheless, this study is the first to test some long standing assumptions that are important to broader theories about cichlid evolution. It provides a new framework for more precise and robust hypotheses about the patterns and processes in this remarkable group of fishes.

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APPENDIX 1: TANGANYIKA SPECIES USED IN THIS STUDY WITH TRIBAL DESIGNATIONS FROM POLL (1986) AND TAKAHASHI (2003). Diet and habitat information are from Konings (1998).

Tanganyika species	Tribe, habitat, diet	Material examined: museum acronym, number, size range in mm SL
<i>Aulonocranus dewindti</i>	Ectodini, intermediate, zoobenthivore	AMNH 58465, 2, 76–66; AMNH 97208, 5, 95–66; AMNH 217370, 6, 66–76; AMNH 225852, 1, 70
<i>Bathybates fasciatus</i>	Bathybatini, the depths, piscivore	UMMZ 199020, 2, 164–120; AMNH 11721, 1, 96; AMNH 217380, 1, 210
<i>Bathybates ferox</i>	Bathybatini, the depths, piscivore	UMMZ 199759, 6, 215–164; AMNH 216020, 1, 184
<i>Bathybates graueri</i>	Bathybatini, the depths, piscivore	UMMZ 199802, 8, 148–120; AMNH 58482, 2, 129–128
<i>Bathybates leo</i>	Bathybatini, the depths, piscivore	UMMZ 199789, 1, 237, UMMZ, 199803, 2, 192–144; AMNH 215727, 1, 270; AMNH 216021, 1, 160
<i>Bathybates vittatus</i>	Bathybatini, the depths, piscivore	UMMZ 199790, 1, 195; UMMZ 199804, 1, 140; AMNH 217410, 1, 272
<i>Boulengerochromis microlepis</i>	Boulengerochromini, sandy, piscivore	UMMZ 199791, 1, 240; UMMZ 199806, 2, 121–105; AMNH 217356, 1, 180; AMNH 215728, 1, 300
<i>Callochromis macrops</i>	Ectodini, shallow sediment rich, zoobenthivore	UMMZ 196124, 1, 91; UMMZ 199866, 6, 98–84; AMNH 11720, 1, 88; AMNH 58485, 1, 91; AMNH 97209, 1, 99
<i>Callochromis pleurospilus</i>	Ectodini, shallow sediment rich, zoobenthivore	AMNH 217381, 14, 74–55
<i>Chalinochromis brichardi</i>	Lamprologini, shallow precipitous rocky, spongivore	UMMZ 196155, 2, 99–55; UMMZ 196156, 1, 75; UMMZ 215995, 1, 95; UMMZ 218325, 1, 47; AMNH 97173, 1, 57; AMNH 97178, 2, 79–78; AMNH 98027, 2, 88–80
<i>Cunningtonia longiventralis</i>	Ectodini, intermediate, algavore	UMMZ 199760, 2, 112–102; UMMZ 199868, 2, 50–46; AMNH 58487, 2, 77–70
<i>Cyathopharynx furcifer</i>	Ectodini, intermediate, algavore	AMNH 58477, 4, 118–86; AMNH 96772, 8, 142–103
<i>Cyphotilapia frontosa</i>	Cyphotilapiini, deep rocky, piscivore	AMNH 58479, 1, 128; AMNH 97212, 2, 166–124; AMNH 98014, 6, 159–91; AMNH 217394, 3, 141–110
<i>Cyprichromis microlepidotus</i>	Cyprichromini, open water, omnivore	AMNH 217387, 15, 93–75
<i>Ectodus descampsi</i>	Ectodini, sandy, zoobenthivore	UMMZ 196157, 2, 50; UMMZ 196158, 4, 90–83; AMNH 11753, 1, 75; AMNH 58464, 3, 77–66
<i>Enantiopus melanogenys</i>	Ectodini, sandy, zoobenthivore	UMMZ 196082, 3, 101–97; UMMZ 196176, 4, 114–80; AMNH 58488, 5, 92–85
<i>Gnathochromis permaxillaris</i>	Limnochromini, deep rocky, zoobenthivore	AMNH 58474, 2, 111–96; AMNH 217350, 2, 120–119; AMNH 217391, 5, 128–80
<i>Grammatotria lemairii</i>	Ectodini, intermediate, zoobenthivore	UMMZ 199763, 1, 117; UMMZ 196159, 3, 113–98; AMNH 58462, 2, 106–101; AMNH 11725, 1, 124.3; AMNH 216019, 2, 160–156; AMNH 217345, 1, 170
<i>Haplotaxodon microlepis</i>	Perissodini, open water, piscivore	UMMZ 199765, 4, 185–145; AMNH 97212, 2, 166–124; AMNH 97214, 1, 141; AMNH 98014, 3, 159–129; AMNH 98028, 4, 205–179; AMNH 98041, 3, 107–91; AMNH 217363, 2, 125–110; AMNH 217394, 3, 141–110

APPENDIX 1: CONTINUED.

Tanganyika species	Tribe, habitat, diet	Material examined: museum acronym, number, size range in mm SL
<i>Julidochromis marlieri</i>	Lamprologini, shallow precipitous rocky, spongivore	UMMZ 196160, 7, 69–41; AMNH 97175, 1, 64; AMNH 217375, 1, 112; AMNH 225775, 1, 58
<i>Julidochromis ornatus</i>	Lamprologini, intermediate, spongivore	AMNH 98005, 1, 56; AMNH 98006, 1, 55; AMNH 98008, 3, 51–40; AMNH 98010, 1, 55; AMNH 98012, 1, 45; AMNH 98013, 1, 60; AMNH 98037, 1, 54; AMNH 98063, 1, 56; AMNH 98064, 1, 50; AMNH 215845, 1, 46; AMNH 225773, 1, 61
<i>Julidochromis regani</i>	Lamprologini, intermediate, spongivore	UMMZ 196161, 3, 91–43; UMMZ 215999, 1, 57; AMNH 97584, 1, 86.2; AMNH 216070, 3, 67–65; AMNH 217353, 1, 86
<i>Julidochromis transcriptus</i>	Lamprologini, shallow precipitous rocky, spongivore	AMNH 97588, 1, 39; AMNH 226102, 3, 32–30
<i>Lepidiolamprologus profundicola</i>	Lamprologini, deep rocky, piscivore	UMMZ 195983, 5, 214–150; UMMZ 199952, 4, 160–95; UMMZ 199782, 4, 214–164; AMNH 225871, 2, 220–205
<i>Limnochromis auritus</i>	Limnochromini, muddy bottoms, zoobenthivore	UMMZ 195997, 1, 86; UMMZ 196016, 1, 102; UMMZ 196139, 1, 116; AMNH 58486, 2, 84–58; AMNH 97222, 2, 148–117
<i>Limnotilapia dardennii</i>	Tropheini, shallow sediment rich, omnivore	UMMZ 199774, 8, 202–121; AMNH 58471, 1, 97; AMNH 97223, 1, 124
<i>Lobochilotes labiatus</i>	Tropheini, intermediate, zoobenthivore	UMMZ 199776, 5, 187–101; UMMZ 199878, 4, 82–62; AMNH 58468, 1, 97
<i>Neolamprologus brevis</i>	Lamprologini, empty shells, zooplanktivore	AMNH 97191, 1, 51; AMNH 217373, 10, 41–35
<i>Neolamprologus caudopunctatus</i>	Lamprologini, intermediate, zoobenthivore	AMNH 97200, 2, 47–41; AMNH 98069, 8, 47–42
<i>Neolamprologus modestus</i>	Lamprologini, intermediate, zoobenthivore	UMMZ 196137, 2, 88–86; AMNH 97193, 1, 69; AMNH 98035, 5, 88–72; AMNH 98047, 1, 76; AMNH 98075, 1, 71
<i>Neolamprologus petricola</i>	Lamprologini, intermediate, zoobenthivore	UMMZ 199913, 1, 93; UMMZ 199772, 1, 104; UMMZ 199875, 1, 96; AMNH 98085, 1, 86
<i>Neolamprologus pulcher</i>	Lamprologini, shallow precipitous rocky, zooplanktivore	AMNH 98049, 8, 51–27
<i>Neolamprologus savoryi</i>	Lamprologini, shallow precipitous rocky, zooplanktivore	UMMZ 194164, 4, 65–48; UMMZ 199840, 2, 52–48; AMNH 77447, 4, 60–56
<i>Neolamprologus sexfasciatus</i>	Lamprologini, intermediate, zoobenthivore	UMMZ 199773, 6, 121–83; UMMZ 199841, 1, 107; UMMZ 199876, 1, 71; AMNH 98022, 1, 84; AMNH 98051, 1, 108
<i>Neolamprologus tetrocephalus</i>	Lamprologini, intermediate, zoobenthivore	AMNH 216213, 2, 87–63
<i>Oreochromis tanganyicae</i>	Tilapiini, shallow sediment rich, algavore	AMNH 10708, 1, 138; AMNH 11717, 1, 105.1; AMNH 97225, 9, 85–62; AMNH 225854, 1, 84
<i>Paracyprichromis nigripinnis</i>	Cyprichromini, open water, omnivore	AMNH 216146, 4, 60–46; AMNH 217392, 2, 71–70; AMNH 225826, 1, 83

APPENDIX 1: CONTINUED.

Tanganyika species	Tribe, habitat, diet	Material examined: museum acronym, number, size range in mm SL
<i>Perissodus microlepis</i>	Perrissodini, shallow precipitous rocky, scale eater	UMMZ 196057, 2, 104–84; AMNH 97226, 1, 81; AMNH 98054, 3, 100–94; AMNH 98080, 4, 109–66
<i>Petrochromis fasciolatus</i>	Tropheini, intermediate, algavore	UMMZ 199779, 5, 114–80; AMNH 58481, 4, 115–80; AMNH 98032, 1, 144
<i>Petrochromis polyodon</i>	Tropheini, shallow precipitous rocky, algavore	UMMZ 199952, 4, 160–95; AMNH 58478, 4, 108–74; AMNH 98040, 1, 168; AMNH 98081, 2, 77–66
<i>Plecodus multidentatus</i>	Perrissodini, the depths, scale eater	UMMZ 196062, 2, 196062; AMNH 217399, 9, 115–81
<i>Simochromis diagramma</i>	Tropheini, shallow sediment rich, algavore	UMMZ 199883, 4, 127–94; AMNH 215567, 1, 97, AMNH 56127 1, 121; AMNH 19639, 1, 91; AMNH 217347, 1, 115
<i>Telmatochromis temporalis</i>	Lamprologini, shallow precipitous rocky, algavore	UMMZ 199885, 4, 81–61; AMNH 97230, 1, 54; AMNH 98054, 1, 44; AMNH 98057, 2, 50–40
<i>Trematocara unimaculatum</i>	Bathybatini, the depths, zoobenthivore	AMNH 217389, 10, 110–84
<i>Tropheus moorei</i>	Tropheini, shallow precipitous rocky, algavore	AMNH 97998, 10, 96–86
<i>Variabilichromis moorii</i>	Lamprologini, shallow precipitous rocky, algavore	AMNH 98019, 10, 72–55
<i>Xenotilapia longispinis</i>	Ectodini, muddy bottoms, zoobenthivore	UMMZ 196079, 6, 110–99; UMMZ 196080, 3, 103–95; AMNH 217355, 2, 101–97
<i>Xenotilapia ornatipinnis</i>	Ectodini, sandy, zoobenthivore	UMMZ 196083, 3, 96–85; AMNH 58466, 4, 71–61; AMNH 217352, 2, 71–67

APPENDIX 2: MALAWI SPECIES SAMPLED IN THIS STUDY. Group designations are from Eccles and Trewavas (1989); diet and habitat information are from Konings (2001).

Malawi species	Tribe, habitat, diet	Material examined: museum acronym, number, size range in mm SL
<i>Alticorpus macrocleithrum</i>	Haplochromini, sandy, zoobenthivore	AMNH 221988, 10, 109–82
<i>Aulonocara guentheri</i>	Haplochromini, sandy, zoobenthivore	AMNH 221259, 1, 120; AMNH 221927, 9, 113–70
<i>Aulonocara macrochir</i>	Haplochromini, sandy, zoobenthivore	AMNH 47991, 2, 125–122; AMNH 47994, 1, 130; AMNH 222075, 7, 105–71
<i>Copadichromis eucinostomus</i>	Haplochromini, open water, zooplanktivore	AMNH 31855, 10, 99–65
<i>Ctenopharynx intermedius</i>	Haplochromini, intermediate, zoobenthivore	AMNH 22024, 7, 141–100; AMNH 31834, 3, 154–146
<i>Ctenopharynx nitidus</i>	Haplochromini, sandy, zoobenthivore	AMNH 31836, 6, 129–112; AMNH 221888, 4, 111–99
<i>Ctenopharynx pictus</i>	Haplochromini, intermediate, zoobenthivore	AMNH 31786, 2, 103–90; AMNH 31788, 4, 103–90; AMNH 221268, 1, 106; AMNH 221270, 2, 75–68; AMNH 222091, 1, 90
<i>Cyrtocara moorii</i>	Haplochromini, sandy, zoobenthivore	UMMZ 218306, 8, 95–70; AMNH 31781, 1, 121; AMNH 31831, 1, 150
<i>Dimidiichromis compressiceps</i>	Haplochromini, shallow sediment rich bays, piscivore	UMMZ 218307, 6, 86–77; UMMZ 218345, 2, 144–124; AMNH 221892, 1, 178; AMNH 222443, 1, 144
<i>Hemitilapia oxyrhynchus</i>	Haplochromini, shallow sediment rich bays, algavore	UMMZ 218294, 3, 98–85; UMMZ 218346, 1, 96; AMNH 31880, 5, 127–103; AMNH 221878, 1, 120; AMNH 222080, 1, 116; AMNH 222445, 1, 108
<i>Labeotropheus fuelleborni</i>	Haplochromini, wave washed upper rocky, algavore	UMMZ 218348, 3, 142–120; UMMZ 218349, 2, 110–109; UMMZ 237733, 4, 119–81; UMMZ 238339, 11, 115–85
<i>Lethrinops albus</i>	Haplochromini, sandy, zoobenthivore	AMNH 221260, 10, 100–78
<i>Lethrinops furcifer</i>	Haplochromini, sandy, zoobenthivore	AMNH 57496, 1, 138; AMNH 221254, 6, 141–98; AMNH 221256, 3, 150–140
<i>Lethrinops mylodon</i>	Haplochromini, sandy, molluscivore	UMMZ 218350, 11, 104–90; UMMZ 218351, 1, 97.8
<i>Lethrinops stridei</i>	Haplochromini, sandy, algavore	AMNH 57494, 10, 118–69
<i>Maravichromis guentheri</i>	Haplochromini, sediment rich rocky, zoobenthivore	AMNH 31808, 7, 97–81
<i>Melanochromis auratus</i>	Haplochromini, sediment free rocky, omnivore	UMMZ 237729, 3, 76–65; 237730, 4, 68–61; AMNH 226049, 1, 84; AMNH 226070, 6, 64–53
<i>Melanochromis</i> sp.	Haplochromini, sediment free rocky, omnivore	UMMZ 238336, 20, 78–52
<i>Melanochromis johannii</i>	Haplochromini, intermediate, omnivore	AMNH 215563, 10, 81–53
<i>Melanochromis vermivorus</i>	Haplochromini, sediment free rocky, omnivore	UMMZ 218352, 3, 107–90; AMNH 31896, 2, 61–55; AMNH 215557, 1, 47
<i>Mylochromis gracilis</i>	Haplochromini, sandy, piscivore	AMNH 31820, 1, 183; AMNH 221873, 1, 117; AMNH 221887, 1, 142; AMNH 221894, 1, 119; AMNH 222045, 3, 158–147

APPENDIX 2: CONTINUED.

Malawi species	Tribe, habitat, diet	Material examined: museum acronym, number, size range in mm SL
<i>Nimbochromis livingstonii</i>	Haplochromini, shallow sediment rich bays, piscivore	UMMZ 218312, 1, 134; UMMZ 218353, 160–148; AMNH 31803, 5, 152–143; AMNH 221959, 1, 161; AMNH 221989, 1, 130
<i>Nimbochromis venustus</i>	Haplochromini, shallow sediment rich bays, piscivore	AMNH 221885, 4, 133–99; AMNH 221889, 1, 165; AMNH 221991, 2, 158–131; AMNH 222064, 3, 141–87
<i>Nyassachromis leuciscus</i>	Haplochromini, sandy, zoobenthivore	AMNH 11730, 1, 83; AMNH 31839, 1, 115; AMNH 221228, 1, 80; AMNH 221949, 6, 103–88
<i>Oreochromis shiranus</i>	Tilapiine, shallow sediment rich bays, detritivore	AMNH 31871, 9, 137–95; AMNH 31930, 2, 131–98
<i>Otopharynx argyrosoma</i>	Haplochromini, sandy, zoobenthivore	AMNH 221217, 5, 111–90; AMNH 221900, 3, 110–97; AMNH 221950, 106–91
<i>Otopharynx heterodon</i>	Haplochromini, intermediate, zoobenthivore	AMNH 221923, 10, 89
<i>Otopharynx lithobates</i>	Haplochromini, intermediate, zoobenthivore	UMMZ 218314, 1, 90; UMMZ 218354, 2, 78–74
<i>Otopharynx ovatus</i>	Haplochromini, open water, egg stealer	UMMZ 218355, 5, 126–86; AMNH 221229, 1, 111
<i>Otopharynx tetrastigma</i>	Haplochromini, shallow sediment rich bays, zoobenthivore	AMNH 43209, 6, 85–74; AMNH 216297, 4, 91–61; AMNH 222036, 1, 81
<i>Placidochromis electra</i>	Haplochromini, sandy, zoobenthivore	UMMZ 218315, 4, 100–80; 218356, 6, 115–80; AMNH 220339, 6, 111–76
<i>Placidochromis johnstoni</i>	Haplochromini, shallow, sediment rich bays, piscivore	AMNH 31775, 1, 102; AMNH 221271, 1, 82; AMNH 221699, 2, 133–100; AMNH 221893, 1, 75; AMNH 221899, 1, 81; AMNH 221958, 3, 102–84; AMNH 222058, 1, 118
<i>Placidochromis subocularis</i>	Haplochromini, sandy, zoobenthivore	AMNH 31821, 1, 137; AMNH 221990, 6, 135–106; AMNH 226026, 1, 113; AMNH 226054, 2, 124–100
<i>Protomelas fenestratus</i>	Haplochromini, intermediate, zoobenthivore	AMNH 221891, 10, 96–76
<i>Protomelas marginatus</i>	Haplochromini, shallow, sediment rich bays, zoobenthivore	UMMZ 218357, 5, 135–110; AMNH 31849, 2, 105–96; AMNH 221984, 1, 105
<i>Pseudotropheus elegans</i>	Haplochromini, sandy, zoobenthivore	AMNH 221875, 6, 87–77
<i>Pseudotropheus elongatus</i>	Haplochromini, sediment free rocky, algavore	UMMZ 237517, 6, 73–67; AMNH 226030, 1, 74
<i>Pseudotropheus macrophthalmus</i>	Haplochromini, sediment free rocky, algavore	UMMZ 218300, 3, 88–81; UMMZ 218360, 3, 108–82
<i>Pseudotropheus tropheops</i>	Haplochromini, sediment free rocky, algavore	UMMZ 237515, 6, 92–80, UMMZ 237516, 23, 86–70; UMMZ 237519, 5, 84–77; UMMZ 237522, 3, 96–78; UMMZ 237524, 5, 81–71
<i>Pseudotropheus zebra</i>	Haplochromini, sediment free rocky, algavore	UMMZ 218301, 8, 83–75; UMMZ 218302, 1, 76; UMMZ 218303, 2, 73–66; 218362, 9, 106–73

APPENDIX 2: CONTINUED.

Malawi species	Tribe, habitat, diet	Material examined: museum acronym, number, size range in mm SL
<i>Sciaenochromis spilostichus</i>	Haplochromini, sandy, piscivore	AMNH 31838, 2, 190–187, AMNH 31885, 1, 148; AMNH 221954, 1, 103; AMNH 222043, 4, 117–105; AMNH 222049, 1, 92; AMNH 222083, 1, 101
<i>Serranochromis robustus</i>	Haplochromini, shallow intermediate, piscivore	AMNH 31877, 1, 150; AMNH 97667, 2, 214–168, AMNH 215574, 2, 170–137
<i>Stigmatochromis modestus</i>	Haplochromini, sediment rich rocky, piscivore	AMNH 31792, 1, 117; AMNH 31794, 1, 137; AMNH 31828, 1, 102; AMNH 215568, 1, 106
<i>Stigmatochromis pholidophorus</i>	Haplochromini, intermediate, piscivore	AMNH 31798, 1, 122; AMNH 216301, 2, 105–103; AMNH 221246, 1, 118; AMNH 221701, 1, 107; AMNH 221895, 1, 117; AMNH 221930, 1, 117; AMNH 221933, 1, 142; AMNH 221995, 1, 150; AMNH 222029, 2, 116–112
<i>Stigmatochromis woodi</i>	Haplochromini, sandy, piscivore	AMNH 31795, 1, 110; AMNH 31796, 1, 146; AMNH 31800, 1, 148; AMNH 221877, 1, 149; AMNH 222026, 3, 129–108
<i>Tramitichromis lituris</i>	Haplochromini, sandy, omnivore	AMNH 222021, 12, 119–90
<i>Trematocranus microstoma</i>	Haplochromini, sandy, zoobenthivore	AMNH 58007, 1, 114; AMNH 222076, 1, 50; AMNH 216101, 3, 154–147
<i>Trematocranus placodon</i>	Haplochromini, sandy, molluscivore	AMNH 31758, 1, 116; AMNH 31823, 1, 135; AMNH 31824, 2, 138–130, AMNH 31883, 1, 82; AMNH 57493, 1, 121; AMNH 57498, 1, 120; AMNH 57499, 1, 113; AMNH 221929, 1, 114; AMNH 222082, 1, 148