GEOMETRIC MORPHOMETRIC ANALYSES PROVIDE EVIDENCE FOR THE ADAPTIVE CHARACTER OF THE TANGANYIKAN CICHLID FISH RADIATIONS

Céline Clabaut,[1,2,3,4] Paul M. E. Bunje,[1,4,5] Walter Salzburger,[1,6,7] and Axel Meyer[1,8]

[1]Lehrstuhl für Zoologie und Evolutionsbiologie, Department of Biology, University of Konstanz, 78457 Konstanz, Germany

[2]Department of Developmental Biology, Harvard School of Dental Medicine, Harvard Medical School, Boston, Massachusetts 02115

[3]E-mail: celine_clabaut@hsdm.harvard.edu

[4]These authors contributed equally to this work.

[5]E-mail: pmebunje@gmail.com

[6]Department of Ecology and Evolution, UNIL Sorge, Le Biophore, CH - 1015 Lausanne, Switzerland

[7]E-mail: walter.salzburger@unil.ch

[8]Corrosponding author e-mail: axel.meyer@uni-konstanz.de

The cichlids of East Africa are renowned as one of the most spectacular examples of adaptive radiation. They provide a unique opportunity to investigate the relationships between ecology, morphological diversity, and phylogeny in producing such remarkable diversity. Nevertheless, the parameters of the adaptive radiations of these fish have not been satisfactorily quantified yet. Lake Tanganyika possesses all of the major lineages of East African cichlid fish, so by using geometric morphometrics and comparative analyses of ecology and morphology, in an explicitly phylogenetic context, we quantify the role of ecology in driving adaptive speciation. We used geometric morphometric methods to describe the body shape of over 1000 specimens of East African cichlid fish, with a focus on the Lake Tanganyika species assemblage, which is composed of more than 200 endemic species. The main differences in shape concern the length of the whole body and the relative sizes of the head and caudal peduncle. We investigated the influence of phylogeny on similarity of shape using both distance-based and variance partitioning methods, finding that phylogenetic inertia exerts little influence on overall body shape. Therefore, we quantified the relative effect of major ecological traits on shape using phylogenetic generalized least squares and disparity analyses. These analyses conclude that body shape is most strongly predicted by feeding preferences (i.e., trophic niches) and the water depths at which species occur. Furthermore, the morphological disparity within tribes indicates that even though the morphological diversification associated with explosive speciation has happened in only a few tribes of the Tanganyikan assemblage, the potential to evolve diverse morphologies exists in all tribes. Quantitative data support the existence of extensive parallelism in several independent adaptive radiations in Lake Tanganyika. Notably, Tanganyikan mouthbrooders belonging to the C-lineage and the substrate spawning Lamprologini have evolved a multitude of different shapes from elongated and *Lamprologus*-like hypothetical ancestors. Together, these data demonstrate strong support for the adaptive character of East African cichlid radiations.

KEY WORDS: Adaptive radiation, body shape, comparative method, ecomorphology, geometric morphometrics, morphological disparity, phylogenetic generalized least squares.

The Great Lakes of East Africa (Victoria, Malawi, and Tanganyika) are among the world's most diverse freshwater ecosystems and contain unique species flocks of cichlid fish composed of hundreds of endemic species each (Fryer and Iles 1972). The large number of species, the high degree of ecological and morphological specialization, and the rapidity of lineage formation make these fish ideal model systems for the study of adaptive radiation and explosive speciation (Fryer and Iles 1972; Meyer 1993; Stiassny and Meyer 1999; Kornfield and Smith 2000; Kocher 2004; Salzburger and Meyer 2004). Adaptive radiation was defined by Simpson (1953) as the "more or less simultaneous divergence of numerous lines from much the same adaptive type into different, also diverging adaptive zones." In the case of the East African cichlids, this diversification process has indeed occurred within a short period of time over wide geographic areas, resulting in unresolved phylogenies and short branches therein (Kornfield and Smith 2000). Though considered one of the best examples of adaptive radiation, the occupation of diverging adaptive zones has not previously been analyzed quantitatively. In addition to the rapidity of speciation, Schluter (2000) defines three other criteria of adaptive radiations: common ancestry, phenotype–environment correlation, and utility of the trait (performance or fitness advantages of the trait in its corresponding environment). Through the quantification of the morphological variation of the body shapes of many cichlid species, we tested the phenotype–environment correlation for the Tanganyikan cichlid species flock, a critical estimate of the breadth of adaptive zone occupation and crucial to the conclusive demonstration of the phenomenon of adaptive radiation.

Lake Tanganyika is the oldest of the Great Lakes with an estimated age of nine to 12 million years (Cohen et al. 1993, 1997). Although lakes Victoria and Malawi are younger, they harbor more species of cichlid fish (~500 and ~1000 species, respectively). However, the estimated 250 cichlids species (Brichard 1989; Snoeks et al. 1994; Turner et al. 2001) in Lake Tanganyika are phylogenetically, morphologically, ecologically, and behaviorally the most diverse. The original assignment to tribes was established by Poll (1986). Recently, Takahashi (2003) suggested the erection of five additional tribes for genera previously assigned to one of Poll's 12 tribes (Poll 1986). These taxonomic studies were based solely on morphological characters. Furthermore, it has been established with molecular markers that the lake was seeded by several ancient lineages (Nishida 1991; Kocher et al. 1995; Salzburger et al. 2002) that evolved in step with changes in the lake's environment: the Tylochromini, Trematocarini, Bathybatini, Tilapiini, Boulengerochromini, Eretmodini, the ancestor of the Lamprologini, and the ancestor of the C-lineage (Clabaut et al. 2005). The C-lineage diversified further from a supposed *Lamprologus*-like ancestor (Salzburger et al. 2002; Koblmueller et al. 2004) into eight tribes, the Cyphotilapi-ini, the Limnochromini, the Cyprichromini, the Perissodini, the Orthochromini, the Ectodini, and the Haplochromini including the Tropheini (Sturmbauer and Meyer 1993; Kocher et al. 1995; Salzburger et al. 2002, 2005; Verheyen et al. 2003; Clabaut et al. 2005).

The cichlids—along with the characids and the catostomids (McCune 1981)—are one of the few fish families with extremely large variation in body shape. High morphological diversity exists among as well as within tribes of cichlids from Lake Tanganyika. Interestingly, convergence in eco-morphological traits and coloration patterns appears to be common between groups that are both distantly (Kocher et al. 1993; Meyer 1993; Rüber et al. 1999; Stiassny and Meyer 1999) and closely (Reinthal and Meyer 1997; Rüber et al. 1999) related. Variation in body form has important fitness consequences (Gatz 1979; Guill et al. 2003). It is therefore important to quantitatively describe differences in body shape that exist between cichlids within a phylogenetic framework to understand the evolutionary processes leading to adaptive spread within Lake Tanganyika.

Morphometrics is the study of shape variation and its covariation with other variables of interests (Bookstein 1991; Dryden and Mardia 1998). Geometric morphometrics is a recently developed approach that explicitly retains information on spatial covariation among landmarks (Rohlf and Marcus 1993). These landmark-based techniques pose no restrictions on the directions of the variation and the localization of shape changes, and they are very effective in capturing meaningful information about the shapes of organisms. Because geometric morphometrics relies on statistically comparable shape variables, it is possible to reconstruct a group consensus shape and the hypothetical shape of a common ancestor. It is also possible to visualize changes and transformations necessary to distinguish one shape from another. Multivariate statistical procedures are complementary to morphometric methods (Rohlf and Marcus 1993; Rohlf et al. 1996; Cavalcanti et al. 1999; Zelditch et al. 2004) because they allow the statistical characterization of the morphological variation itself. They are also used to test for significant correlations between body shape and ecological traits or to evaluate the importance of phylogenetic inertia on shape similarity. Closely related taxa are expected to be more similar to one another than they would be without shared evolutionary history (Felsenstein 1985; Rüber and Adams 2001; Rosenberg 2002; Guill et al. 2003). It is therefore important to include phylogenetic information with geometric morphometric approaches to reliably establish a link between an observed pattern of morphological variation and a hypothesized process driving adaptive divergence (Coddington 1990; Linde et al. 2004).

In the past 15 years, the use of geometric morphometrics methods to study cichlids has grown rapidly relative to studies that use traditional morphometrics (Hanssens et al. 1999; Kassam

et al. 2003a). Bouton et al. (2002) found that the head shapes of haplochromines of Lake Victoria are correlated with eight environmental variables; Rüber and Adams (2001) established a correlation between body shape and trophic morphology for the Tanganyikan tribe Eretmodini, features that turned out to be independent of their phylogenetic relationships. The same type of correlation was also studied in the case of some haplochromines from Lake Malawi (Kassam et al. 2003a, 2004). Studies on whole body shape variation have also helped to distinguish morphologically different species that belong to the same species complex (Klingenberg et al. 2003) and to demonstrate morphological convergence between distantly related species (Kassam et al. 2003b). Recently, geometric morphometrics were used to test conjectures about the relative degree of morphological diversity among the Lake Malawi and Tanganyika cichlid species flocks (Chakrabarty 2005).

Here we present a geometric morphometric study based on the largest dataset so far for Lake Tanganyika cichlids, including 1002 specimens from 45 species representing the full spectrum of phylogenetic and morphological diversity in Lake Tanganyika. Utilizing a robust phylogenetic hypothesis of relationships for these taxa, we use several methods to test for the influence of phylogeny on body form evolution. Variation among species is also discussed with reference to several ecological traits (trophic preferences, habitat differentiation, various mating and breeding systems) using various statistical tools to assess what, if any, ecological features may be driving morphological divergence. Finally, we describe morphological disparity within and among tribes and, using disparity metrics, apply a novel evaluation of morphospace structure to assess the patterns of diversity within and among clades and ecological groups. These analyses enable us to confirm the adaptive character of the radiations, as well as to discuss the role of particular body shapes and their potential for invading different adaptive zones. These patterns and processes are most likely central to the origin of the spectacular diversity of cichlid species in Lake Tanganyika.

Materials and Methods
SPECIMENS
Specimens included in this study, their origins, the number of specimens per species, their assignment to one of the 17 tribes according to Takahashi (2003), and GenBank accession numbers of DNA sequences are listed in Table 1. Voucher specimens are deposited in the Royal Museum for Central Africa in Tervuren, Belgium.

DATA COLLECTION
Images of the left side of more than 1000 individuals were taken with a digital camera (Nikon Coolpix 995) in the Museum for Central Africa in Tervuren, Belgium. Specimens belong to 45 different species representing 14 of the 17 tribes to which Tanganyikan cichlids have been assigned (only rare, monogeneric tribes were not included; see Takahashi 2003). The *x*, *y* coordinates of 17 landmarks (Fig. 1) were digitized as described elsewhere (Klingenberg et al. 2003). These were measured twice by the same person, and the mean of the two measurements was used as raw data for subsequent analyses. Direct analysis of the coordinates would be inappropriate as the effects of variation in position, orientation, and sizes of the specimens can introduce bias. Nonshape variation was therefore mathematically removed using generalized procrustes analysis (GPA) in tpsSuper (Rohlf 2004b). The GPA superimposes landmark configurations of various specimens using least-squares estimates for translation and rotation. The centroid of each configuration is translated to the origin and configurations are scaled to a common unit size. Finally, the configurations are optimally rotated to minimize the squared differences between corresponding landmarks (Gower 1975; Rohlf and Slice 1990). Procrustes analysis fits minimized least squared distances between each landmark in all specimens, whereas the relative distances of the 17 landmarks to each other remain constant. The resulting coordinates lie in a tangent space, whose variation was determined to be minimal (Rohlf 2002) using tpsSmall (Rohlf 2003), therefore transformed landmarks were used in subsequent analyses. Principal components analysis (PCA) was performed for each tribe in PAST (Hammer et al. 2001) to identify outliers (specimens not belonging to the 95% ellipse after PCA). After discarding these nonrepresentative specimens, the matrix contained 1002 samples with 34 coordinates each. From this matrix we calculated the consensus shape for each species and for each tribe using tpsSuper (Rohlf 2004b).

We collected information about ecological characteristics of each species from the literature, disregarding general information at the level of the tribe to avoid the influence of phylogeny on the calculation of correlations (Table 2). We used the following references to complete the ecological character data-matrix for all taxa included in our analysis (Poll 1956; Konings 1988; Barlow 1991; Coulter 1991; Hori 1991; Ribbink 1991; Winemiller et al. 1995; Kuwamura 1997; Nishida 1997; Nagoshi and Yanagisawa 1997; Gerbrand 1998; Goodwin et al. 1998; Rüber and Adams 2001; Lowe-McConnell 2002; Kassam et al. 2003a; Parsons 2003).

Ecological data included differentiation of the habitat by preferred depths in the water column. This assignment (Poll 1956) was binned into four categories: shallow water (0 to 5 m), medium water (0 to 30 m), deep water (more than 30 m), and rivers. We also coded the substrate of the preferred habitat: mud, sand, rock, intermediate substrate between these categories or ubiquitous, a fifth category for rivers, and a sixth category for other habitats not involving any substrate (e.g., deep or open water species).

Table 1. Characterization of analyzed species of Lake Tanganyika cichlids.

Taxonomy information		Sampling locality	GenBank accession no.	No. of specimens
Tribe	Taxon		ND2	
Bathybatini	*Bathybates* sp.	Lake Tanganyika	U07239	22
Cyphotilapiini	*Cyphotilapia frontosa*	Lake Tanganyika	U07247	8
Cyprichromini	*Cyprichromis leptosoma*	Lake Tanganyika	AF398224	29
	Paracyprichomis brieni	Lake Tanganyika	AF398223	24
Ectodini	*Callochromis stappersi*	Lake Tanganyika	AY337775	14
	Cunningtonia longiventralis	Lake Tanganyika	AY337780	24
	Cyathopharynx furcifer	Lake Tanganyika	AY337781	18
	Ectodus descampsi	Lake Tanganyika	AY337790	15
	Enantiopus melanogenys	Lake Tanganyika	AY337770	25
	Grammatotria lemairii	Lake Tanganyika	AY337787	46
	Ophthalmotilapia nasuta	Lake Tanganyika	AY337783	30
	Xenotilapia ochrogenys	Lake Tanganyika	AY337767	32
Eretmodini	*Eretmodus cyanostictus*	Lake Tanganyika	AF398220	20
	Spathodus erythrodon	Lake Tanganyika	AF398218	16
Haplochromini	*Astatoreochromis alluaudi*	Lake Kanyaboli	AY930075	19
	Haplochromis paludinosus	Nanganga River	AY930107	15
	Melanochromis auritus	Lake Malawi	AY930069	28
	Metriaclima zebra	Lake Malawi	U07263	25
	Pseudocrenilabrus multicolor	Lake Kanyaboli	AY930070	16
Lamprologini	*Altolamprologus compressiceps*	Lake Tanganyika	AF398229	21
	Julidochromis ornatus	Lake Tanganyika	AF398230	18
	Lamprologus congoensis	Congo River	AF317272	6
	Lamprologus cylindricus	Lake Tanganyika	DQ093115	4
	Lamprologus teugelsi	Congo River	AF398225	16
	Telmatochromis vittatus	Lake Tanganyika	AY740396	25
	Neolamprologus leleupi	Lake Tanganyika	DQ093113	28
	Julidochromis regani	Lake Tanganyika	EF210777	20
	Neolamprologus calliurus	Lake Tanganyika	AF398227	30
Limnochromini	*Limnochromis auritus*	Lake Tanganyika	AF398216	15
Orthochomini	*Orthochromis malagaraziensis*	Malagarazi River	AF398232	30
	Orthochromis uvinzae	Malagarazi River	AY930048	9
	Orthochromis mazimeroensis	Mazimero River	AY930053	17
Perissodini	*Perissodus microlepis*	Lake Tanganyika	AF398222	18
	Plecodus straeleni	Lake Tanganyika	AF398221	12
Tilapiini	*Tilapia rendalli*	East Africa	AF317259	31
	Oreochromis tanganicae	Lake Tanganyika	AF317240	29
Trematocarini	*Trematocara unimaculatum*	Lake Tanganyika	AF317268	30
Tropheini	*Ctenochromis horei*	Lake Tanganyika	AY930100	18
	Limnotilapia dardennii	Lake Tanganyika	DQ093109	35
	Lobochilotes labiatus	Lake Tanganyika	U07254	16
	Petrochromis polyodon	Lake Tanganyika	AY930068	29
	Simochromis babaulti	Lake Tanganyika	DQ093110	23
	Simochromis diagramma	Lake Tanganyika	AY930087	22
	Tropheus duboisi	Lake Tanganyika	AY930085	37
Tylochromini	*Tylochromis polylepis*	Lake Tanganyika	AF398215	37

Feeding preferences were assigned to six different categories: exclusively vegetal, zooplankton and detritus, benthic invertebrates, fish, scales, and a final category called "generalist" for species that are especially opportunistic feeders. These categories were also reduced into three categories of prey type: nektonic prey, represented by organisms that move actively in the water column, planktonic prey, a category that grouped organisms suspended in the water column, and benthic prey, including sessile prey or slow
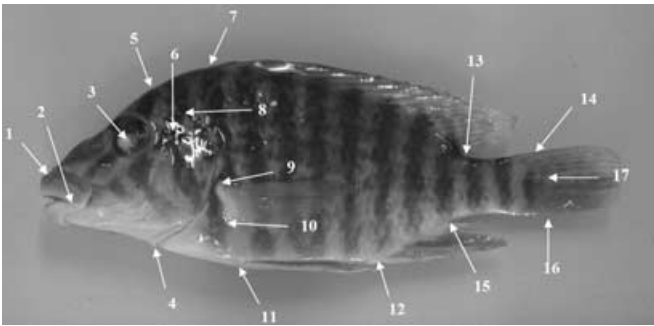
Figure 1. Description of the landmarks: 1, tip of the snout at the fold anterior to the ethmoid/nasal bones, touching the upper lip when the premaxilla is retracted (mouth closed); 2, corner of the mouth, at the corner of the skin fold where the maxillary angle rests when the mouth is closed; 3, center of the eye; 4, base of the isthmus; 5, boundary between smooth and scaly skin; 6, dorsal end of the pre-occular groove; 7, anterior base of the dorsal fin; 8, opercular origin; 9, base of the leading edge (upper, anterior) of the pectoral fin; 10, base of the trailing edge (lower, posterior) of the pectoral fin; 11, anterior base of the pelvic fin; 12, anterior base of the anal fin; 13, posterior end of the dorsal fin base; 14, base of the caudal fin, dorsal; 15, posterior end of the anal fin base; 16, base of the caudal fin, ventral; 17, base of the caudal fin at the level of the lateral line.

moving organisms living on the substrate (Linde et al. 2004). Additionally, feeding preference was simply coded as having mobile or nonmobile prey. These groupings may influence the strategy used by a cichlid to capture prey, and thus influencing the shape of the fish predator.

Information was also collected on the type of parental care given (maternal, biparental or involving helpers, i.e., cooperative breeding), on mating system (monogamy, polygamy, polygyny, and a fourth category for more complex mating behavior), and on breeding type (mouthbreeders or substrate guarders).

PHYLOGENETIC ANALYSES

Forty-five complete sequences of the mitochondrial NADH Dehydrogenase Subunit II gene (ND2, 1047bp; Salzburger et al. 2002, 2005; Koblmueller et al. 2004; Salzburger and Meyer 2004; Clabaut et al. 2005) were analyzed using maximum likelihood (ML) methods with PAUP∗ 4.0b10 (Swofford 2002). *Tylochromis polylepis* was declared as outgroup (according to Stiassny 1990; Lippitsch 1995; Farias et al. 2000; Salzburger et al. 2002). We ran the Modeltest 3.06 routine (Posada and Crandall 1998) to determine, with a hierarchical likelihood ratio test, the appropriate model of molecular evolution for the ML analyses. We used the GTR+I+γ model (Rodriguez et al. 1990) with $A = 0.297$; $C = 0.3795$; $G = 0.0846$; $\alpha = 0.9192$; $I = 0.3565$; and A–$C = 0.4049$, A–$G = 11.3001$, A–$T = 0.6488$, C–$G = 0.8348$, C–$T = 4.2669$, G–$T = 1$. Previous analyses have demonstrated that the ND2 gene contains enough informative characters to achieve a well

supported topology for the Lake Tanganyika species assemblage (Salzburger et al. 2002; Clabaut et al. 2005).

PHYLOGENETIC PATTERNS OF SHAPE VARIATION

We used two distance-based and three variance partitioning methods to evaluate the influence of phylogeny on the body shapes of the Tanganyikan cichlid assemblage. For the first distance-based method, a cluster analysis was performed in PAST on the 34 coordinates of the landmarks using three different algorithms on the 34 tangent space coordinates (UPGMA, Ward's method, and single linkage with Procustes distances). These multivariate algorithms group species were based on their overall morphological similarities, and enabled us to visualize which groups are congruent with those defined by phylogeny. The second distance-based method used Procrustes distances between each pair of taxa in the morphospace. Normalized Mantel statistics (Mantel 1967; Smouse et al. 1986) were then used to evaluate the correlation between the phylogenetic distances and the Procrustes distances between all pairs of taxa. The program MANTEL (Cavalcanti 2005) was used to estimate the probability of obtaining a correlation equal to or greater than the calculated value over 10,000 random matrix permutations.

COMPARATIVE ANALYSES

To evaluate the influence of ecology on body shape, we fitted the ecological characters to the partial warp scores describing shape variation using the phylogenetic generalized linear model suggested by Martins and Hansen (1997). Partial warp scores effectively capture spatial variation in a sample that can then be analyzed meaningfully using multivariate statistical modeling (Rohlf 2002). We calculated the partial warp scores in tpsRelw (Rohlf 2005) and then fit a linear model using ecological characters as predictors. Fitting this model used a maximum-likelihood generalized least squares (PGLS) approach and took the form

$$\mathbf{W} = \beta\mathbf{X} + \varepsilon,$$

where $\mathbf{W}$ is the partial warp scores matrix, $\mathbf{X}$ is the matrix of ecological characters, β is the regression coefficient for each predictor, and ε is the error term. To account for phylogenetic nonindependence, PGLS allows the ε to have a correlation matrix derived from the phylogenetic tree. We used a matrix for the variance error due to phylogenetic relationships ($\mathbf{v}_{ij}$) that took the form

$$\mathbf{v}_{ij} = \gamma^{-\alpha t_{ij}},$$

where α represents the magnitude of the force of phylogenetic restraint, t_{ij} is the phylogenetic distance between taxa, and γ is a constant. This variance matrix is based on the Ornstein–Uhlenbeck model wherein the strength of evolution toward an optimum is captured in the α term (Martins and Hansen 1997). When a variance

Table 2. Ecological characters of included species.

Species	Habitat	Parental care	Mating system	Breeding type	Feeding preferences	Preferred depth (m)
Bathybatini						
Bathybathes sp.	bathypelagic	maternal		Mb	fish	0–25–80
Cyphotilapiini						
Cyphotilapia frontosa	rock	maternal	polygyny, harem	Mb	fish, large invertebrates	0–20–30
Cyprichromini						
Cyprichromis leptosoma	rock	maternal	polygamy	Mb	pelagic zooplankton, copepods	
Paracyprichromis brieni	littoral zone pelagic	maternal	polygamy	Mb	zooplankton and microbenthos	
Ectodini						
Ectodus descampsi	sand	maternal	polygamy	Mb	insects, invertebrates, plants	0–5–25
Callochromis stappersi	sand	maternal	polygamy	Mb	invertebrates	
Eniantiopus melanogenys	sand	maternal	polygamy	Mb	invertebrates	
Ophthalmotilapia nasuta	intermediate	maternal	polygamy	Mb	Aufwuchs	
Cyathopharynx furcifer	intermediate	maternal	polygamy	Mb	Aufwuchs	0–5–15
Grammatotria lemairii	sand	maternal	polygyny, harem	Mb	invertebrates and small snails	0–15–60
Cunningtonia longiventralis	intermediate	maternal	polygamy	Mb	filamentous algae, diatoms	
Xenotilapia ochrogenys	sand and mud	biparental	polygamy; polyandry school	Mb	copepods, larvae, ostracods, benthos	0–5–35
Eretmodini						
Eretmodus cyanosticus	rock, surge water	biparental	monogamy	Mb	filamentous algae	0–5
Spathodus erythrodon	rock, surge water	biparental		Mb	diatoms, Aufwuchs and insects larvae	0–5
Haplochromini						
Haplochromis paludinosus	river	maternal	polygyny	Mb	generalist	river
Pseudotropheus zebra	rock	maternal		Mb	vegetarian	
Astatoreochromis alluaudi	ubiquitous	maternal	polygyny	Mb	molluscs	
Pseudocrenilabus multicolor	river	maternal	polygamy	Mb	generalist	
Melanochromis auratus	rock	maternal	polygyny	Mb	omnivore	
Lamprologini						
Lamprologus teugelsi	river	maternal	polygyny, harem	Ss	invertebrates	river

Table 2. continued

Species	Habitat	Parental care	Mating system	Breeding type	Feeding preferences	Preferred depth (m)
Lamprologus congoensis	river	maternal	polygyny, harem	Ss	invertebrates	river
Julidochromis ornatus	rock	cooperative	monogamy	Ss	zoobiocover	0–10
Lamprologus leleupi	rock	biparental	monogamy	Ss	zooplankton, benthic arthropods, invertebrates	0–5
Lamprologus cylindricus	rock	biparental	polygamy	Ss	invertebrates	
Altolamprologus calvus	rock and sediment	maternal	monogamy	Ss	zoobiocover	
Telmatochromis vittatus	intermediate	maternal	monogamy	Ss	Aufwuchs and invertebrates	0–5
Julidochromis reganii	intermediate	biparental	monogamy	Ss	zoobiocover	0–5
Lamprologus brichardi	rock	cooperative	mono/polygamy/ polygyny	Ss	zooplankton, algae	
Limnochromini						
Limnochromis auritus	mud	biparental	monogamy	Mb	invertebrates, snails and small fish	0–35–115
Orthochromini						
Orthochromis malagaraziensis	river	maternal		Mb	plankton	river
Orthochromis uvinzae	river	maternal		Mb	algae	river
Orthochromis mazimeroensis	river	maternal		Mb	algae	river
Perissodini						
Perissodus microlepis	ubiquitous	maternal/biparental	monogamy	Mb	scales and microbenthos	0–15–95
Plecodus straeleni	rock	biparental	monogamy	Mb	scales and eggs	0–5
Tilapiini						
Tilapia rendalli	river	biparental	monogamy	Ss	aquatic plants	river
Oreochromis tanganicae	ubiquitous	maternal	polygyyamy	Mb	detritus, phytoplankton	0–5–25
Trematocarini						
Trematocara unimaculatum	mud	maternal		Mb	diatoms, detritus, gastropods, crustaceans, zooplankton	0–50–120
Tropheini						
Simochromis diagramma	mud	maternal	polygamy	Mb	aquatics weeds, algae	river 0–15
Ctenochromis horei	ubiquitous	maternal	polygyny	Mb	omnivore (benthos, fish, invertebrates)	
Lobochilotes labiatus	rock	maternal	polygyny	Mb	gastropods, crabs, benthos	0–5–30
Petrochromis polyodon	rock	maternal	polygamy	Mb	Aufwuchs, algae	0–5–25
Tropheus duboisi	rock	maternal	polygamy	Mb	Aufwuchs	
Limnotilapia dardennii	rock and sand	maternal	polygyny	Mb	omnivore (algae, plants and invertebrates)	0–5–85
Simochromis babaulti	mud	maternal		Mb	vegetarian	0–30
Tylochromini						
Tylochromis polylepsis	sand and mud	maternal	polygyny	Mb	molluscs, vegetal matters, water plants	river 0–5–75

Mb, mouth-brooder; Ss, substrate spawner.

matrix representing Brownian motion was used, the results did not change. To test the effects of ecology on shape, we regressed each of the ecological characters (**X**) on the matrix of partial warp scores (**W**). We also regressed ecology on shape using more complex models that included each of the ecological characters in permutations of every possible additive combination (i.e., models with 1, 2, . . ., 6 characters used as predictors). The restricted maximum log-likelihood value for each model, which is based on a function of the determinant of the error variance-covariance matrix (Pinheiro and Bates 1998), was used to perform likelihood-ratio tests to determine if models including iteratively more predictors significantly improved the fit. To assess the relative importance of each of the characters, we used the F-statistic from each model following analysis of variance, using marginal sums of squares when comparing predictors within models with multiple predictors to perform the ANOVA. One-tailed t-tests were used to determine which trait values of each character had significant regression coefficients. PGLS was performed using APE (Paradis et al. 2004).

DISPARITY WITHIN AND AMONG LINEAGES

Statistical analyses of morphological disparity allow us to examine the structure of the morphospace defined by the Lake Tanganyika species flock. We used two related methods to investigate the phylogenetic and ecological impacts on the morphospace. First, to estimate the distribution of morphological diversity among tribes, we calculate values of partial disparity for each of the tribes (Foote 1993). We can thus test the degree of constraint on morphological diversification of Lake Tanganyika cichlids. Disparity is a measure of the amount of morphological variation in a group of samples, taking into account the volume of the hyperdimensional morphospace occupied, the relative distances between samples, and the number of samples. We used tangent space coordinates of all specimens included in each tribe. Using IMP software (Sheets 2005), we then estimated the disparity of each tribe according to Foote's (1993) formula for partial disparity:

$$\mathrm{PD}_i = \sum_j d_{ij}^2 \big/ (N - 1),$$

where group i contains n_i points, each of which is a Procrustes distance d_{ij}^2 from the overall group centroid, and N is the total number of points in all groups (monophyletic tribes). Furthermore, we calculated the correlation between disparity and number of specimens or species contained in each tribe in our dataset. We estimated confidence intervals for the morphological disparity of the whole group, the contribution of each tribe to the overall disparity, and the correlations of disparity with the number of species and specimens per tribe by performing 100 bootstrap replicates of specimens in tribes (Smith and Bunje 1999). To determine which of the tribes have a statistically significant effect on total morphological disparity, we used the approach of Foote (1993), in which

the morphological disparity of the whole group was measured after iterative exclusion of each of the 14 tribes. If the disparity value of a given tribe falls outside of the 95% confidence interval of the entire morphospace excluding that tribe, then it is considered to have a significant effect on total morphological disparity (Foote 1993).

A related method allows us to estimate the relative contribution of grouping variables (e.g., ecology or phylogeny) to morphological diversity. Specifically, calculating the variability of Procrustes distances within, among, and between groups allows us to determine the geometric relationships between those groups, that is, which parts of the total morphospace the groups occupy relative to each other (Foote 1991; Smith and Bunje 1999). Using species consensuses of tangent space coordinates, we computed within-group variability (W), among-group variability (A), and discreteness (D) according to the formulae (Foote 1991)

$$W = \frac{1}{N'} \sum_{i=1}^{G} \bar{d}_i n_i$$

$$A = \frac{1}{2\bar{n}M} \sum_{i=1}^{G} \sum_{j=i+1}^{G} d_{ij}(n_i + n_j)$$

$$D = \frac{A}{W},$$

where N' is the total number of taxa in groups with more than one member (one-taxon groups are excluded because $d_i n_i = 0$), G is the number of groups, $\bar{d}_i$ is the mean of all pairwise distances within group i, n_i is the number of species in group i, n_j is the number of species in group j, $\bar{n}$ is the average number of species in each group, $M = G(G-1)/2$ is the number of comparisons among groups, and d_{ij} is the distance between the centroids of groups and i and j. We estimated confidence intervals for these parameters by performing 10,000 bootstrap replicates of specimens in groups. We performed these calculations for species grouped by tribe (14 groups), by feeding preferences (six groups), and by depth of habitat where the species occur (four groups). This method is used for the first time to assess the relationships (distance and overlap) between taxonomically and ecologically pre-defined groups (tribe assignment, habitat and feeding preferences). This constitutes a test of which characteristics significantly structure variation in the morphospace.

MORPHOSPACE VISUALIZATION OF SHAPE VARIATION AND CHANGE

Differences in shape among objects can be described in terms of differences in the deformation grids depicting these objects, following the principle of d'Arcy Thompson's transformation grids (Thompson 1917). The shape differences of one specimen

to another are represented as a bent grid superimposed over the coordinates of the initial specimen. For normalized shape coordinates, we used the thin-plate spline (Bookstein 1991; Dryden and Mardia 1998) to map the deformation in shape along axes of the morphospace. For ecological characters that were found to be correlated with body shape, we calculated the average shape of each ecological cluster, as well as the consensus shape of these averages (consensus calculated with tpsSuper; Rohlf 2004b). We then depicted the transformation grid of each ecological group to this consensus, highlighting the principal differences in morphology existing between the different ecological clusters found to have an influence on body shape evolution.

For visualization purposes, the morphometric data were reduced using a principal component analysis (PCA) implemented in PAST (Hammer et al. 2001) into three axes explaining 75% (in decreasing order 55.4%, 10.6%, and 9%) of the variance. Using Mesquite (Maddison and Maddison 2004), we mapped our phylogenetic tree in the morphospace defined by the coordinates of the

first three axes of the PCA. Mesquite also calculates the coordinates of the landmarks of the hypothetical ancestral shape at each node using a parsimony model and the 34 coordinates. Additionally, we plotted the shape of the ancestor of the C-lineage in the morphospace using Mesquite (Maddison and Maddison 2004) to test the hypothesis that the ancestor of the C-lineage was *Lamprologus*-like as assumed by Salzburger et al. (2002) and Koblmüller et al. (2004).

Results
PHYLOGENETIC ANALYSIS
The ML tree is shown in Fig. 2. Results are similar to previous studies (Kocher et al. 1995; Salzburger et al. 2002; Clabaut et al. 2005) with *Tilapia rendalli* (it does not belong to the Tanganyiakan assemblage) occupying the most ancestral position, followed by a clade formed by *Bathybates minor, Oreochromis tanganicae,* and *Trematocara unimaculatum.* These tribes are basal to
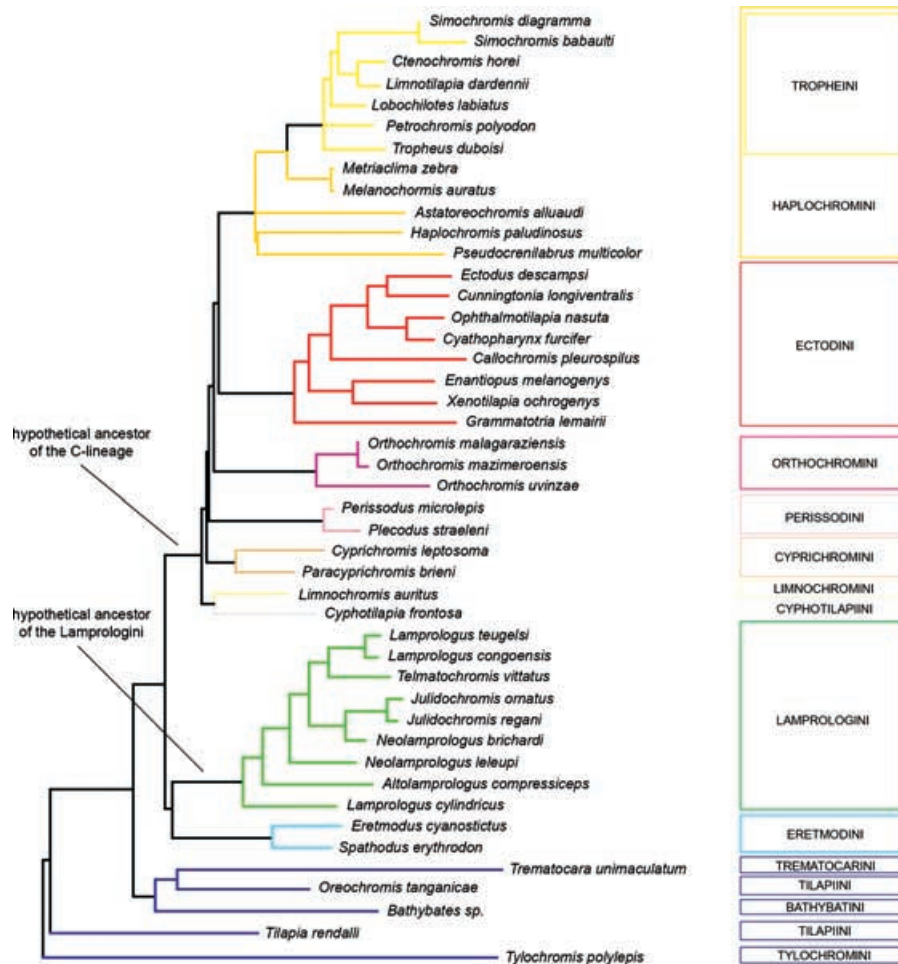

Figure 2. Maximum likelihood phylogram of Lake Tanganyika cichlids based on ND2 of 45 taxa. *Tylochromis polylepsis* was designated as the outgroup.

two major clades, a clade formed by the Eretmodini plus Lamprologini and a clade including all remaining taxa called the C-lineage (Clabaut et al. 2005). In the C-lineage, *Limnochromis auritus* and *Cyphotilapia frontosa* form the most ancestral lineages and are the sister groups to the Cyprichromini, the Perissodini, the Orthochromini, the Ectodini, and the Haplochromini including the tribe Tropheini.

INFLUENCE OF PHYLOGENY ON BODY SHAPE EVOLUTION

None of the cluster analyses managed to recover the taxonomy at the tribe level. Only two tribes were recovered consistently with the three different algorithms: the Eretmodini and the Tilapiini. All other tribes were morphologically too diverse to be clustered with any statistical support. Some species that belong to the same tribe were consistently found to cluster together: among the Tropheini, the two *Simochromis* (*S. diagramma* and *S. babaulti*) with *Limnotilapia dardenni*; among the Ectodini, *Callochromis stappersi*, *Ectodus melanogenys,* and *Grammatotria lemarii*; and *Cyathopharynx furcifer* and *Cunningtonia longiventralis*. This latter pair of Ectodini was always found to cluster with three Haplochromini/Tropheini (*Haplochromis paludinosus, Astatoreochromis alluaudi,* and *Ctenochromis horei*). The Orthochromini were not clustered, with *Orthochromis uvinzae* being assigned to a different part of the cluster analysis space. However, the Orthochromini are always clustered with some lamprologine representatives: *Orthochromis uvinzae* with *Telmatochromis*, and *O. mazimeroensis* and *O. malagarasiensis* with *N. calliurus*, *L. congoensis* and *L. leleupi. L. cylindricus* is associated with *Paracyprichromis brieni*; *Bathybates minor* with *Perissodus microlepis*.

The assumption that sister species are not necessarily close morphologically is also confirmed by the calculation of distances between species in the first three components of the morphospace: the smallest distances are not even found between two species that belong to the same tribe. Furthermore, the Mantel test (Mantel 1967) revealed no significant correlation between phylogenetic distances and Procrustes distances. For the total dataset, the probability of having a random Mantel statistic greater than the observed one is $P = 0.99$. The same result was found for all subsets tested: the C-lineage ($P = 1$), the Ectodini ($P = 1$), the Lamprologini ($P = 1$), the Haplochromini ($P = 1$), or within the ancestral lineages ($P = 1$).

INFLUENCE OF ECOLOGY ON BODY SHAPE EVOLUTION

Independent regression of ecological characters using PGLS indicated that only feeding preference was a significant predictor (also after correction for multiple comparisons), though water depth approached a P of 0.05 (see Table 3). These two characters also explained the most variance (standard error of the residuals were 2.89 $\times 10^{-3}$ and 2.85 $\times 10^{-3}$, respectively). Coding feeding preference by less discriminate methods did not result in any significant fits. Likelihood-ratio tests of more complex models revealed that only models that also included mating system, breeding type, substrate type, and water depth improved the fit of the regression over a model including only feeding preference ($P = 0.01$, though $P > 0.05$ after sequential Bonferonni correction for multiple comparisons of more complex models compared to the single predictor). Marginal F-statistics for these more complex models revealed that breeding type ($F = 4.11$, df $= 2$, $P = 0.03$) and water depth ($F = 2.91$, df $= 4$, $P = 0.04$) also have a significant effect on shape, though not after correction for multiple comparisons. Indeed, the effects of feeding preference appear to be accounted for in other ecological variables as it is not a significant predictor ($F = 1.88$, df $= 5$, $P = 0.14$) when mating system, breeding type, substrate

Table 3. *F*-tests based on analyses of variance of fitted PGLS models to determine which ecological traits influence shape variation (W). We show the results for models in which only one ecological character is used as a predictor (X) at a time, the model that includes all characters, and the best-fit model (i.e., the one that significantly improved the fit over the single predictor model of feeding preference). Following correction for multiple comparisons (sequential Bonferroni method), the only *P*-value less than 0.05 is feeding preference in the single predictor model for that character (i.e., 0.006).

| Trait	df	Single predictors		X=pc+ms+bt+fp+st+wd		X=ms+bt+fp+st+wd	
		F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Parental care (pc)	2	0.107	0.898	1.353	0.279	–	–
Mating system (ms)	4	1.066	0.386	2.000	0.130	1.931	0.138
Breeding type (bt)	2	0.608	0.549	3.652	0.043	4.113	0.029
Feeding preferences (fp)	5	3.874	0.006	2.195	0.092	1.879	0.136
Substrate type (st)	5	0.566	0.725	1.654	0.188	1.389	0.264
Water depth (wd)	4	2.308	0.075	2.411	0.080	2.915	0.043
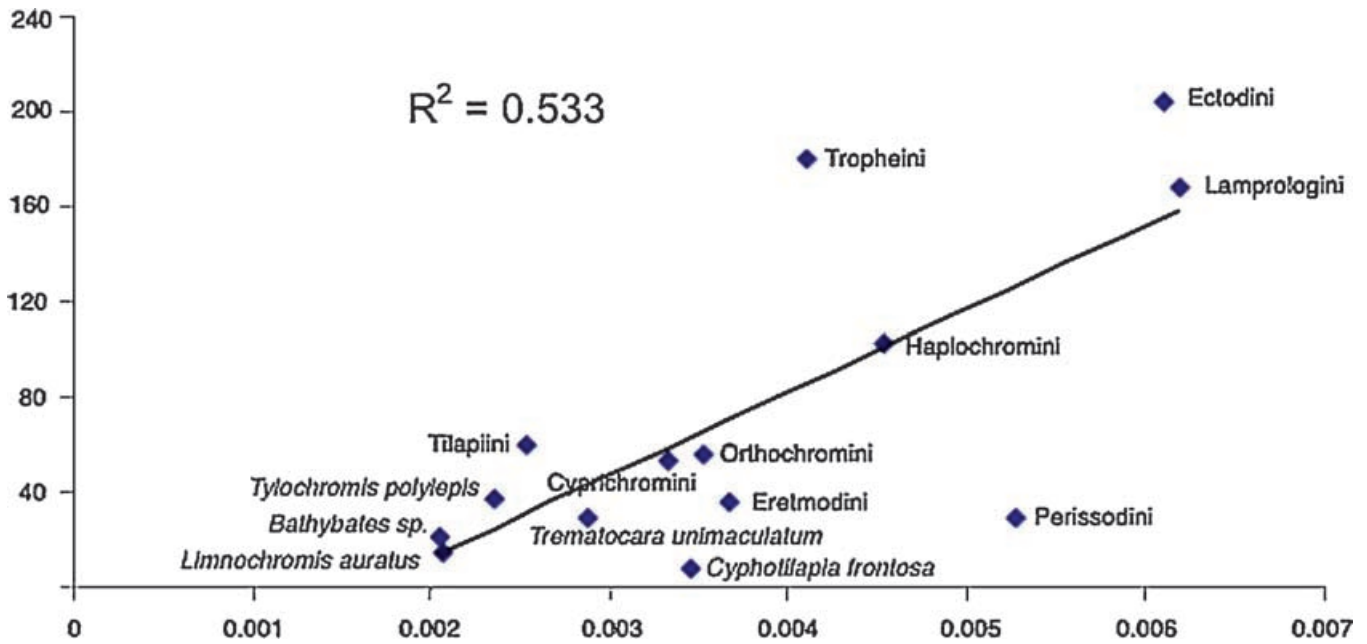
Figure 3. Correlation between the morphological disparity within a tribe and the number of specimens included in this tribe.

type, and water depth are included in the model (but it is when only breeding type and water depth are included as additional predictors; $F = 3.04$, df $= 5$, $P = 0.02$). As a result of the F-tests and likelihood-ratio tests, we are able to hypothesize that the most important ecological variable for predicting shape is feeding preference followed by water depth (this is borne out by our stepwise approach to the likelihood ratio tests, though not with statistical significance). The importance of feeding preference and water depth are also highlighted by the particular trait values that effectively predict shape. Invertebrate feeders, piscivores, and gener-

alists all possess significant regression coefficients, as do species that live in intermediate or deep water habitats. No other trait values had significant regression coefficients, indicating that for the whole Tanganyikan species assemblage only feeding preference and water depth are likely to be consistently relevant to shape.

DISPARITY WITHIN AND AMONG SPECIES

The disparity of tribes is slightly correlated with the number of specimens per tribe ($R^2 = 0.533$), and even more to the number of species per tribe ($R^2 = 0.671$). Figure 3 shows that the

Table 4. Disparity values for the whole morphospace, excluding each of the tribes one by one, and 95% confidence interval values. The partial disparity in each row is that of all tribes excluding the one that is named in that row. Only the morphospace without Cyphotilapiini is significantly smaller than the total morphospace ($3.87 \times 10^{-3} < 4.15 \times 10^{-3}$).

| Tribe	Total partial disparity	Lower 95% bound	Upper 95% bound
Cyphotilapiini	0.00367	0.00354	0.00387
Tilapini	0.00400	0.00367	0.00438
Bathybatini	0.00412	0.00382	0.00453
Cyprichromini	0.00421	0.00392	0.00467
Perissodini	0.00439	0.00416	0.00483
Trematocarini	0.00448	0.00422	0.00498
Lamprologini	0.00452	0.00430	0.00506
Tylochromini	0.00454	0.00431	0.00508
Ectodini	0.00457	0.00426	0.00495
Orthochromini	0.00457	0.00430	0.00498
Tropheini	0.00458	0.00432	0.00509
Eretmodini	0.00461	0.00438	0.00511
Limnochromini	0.00462	0.00438	0.00509
Haplochromini	0.00469	0.00444	0.00507
All Included	0.00440	0.00415	0.00483
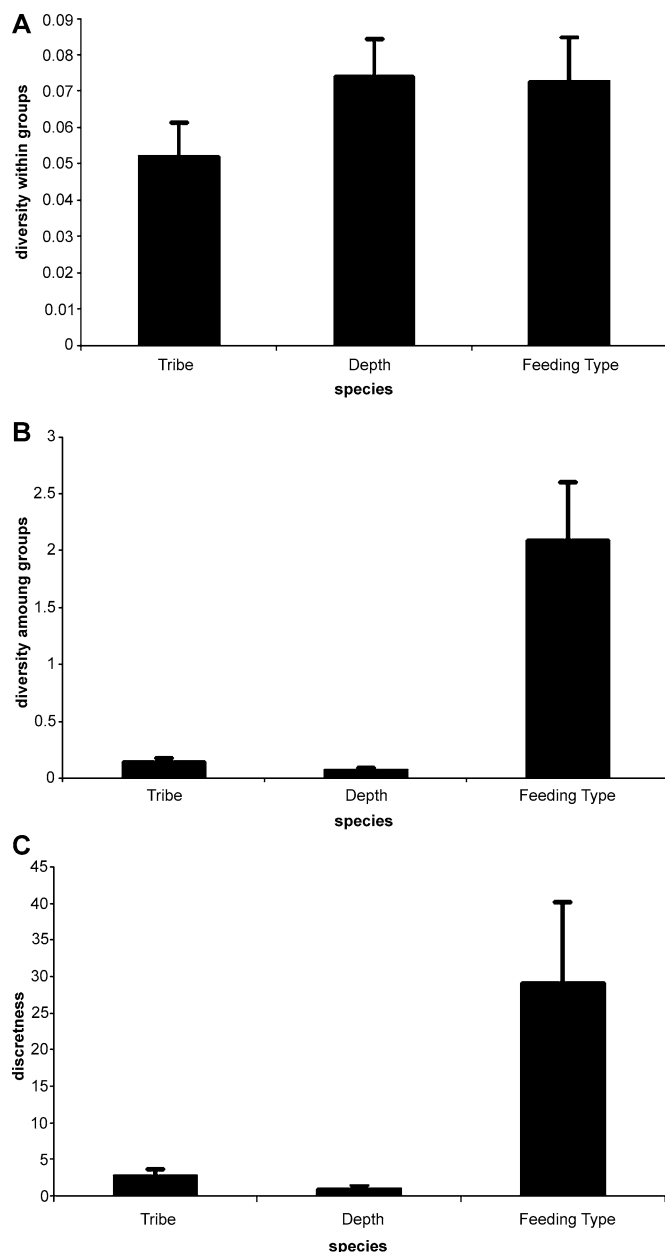
Figure 4. Graphs showing values of morphological diversity (A) within groups and (B) among groups for the different groupings. (C) Discreteness values for those groupings (discreteness = variability among groups/variability within groups).

Tropheini and the Perissodini are particularly far from the regression line. The Tropheini has a low disparity value despite its relatively large number of species, whereas the Perissodini, a bigeneric tribe, shows very high disparity. When these two tribes are eliminated from the correlation analysis, we observe a marked increase in the correlation factor ($R^2 = 0.823$ and 0.899, respectively). The Lamprologini (PD $= 6.20 \times 10^{-3}$) and the Ectodini (PD $= 6.10 \times 10^{-3}$) are the most morphologically diverse tribes whereas the Limnochromini (PD $= 2.08 \times 10^{-3}$) and the Bathybatini (PD $= 2.05 \times 10^{-3}$) are the least.

The results of the disparity analysis are shown in Table 4 and in Figure 3. *Cyphotilapia frontosa*, which is characterized by a hump on its head, is found to have the largest influence on the disparity of the whole morphospace. The value of its contribution to the disparity of the whole morphophace is the highest, and after the exclusion method (Foote 1993), only it significantly affects the disparity of the morphospace outside of the 95% confidence interval. This also implies that all the other tribes cannot be statistically discriminated in the morphospace (Foote 1993). No correlation was found between disparity values of the different subgroups and the number of specimens used for the calculation of the disparity ($R^2 = 0.164$), nor with the number of different species comprised in the tribe in our study ($R^2 = 0.169$).

The two most important ecological characters, feeding preference and water depth, were further analyzed using disparity methods. Estimating the discreteness of these groups in the multidimensional morphospace allows us to determine if any a priori grouping better discriminates specimens in the morphospace. Even though within-group variability (W) for our pre-defined groups (tribes and ecological groups) seems to be similar (Fig. 4A), assignment to tribes produces lower values of W than assignment by feeding preference or water depth. This is probably a consequence of having more tribes than ecological distinct groups. However, we observe a dramatic increase of the variability among groups (Fig. 4B) and therefore discreteness (Fig. 4C) when species are grouped by feeding preferences. This result enables us to reject, in the case of feeding preferences, the null hypothesis under which groups are equally overlapping in the morphospace (i.e., nondiscrete). This means that feeding types structure the morphological variation better than grouping of the species by tribe or preferred habitat depth, in agreement with the results of PGLS.

VISUALIZATION AND DESCRIPTION OF MORPHOLOGICAL DIVERSITY

We calculated the average shapes of each feeding preference cluster (vegetal prey, zooplankton and detritus, benthic invertebrates, fish, scales, generalist) and the consensus of these six averages. Using thin-plate splines to describe these different categories (Fig. 5), we observed that fish feeding on passive prey items such as plants and plankton have a shape close to the average shape, but with a short caudal peduncle. Benthic prey feeders are slender and elongated. Among the nektonic prey feeders, we can distinguish between scale eaters and piscivorous fish. The Perissodini, a tribe of scale eaters, have a mouth shifted up compared to the rest of the landmarks describing their anterior body, the latter being shorter than average. *Bathybates minor* and *Cyphotilapia frontosa*, both piscivorous fish, have a much larger anterior body.

In the PCA representation of total shape variation, the first two principle components explain 55.4% and 10.6% of the variation, respectively (Fig. 6). The first axis is strongly loaded by
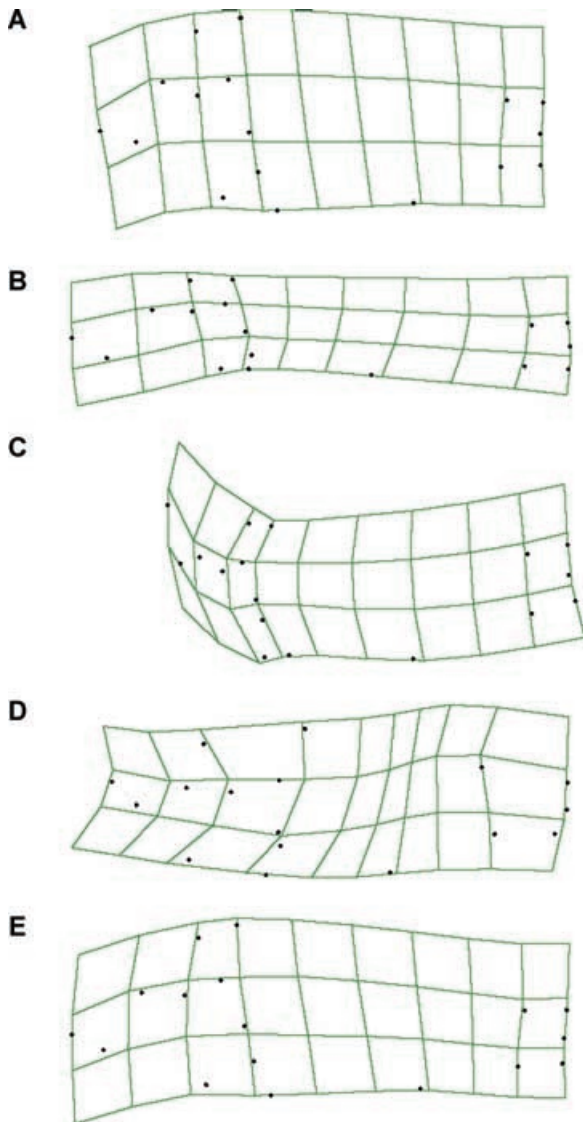
Figure 5. Deformation grids from the consensus shape of the four ecological groups of different feeding habits to the consensus shape of each of these groups individually: (A) planktonic prey, (B) benthic prey, (C) nektonic prey: scale eaters, (D) nektonic prey: piscivores, and (E) generalists.

variables that represent the length and height of the body. Specimens on the left side of the graph are elongated and thin, whereas the ones on the right side are stouter and deeper. The second axis mostly describes variation in head shape. The lower the specimens are in the graph, the smaller and shorter their head is, the most posterior is their anal fin at the body, and the shorter is their caudal peduncle. The third axis (not shown) explains 8.96% of the variation and this axis is loaded by the position of the mouth and the caudal peduncle, shifted up to the rest of the landmarks and therefore expanding the ventral part of the body.

The superimposition of the phylogenetic tree on the morphospace shows no directional trend in the evolution of body shape at the Tanganyikan assemblage level, nor at the tribe level. More ancestral tribes present a wide range of shapes: some have a wide and round body and head shape (like *Oreochromis tanganicae*), whereas others have a thin body and head shape (like *Bathybates minor* and *Trematocara unimaculatum*). The Lamprologini occupy a large portion of the morphospace because some species have extreme shapes such as the deep-bodied *Altolamprologus calvus* and the elongated, short-headed *Telmatochromis vittatus*. Between these two species, a range of intermediate forms exists. The eight species that represent the Ectodini in our study are, in general, elongated fish but with a more pointed head than the majority of Tanganyikan cichlids. Variation in this tribe follows the transformation of the first axis, that is, changes in the length of their body. On the other hand, the Haplochromini (including the Tropheini) have a deeper body, and are differentiated also on the second axis, that is, they show an extensive range of head shapes.

Interestingly, the trajectory of shape evolution within tribes seems to be different for each of them. For example, the derived species of the Ectodini tend to be more elongated than ancestral ones, whereas the inverse pattern is observed for the Tropheini. The other species-rich groups (Haplochromini, Lamprologini) do not seem to show any discernable trend at all (at least within the morphospace defined by the first two axes of the PCA). Sister taxa in our phylogeny are often rather distant from each other in the morphospace: *Perissodus microlepis*, for example, has a shape similar to the average Lamprologini, and *Plecodus straeleni* is found nested within the morphospace occupied by the Haplochromini/Tropheini. Some species are placed in the area of the morphospace occupied by species of a different tribe. The Cyprichromini, for example, are found within the morphospace occupied by the Ectodini, the Orthochromini within the Lamprologini, and the Eretmodini within Haplochromini/Tropheini. Phylogenetically unrelated species are characterized by similar coordinates in the space defined by the two first axes: *Tilapia rendalli*, *Cyphotilapia frontosa,* and *Petrochromis polyodon*, for example.

The coordinates of the hypothetical ancestor of the C-lineage (in which the Lamprologini are not included) are found within the subspace occupied by the Lamprologini and close to the coordinates defining the position of the hypothetical ancestor of the Lamprologini. The cluster analyses also group this hypothetical ancestor within a group containing *Lamprologus lelupi*, *L. brichardi,* and *L. congoensis*. This is consistent with the assumption that the ancestor of the C-lineage was probably a *Lamprologus*-like cichlid (Salzburger et al. 2002; Koblmueller et al. 2004), albeit somewhat shorter and wider than the hypothetical ancestor of the Lamprologini.
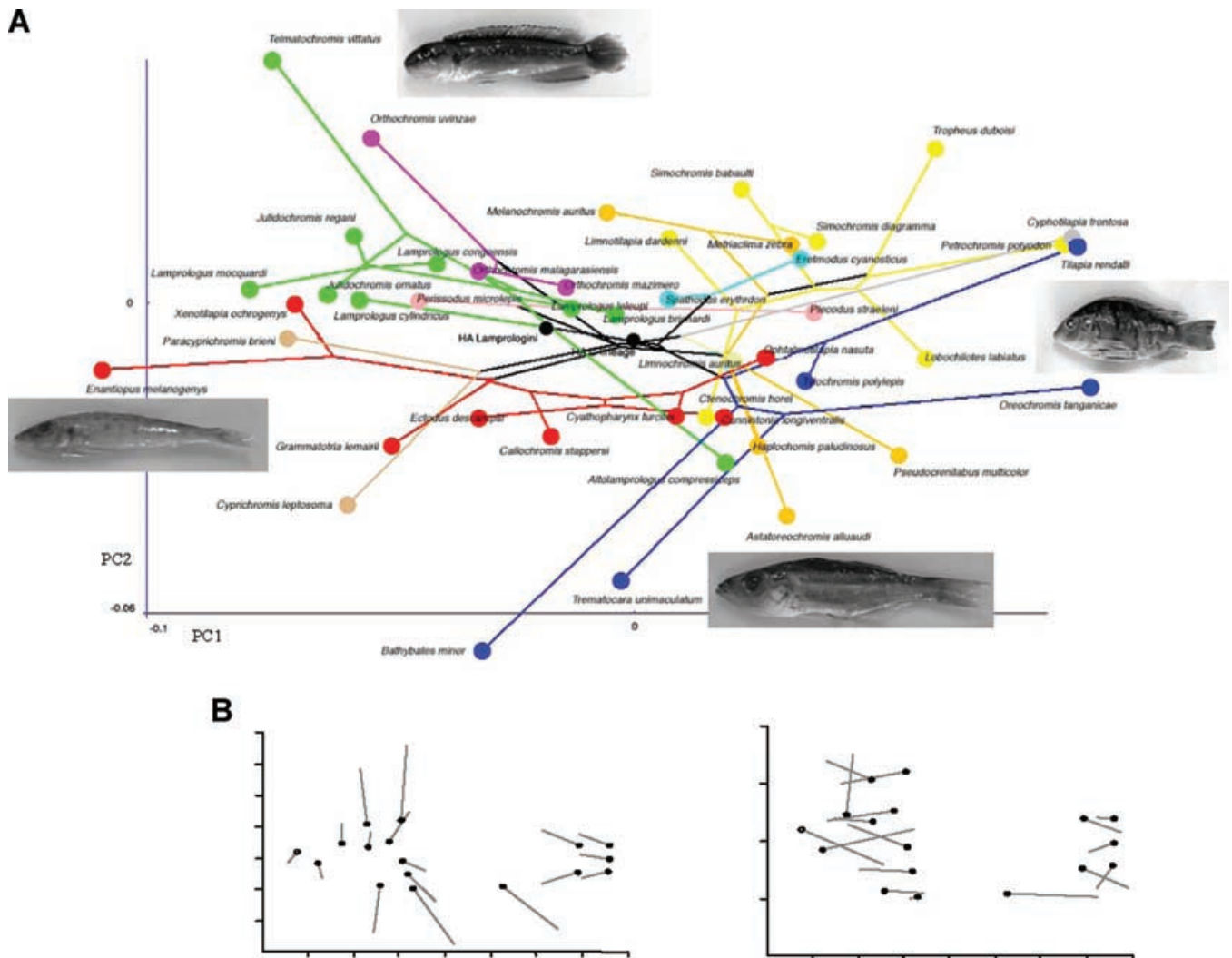
Figure 6. (A) PCA plot (origin at the center of the plot) with phylogenetic relationships among species. The pictures of the most extreme shapes of this morphospace are shown to illustrate the differences. The deformation vectors from individuals showing minimal scores to individuals showing maximal scores along the (B) horizontal axis (PC1) and (C) vertical axis (PC2) are also given. HA stands for hypothetical ancestor.

Discussion

The cichlids of East Africa are viewed as an ideal model system for the study of adaptive radiation (Fryer and Iles 1972; Stiassny and Meyer 1999; Kornfield and Smith 2000; Kocher 2004; Salzburger and Meyer 2004). We used geometric morphometric methods to describe the body shape of 45 species of East African cichlid fish, with a focus on the Lake Tanganyika species assemblage. This assemblage contains the largest degree of morphological variation of all East African cichlid radiations as well as their ancestral lineages (e.g., Salzburger et al. 2005). We presented quantitative data supporting the parallel evolution of several adaptive radiations within Lake Tanganyika. Indeed, the Tanganyikan mouthbrooders (C-lineage) and the substrate spawning Lamprologini have evolved a multitude of different shapes from two very similar hy-

pothetical ancestors. We confirm the adaptative character of these independent radiations through the presentation of correlations between body shape and ecological characters. Finally, the impressive morphological diversity contained in the tribes included in our study, even those represented by very few specimens or species, illustrates the singular potential for radiation that characterizes cichlid fish.

LITTLE INFLUENCE OF PHYLOGENETIC CONSTRAINT ON BODY SHAPE EVOLUTION OF THE TANGANYIKAN CICHLID ASSEMBLAGE

In previous studies on cichlids and other organisms (Rüber and Adams 2001; Rosenberg 2002; Guill et al. 2003) phylogenetic relationships between species were found to be of great importance to the evolution of shape, resulting in closely related species that

resemble each other more than distant relatives. As expected in the case of rapid morphological diversification, however, cluster analyses of the Tanganyikan cichlid assemblage showed little similarity with phylogenetic assignment. We therefore investigated correlations between phylogenetic distances and Procrustes distances using Mantel statistics. However, no statistically significant correlation could be found, highlighting the surprisingly small influence of phylogeny on the shapes of cichlids. These results were predictable at the scale of the whole Tanganyikan assemblage because Lake Tanganyika does not comprise a monophyletic flock (Nishida 1991; Kocher et al. 1995; Salzburger et al. 2002). Even so, when we tested homogeneity within a monophyletic entity such as the whole C-lineage, the Haplochromini (including the Tropheini), the Ectodini, or the Lamprologini, we could still find no significant correlations. These results suggest that multiple cases of extensive intralake parallelism and rapid morphological diversification exist within Lake Tanganyika.

The absence of phylogenetic inertia in our morphometric data is particular to adaptive radiations (Schluter 2000). In general, smaller distances in the morphospace are expected to be found within a family of closely related organisms (Gatz 1979). In the darters (Percidae), for example, a significant correlation between phylogenetic distances and distances in the morphospace indicated that body shape is greatly influenced by phylogenetic history (Guill et al. 2003). Our results statistically support the assumption that there is no correlation between the degree of phylogenetic and morphological variation among cichlid adaptive radiations (see also Sturmbauer and Meyer 1992; Verheyen et al. 2003; Clabaut et al. 2005).

THE ADAPTIVE CHARACTER OF THE LAKE TANGANYIKA RADIATIONS

In the case of adaptive radiation, body shapes are similar among species not only because of shared evolutionary history, but also because of common ecological characteristics (Claude et al. 2004). These characteristics are of course indirectly and to a certain extent linked to shared evolutionarily history, but it has been shown that characters such as body size, morphology, life history, and physiology are also evolutionary more labile than others (deQueiroz and Wimberger 1993; Blomberg et al. 2003). If shared evolutionary history is not the main cause of similarity in shape, then the most likely cause of parallel and convergent evolution of a multitude of geographically isolated founder populations is equivalent ecological conditions (Sturmbauer et al. 2003).

Lake fish are distributed according to water depth and the nature of the substrate. Species have a particular depth range, which may be extremely narrow (less than 5 m) or broad (up to 100 m; Ribbink 1991). Divergent selection for fish inhabiting near shore, littoral zones, and off-shore, open water habitats might arise from two major differences between these environ-

ments: water velocity and the difference in resource composition and availability. Hydrodynamic theory posits that a more fusiform body shape reduces drag, and hence reduces the energetic expenditure necessary to maintain position in flowing water (reviewed in Langherans 2003). In our study, the most important global differences in body shape are related to body length. This is particularly the case for the transformation from one shape to another within the Ectodini which have colonized different habitats during their radiation, from shallow water to more open water. As might be expected then, we found some limited evidence for a relationship between depth of preferred habitat and shape using PGLS, though this relationship was not statistically significant. Furthermore, we observe a correlation in the PCA between the length of the body of *Grammatotria lemairii*, *Ectodus descampsi,* and *Cyathopharynx furcifer* and their preferred water depth (Poll 1956). Specifically, the deeper a cichlid species lives, the more elongated is its body.

Also, in the cluster analysis, *Cyathopharynx furcifer* and *Cunningtonia longiventralis* were always grouped with *Haplochromis paludinosus, Astatoreochromis alluaudi* (Lake Victoria and surroundings) and *Ctenochromis horei*. The latter three species also occur in rivers, a fact that could explain why they are morphologically close to each other. They are characterized by a deep body shape, whereas the Orthochromini, also riverine, have a more elongated body shape. The Orthochromini are grouped into two morphological clusters, which is consistent with the findings of De Vos and Seegers (1998) who place *O. mazimeroensis* and *O. malagarasiensis* in a monophyletic group. These two *Orthochromis* species are riverine, as well as *Lamprologus congoensis*, and they are grouped together in our cluster analyses. Two other Lamprologini, *N. calliurus* and *L. leleupi* are also found in this group. *Orthochromis uvinzae*, on the other hand, is clustered apart from the rest of the Orthochromini with *Telmatochromis vittatus.* We therefore suggest the existence of two types of body shapes in riverine cichlids. A deep-bodied morphotype adapted to rivers with slow water current (Haplochromini), and an elongated type living in surge waters (riverine Lamprologini and Orthochromini). The deep-bodied type may be more generalist in terms of habitat, enabling such fish to readily colonize new habitats and eventually become precursors of radiations in other lakes (see, e.g., Schelly and Stiassny 2004; Salzburger et al. 2005).

Another characteristic change revealed by the second axis of the PCA (Fig. 6) concerns the proportion of sizes of the different body parts (head and caudal peduncle). This is particularly the case for the Haplochromini, generally deep-bodied fish but whose head and caudal peduncle contain a large amount of shape variation compared to the rest of the body. The Haplochromini, and especially the nested Tropheini, show little variation in their habitat preferences because they are mainly restricted to rocky shore areas and they diversified primarily in their feeding habits.

As a consequence, the Tropheini also present a surprisingly low disparity value even when the number of species and specimens analyzed is taken into account.

Despite the inferred importance of water depth on shape, and the ease with which correlations between gross shape differences and habitat can be determined, this does not appear to be the most important ecological characteristic in generating cichlid shape diversity. Indeed, there is little statistical support for using complex models to describe cichlid body shape. Given that diverging lineages in an adaptive radiation are expected to evolve according to disparate ecological pressures and considering that evolutionary responses in morphology to different adaptive dynamics may be similar or unpredictable, it is perhaps not surprising that the complex models regressing ecology on shape are statistically unreliable and confound various ecological characters. This difficulty in identifying specific ecological characters as the most important in defining Tanganyikan cichlid shape serves to highlight the extreme ecological diversity of this adaptive radiation. Nonetheless, one single predictor model did have a significant effect on partial warp scores, that which coded feeding preference into six types of food source. Feeding preference was found by PGLS and by the analysis of morphospace variability (Fig. 4), the main characteristic structuring the morphospace. In other words, species with similar feeding behavior occupy discrete regions of the morphospace, leading to the conclusion that morphological variation is strongly related to what a species specializes on trophically. With such high rates of speciation, such small scale differentiation may play a huge role in generating behavioral and geographic differences necessary for barriers to reproduction to evolve. As a result, it appears that such types of ecological divergence may play a central role in producing the rapid evolution of new types that is a signature of adaptive radiations (Schluter 2000).

Additionally, the scale eaters *Plecodus straeleni* and *Perissodus microlepis* show different body shapes but are similar in the position of the mouth and the size and characteristic shape of their head according to PCA (Fig. 6). Their very specific feeding habit (scale eating) may constrain the features involved in the feeding behavior, whereas the rest of the body is evolving in response to other environmental pressures, as evidenced by the high disparity value of this tribe. One possible explanation for the evolution of overall body shape among scale eaters is mimicry of the shape of their prey, as observed in *P. straeleni* preying on *Cyphotilapia frontosa* (Brichard 1978; Coulter 1991). The resemblance of these species is supported by the cluster analysis using Ward's method and the UPGMA algorithms. *Perissodus microlepis*, on the other hand, is long and thin, characteristics probably related to the fact that these fish need to be good open water swimmers to easily attack pelagic prey (Winemiller 1991). It seems likely, though, that these scale eaters mimic the abundant Tanganyika killifish (*Lamprichthys tanganicanus*).

The examples above highlight the adaptive character of Tanganyikan cichlid body shape evolution, even though specific interpretations of the results are difficult as various ecological parameters are acting simultaneously on body shape evolution. For instance, cichlids consume abundant prey when available, even outside their speciality (McKaye and Marsch 1983; Winemiller 1990; Langerhans et al. 2003), leading Liem to call them "jacks of all trades" (Liem 1980). This opportunism in their feeding habits, though some species are extremely specialized, might also have an influence on body shape, constraining it to a more average form. A geometric morphometric analysis more focused on the head shape would probably strengthen this result and enable a more explicit interpretation of the changes in shape in relation to ecology.

POTENTIAL FOR DIVERSIFICATION

The Lamprologini and Ectodini are the most morphologically diverse tribes of Lake Tanganyika (Fig. 3), which can be explained by the great amount of trophic and habitat diversity that characterize the fish of these two tribes (Sturmbauer and Meyer 1993; Stiassny 1997; Barlow 2000; Chakrabarty 2005).

The influence of the Cyphotilapiini on morphospace disparity is characteristic of the peripheral position of this tribe. The fact that the position of this subgroup in the overall morphospace is far from the centroid is probably due to the pronounced bump on their forehead. This very peculiar feature has a strong influence on the description of shape after Procustres analysis, because the displacement of the landmarks located on the head will be carried through to all other landmarks. The fact that no other subgroup significantly influences the disparity of the total morphospace indicates that all other tribes strongly overlap in the morphospace. Therefore, we conclude that the morphology of Tanganyikan cichlids is not constrained by tribe affiliation, because even species-poor tribes with a few specimens tend to occupy large portions of the entire morphospace (Figs. 3 and 6). This implies that even though only a few tribes (Haplochromini, Ectodini, Lamprologini) are extremely species rich, the other tribes, irrespective of whether they are ancient or young lineages, and irrespective of whether they contain many or a few species, still contain an impressive diversity of morphologies. This illustrates the potential for radiation that exists in cichlid lineages. However, the absence of evolutionary novelties in the cichlid body shape has been noted before (Stiassny 1991). The disparity analysis gives compelling quantitative evidence for the fact that cichlids are tinkering with an ancestral toolkit of shape.

INDEPENDENT ADAPTIVE RADIATIONS IN LAKE TANGANYIKA

Our study reveals that for the adaptive radiations of the Lake Tanganyika cichlids, the influence of phylogeny on the evolution of

form is small. In contrast, body shape evolution is strongly affected by ecology. We suggest the presence of two general patterns of diversification within the lake´s species flock. One trend in diversification is constrained by habitat preferences, and is characterized by body shape being more or less elongated (Ectodini, Lamprologini). The other evolutionary trajectory is correlated with trophic habits, leading to changes in the different proportions of sizes of the different parts of the body (Haplochromini, see Fig. 5). The ancestor of the C-lineage was *Lamprologus*-like as indicated by our analysis and could have undergone first an expansion in different habitat types, and later a specialization in feeding behaviors. In the case of the mouthbrooders of the C-lineage as well as in the case of the lamprologine substrate spawners, sexual selection would then be a speciation mechanism happening only after morphological diversification (Danley and Kocher 2001). In either case, it is apparent from these analyses that ecology plays a remarkably strong role in generating morphological diversity. This fact confirms the presence of a strong correlation between phenotype and environment, precisely as expected for an adaptive radiation (Schluter 2000).

LITERATURE CITED

Barlow, G. W. 1991. Mating system among cichlid fishes. Pp. 173–190 *in* M. H. A. Keenleyside, ed. Cichlid fishes: behavior, ecology and evolution. Chapman and Hall, London.

———. 2000. The cichlid fishes: nature's grand experiment. Perseus Publishing, Cambridge, MA.

Blomberg, S. P., T. J. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745.

Bookstein, F. L. 1991. Morphometric tools for landmark data: geometry and biology. Cambridge Univ. Press, New York.

Brichard, P. 1978. Fishes of Lake Tanganyika. TFH Publications, Neptune City, NJ.

———. 1989. Cichlids and all the other fishes of Lake Tanganyika. TFH Publications, Neptune City, NJ.

Cavalcanti, M. J. 2005. MANTEL, Ver. 1.16. Dept. de Zoologia, Univ. Estado Rio de Janeiro, Brazil. Available at http://acd.ufrj.br/~maurobio/en/?Available_Software.

Cavalcanti, M. J., L. R. Monteiro, and P. R. Duarte Lopes. 1999. Landmark-based morphometric analysis in selected species of Serranid fishes (Perciformes: Teleostei). Zool. Stud. 38:287–294.

Chakrabarty, P. 2005. Testing conjectures about morphological diversity in Cichlids of Lake Malawi and Tanganyika. Copeia 2:359–373.

Clabaut, C., W. Salzburger, and A. Meyer. 2005. Comparative phylogenetic analyses of the adaptive radiation in Lake Tanganyika cichlid fishes: nuclear sequences are less homoplasious but also less informative than mitochondrial DNA. J. Mol. Evol. 31:666–681.

Claude, J., P. Pritchard, H. Tong, E. Paradis, and J.-C. Auffray. 2004. Ecological correlates and evolutionary divergence in the skull of turtles: a geometric morphometric assessment. Syst. Biol. 53:933–948.

Coddington, J. A. 1990. Bridges between evolutionary patterns and process. Cladistics 6:379–386.

Cohen, A., K. Lezzar, J. Tiercelin, and M. Soreghan. 1997. New paleontologic and lake level reconstructions of Lake Tanganyika: implication for tectonic, climatic and biological evoluion in a rift lake. Basin Res. 7:107–132.

Cohen, A., M. Soreghan, and C. Scholz. 1993. Estimating the age of formation of lakes: an example from Lake Tanganyika, East African Rift system. Geology 21:511–514.

Coulter, G. W. 1991. The benthic fish community in Lake Tanganyika and its life. Oxford Univ. Press, Oxford, U.K.

Danley, P. D., and T. D. Kocher. 2001. Speciation in rapidly diverging systems: lessons from Lake Malawi. Mol. Ecol. 10:1075–1086.

deQueiroz, A., and P. H. Wimberger. 1993. The usefulness of behavior for phylogeny estimation: levels of homoplasy in behavioral and morphological characters. Evolution 47:46–60.

Dryden, I. L., and K. V. Mardia. 1998. Statistical shape analysis. John Wiley and Sons, New York.

Farias, I. P., G. Orti, and A. Meyer. 2000. Total evidence: molecules, morphology, and the phylogenetics of cichlids fishes. Mol. Dev. Evol. 288:76–92.

Felsenstein, J. 1985. Phylogenies and the comparative method. Am. Nat. 125:1–15.

Foote, M. 1991. Morphologic patterns of diversification, examples from trilobites. Palaeontology 34:461–485.

———. 1993. Contributions of individual taxa to overall morphological disparity. Paleobiology 19:403–419.

Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of the evidence. Am. Nat. 160:712–726.

Fryer, G., and T. D. Iles. 1972. The cichlids fishes of the Great Lakes of Africa. THF Publications, Neptune City, NJ.

Gatz, A. J. J. 1979. Community organization in fishes as indicated by morphological features. Ecology 60:711–718.

Gerbrand, J. P. 1998. Ecomorphology of a size-structured tropical freshwater fish community. Env. Biol. Fishes 51:67–86.

Goodwin, N. B., S. Balshine-Earn, and J. D. Reynolds. 1998. Evolutionary transitions in parental care in cichlid fish. Proc. R. Soc. Lond. B 265:2265–2272.

Gower, J. C. 1975. Generalized Procrustes analysis. Psychometrika 40:33–51.

Guill, J. M., D. C. Heins, and C. S. Hood. 2003. The effect of phylogeny on interspecific body shape variation in Darters (Pisces: Percidae). Syst. Biol. 52:488–500.

Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4:1.

Hansen, T. F., and S. H. Orzack. 2005. Assessing current adaptation and phylogenetic inertia as explanations of trait evolution: the need for controlled comparisons. Evolution 59:2063–2072.

Hanssens, M., J. Snoeks, and E. Verheyen. 1999. A morphometric revision

of the genus *Ophthalmotilapia* (Teleostei, Cichlidae) from Lake Tanganyika (East Africa). Zool. J. Linn. Soc. 125:487–512.

Hori, M. 1991. Feeding relationships among cichlid fishes in Lake Tanganyika: effects of intra- and interspecific variations of feeding behavior on their coexistence. Eco. Int. Bull. 19:89–101.

Housworth, E. A., E. P. Martins, and M. Lynch. 2004. The phylogenetic mixed model. Am. Nat. 163:84–96.

Kassam, D., D. C. Adams, and K. Yamaoka. 2004. Functional significance of variation in trophic morphology within feeding microhabitat-differentiated cichlid species in Lake Malawi. Anim. Biol. 54:77–90.

Kassam, D. D., D. C. Adams, A. J. D. Amballi, and K. Yamaoka. 2003a. Body shape variation in relation to resource partitioning within cichlid trophic guilds coexisting along the rocky shore of Lake Malawi. Anim. Biol. 53:59–70.

Kassam, D. D., D. C. Adams, M. Hori, and K. Yamaoka. 2003b. Morphometric analysis on ecomorphologically equivalent cichlid species from lakes Malawi and Tanganyika. J. Zool. 260:153–157.

Klingenberg, C., M. Barluenga, and A. Meyer. 2003. Body shape variation in cichlid fishes of the Amphilophus citrinellus species complex. Biol. J. Linn. Soc. 80:397–408.

Koblmueller, S., W. Salzburger, and C. Stumbauer. 2004. Evolutionary relationships in the sand-dwelling cichlid lineage of Lake Tanganyika suggest multiple colonization of rocky habitats and convergent origin of biparental mouthbrooding. J. Mol. Evol. 58:79–96.

Kocher, T. D. 2004. Adaptive evolution and explosive speciation: the cichlid fish model. Nat. Rev. Genet. 5:288–298.

Kocher, T. D., J. A. Conroy, K. R. McKaye, and J. R. Stauffer. 1993. Similar morphologies of cichlid fishes in Lakes Tanganyika and Malawi are due to convergence. Mol. Phyl. Evol. 4:420–432.

Kocher, T. D., J. A. Conroy, K. R. McKaye, J. R. Stauffer, and S. F. Lockwood. 1995. Evolution of NADH Dehydrogenase Subunit 2 in East African cichlid fish. Mol. Phyl. Evol. 4:420–432.

Konings, A. 1988. Tanganyika cichlids. Pp 272. Verduijn Cichlids, Zevenhuizen, The Netherlands.

Kornfield, I., and P. F. Smith. 2000. African cichlid fishes: model systems for evolutionary biology. Annu. Rev. Ecol. Syst. 31:163–196.

Kuwamura, T. 1997. The evolution of parental care and mating systems among Tanganyikan cichlids. Pp. 59–86 *in* H. Kawanabe, M. Hori, and M. Nagoshi, eds. Fish communities in Lake Tanganyika. Kyoto Univ. Press, Kyoto.

Langerhans, R. B., C. A. Layman, A. K. Langerhans, and T. J. Dewitt. 2003. Habitat-associated morphological divergence in two Neotropical fish species. Biol. J. Linn. Soc. 80:689–698.

Liem, K. F. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. Am. Zool. 20:295–314.

Linde, M., M. Palmer, and J. Gòmez-Zurita. 2004. Differential correlates of diet and phylogeny on the shape of the premaxilla and anterior tooth in sparid fishes (Perciformes: Sparidae). J. Evol. Biol. 17:941–952.

Lippitsch, E. 1995. Scale and squamation character polarity and phyletic assessment in the family Cichlidae. J. Fish. Biol. 47:91–106.

Lowe-McConnell, R. 2002. Cichlids all! With an ecological view of African cichlids. Environ. Biol. Fishes 63:459–463.

Maddison, W. P., and D. R. Maddison. 2004. Mesquite: a modular system for evolutionary analysis. Ver. 1.05. http:// mesquiteproject.org

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer. Res. 27:209–220.

Martins, E. P., and T. F. Hansen. 2004. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am. Nat. 149:646–667.

McCune, A. R. 1981. Quantitative description of body form in fishes: implication for species level taxonomy and ecological inferences. Copeia 4:897–901.

McKaye, K. R., and A. Marsch. 1983. Food switching by two specialized algae-scraping cichlid fishes in Lake Malawi, Africa. Oecologia 56:245–248.

Meyer, A. 1993. Phylogenetic relationships and evolutionary processes in East African cichid fishes. Trends Ecol. Evol. 8:279–284.

Nagoshi, M., and Y. Yanagisawa. 1997. Parental care patterns and growth and survival of dependant offspring in cichlids. Pp. 177–192 *in* H. Kawanabe, M. Hori, and M. Nagoshi, eds. Fish communities in Lake Tanganyika. Kyoto Univ. Press, Kyoto.

Nishida, M. 1991. Lake Tanganyika as an evolutionary reservoir of old lineages of East African fishes: inferring from allozymes data. Experientia 47:974–979.

———. 1997. Phylogenetic relationships and evolution of Lake Tanganyika cichlids: a molecular perspective. Pp. 1–24 *in* M. Nagoshi, ed. Fish communities in Lake Tanganyika. Kyoto Univ. Press, Kyoto.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Parsons, K. J. 2003. Getting into shapes. Env. Biol. Fishes 67:417–431.

Pinheiro, J. C., and D. M. Bates. 1998. Computational methods for multilevel models. Bell Labs technical memorandum. Available at http://stat.bell-labs.com/NLME/CompMulti.pdf.

Poll, M. 1956. Resultats scientifique. Exploration hydrobiologique belge au lac Tanganyika (1946–1947). Poissons Cichlidae. Institut Royal des Sciences Naturelles de Belgique, Belgium.

———. 1986. Classification des Cichlidae du lac Tanganyika: tribus, genres et espèces. Acad. R. Belg. Mem. Classe Sci (Collection in –8°–2° serie) T. 45:1–163.

Posada, D., and K. A. Crandall. 1998. ModelTest: testing the model of DNA substitution. Bioinformatics 14:817–818.

Reinthal, P., and A. Meyer. 1997. Molecular phylogenetic tests of speciation models in African cichlid fishes. Pp. 375–390 *in* T. Givinish and K. Sytsma, eds. Molecular phylogenetics of adaptive radiations. Cambridge Univ. Press, Boston.

Ribbink, A. J. 1991. Ecology of the cichlids of the African Great Lakes. *In* M. H. A. Keenleyside, ed. Cichlid fishes: behavior, ecology and evolution. Chapman and Hall, London.

Rodriguez, F., J. F. Oliver, A. Marin, and J. R. Medina. 1990. The general stochastic model of nucleotide substitutions. J. Theor. Biol. 142:485–501.

Rohlf, F. J. 2002. Geometric morphometrics and phylogeny. Pp. 175–193 *in* N. MacLeod and P. L. Forey, eds. Morpholgy, shape and phylogeny. Taylor and Francis, London.

———. 2003. tpsSmall, Ver. 1.20. Department of Ecology and Evolution, State University of New York at Stony Brook. Available at http://life.bio.sunysb.edu/morph/.

———. 2004a. tpsSpline. Department of Ecology and Evolution, State University of New York at Stony Brook. Available at http://life.bio.sunysb.edu/morph/.

———. 2004b. tpsSuper, superimposition and image averaging, Ver. 1.13. Department of Ecology and Evolution, State University of New York at Stony Brook. Available at http://life.bio.sunysb.edu/morph/.

———. 2005. tpsRelw, relative warps analysis, Ver. 1.42. Department of Ecology and Evolution, State University of New York at Stony Brook. Available at http://life.bio.sunysb.edu/morph/.

Rohlf, F. J., A. Loy, and M. Corti. 1996. Morphometric analysis of Old World Talpidae (Mammalia, Insectivora) using partial-warp scores. Syst. Biol. 45:129–132.

Rohlf, F. J., and L. F. Marcus. 1993. A revolution in morphometrics. Trends Ecol. Evol. 8:129–132.

Rohlf, F. J., and D. E. Slice. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Syst. Zool. 39:40–59.

Rosenberg, M. S. 2002. Fiddler crab claw shape variation: ageometric morphometric analysis accross the genus *Uca* (Vrustacea: Brachyura: Ocypodidae). Biol. J. Linn. Soc 75:147–162.

Rüber, L., and D. C. Adams. 2001. Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika. J. Evol. Biol. 14:325–332.

Rüber, L., E. Verheyen, and A. Meyer. 1999. Replicated evolution of trophic specializations in an endemic cichlid fish lineages from Lake Tanganyika. PNAS 96:10230–10235.

Salzburger, W., T. Mack, E. Verheyen, and A. Meyer. 2005. Out of Tanganyika: genesis, explosive speciation, key-innovations and phylogeography of the haplochromine cichlid fishes. BMC Evol. Biol. 5:17.

Salzburger, W., and A. Meyer. 2004. The species flocks of East African cichlid fishes: recent advances in molecular phylogenetics and population genetics. Naturwissenschaften 91:277–290.

Salzburger, W., A. Meyer, S. Baric, E. Verheyen, and C. Stumbauer. 2002. Phylogeny of the Lake Tanganyika Cichlid species flock and its relationship to the central and east African Haplochromine cichlid fish faunas. Syst. Biol. 51:113–135.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford Univ. Press, Oxford, U.K.

Sheets, H. D. 2005. IMP. Department of Physics, Canisius College, New York. Available at http://www.canisius.edu/s̄heets/morphsoft.html.

Smith, L. H., and P. M. Bunje. 1999. Morphologic diversity of inarticulate brachiopods through the Phanerozoic. Paleobiology 25:396–408.

Smouse, P. E., J. C. Long, and R. R. Sokal. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Syst. Zool. 35: 627–632.

Snoeks, J., L. Rüber, and E. Verheyen. 1994. The Tanganyika problem: comments on the taxonomy and distribution patterns of its cichlid fauna. Adv. Limnol. 44:355–372.

Stiassny, M. L. J. 1990. *Tylochromis*, relationships and the phylogenetic status of the African Cichlidae. Am. Mus. Novit. 1993:1–14.

———. 1991. Phylogenetic relationships of the family Cichlidae: an overview. *In* M. H. A. Keenleyside, ed. Cichlid fishes: behavior, ecology and evolution. Chapman and Hall, London.

———. 1997. A phylogenetic overview of the Lamprologine cichlids of the Africa (Teleostei, Cichlidae): a morphological perspective. S. Afr. J. Sci. 93:513–523.

Stiassny, M. L. J., and A. Meyer. 1999. Cichlids of the African rift lakes. Sci. Am. 280: 44–49.

Sturmbauer, C., U. Hainz, S. Baric, E. Verheyen, and W. Salzburger. 2003. Evolution of the tribe Tropheini from Lake Tanganyika: synchronized explosive speciation producing multiple evolutionary parallelism. Hydrobiologia 500:51–64.

Sturmbauer, C., and A. Meyer. 1992. Genetic divergence, speciation and morphological stasis in a lineage of African cichlid fishes. Nature 358:578–581.

———. 1993. Mitochondrial phylogeny of the endemic mouthbrooding lineages of cichlid fishes of Lake Tanganyika, East Africa. Mol. Biol. Evol. 10:751–768.

Swofford, D. L. 2002. PAUP*, Ver. 4.0b10. Sinauer, Sunderland, MA.

Takahashi, T. 2003. Systematics of Tanganyikan cichlids fishes (Teleostei: Perciformes). Ichthyol. Res. 50:367–382.

Thompson, D. W. 1917. On growth and form. Cambridge Univ. Press, Cambridge, U.K.

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? Mol. Ecol. 10:793–806.

Verheyen, E., W. Salzburger, J. Snoeks, and A. Meyer. 2003. Origin of the superflock of cichlid fishes from Lake Victoria East Africa. Science 300:325–329.

Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecol. Monogr. 60:331–367.

———. 1991. Ecomorphological diversification in low-land freshwater fish assemblages from five biotic regions. Ecol. Monogr. 61:343–365.

Winemiller, K. O., L. C. Kelso-Winemiller, and A. L. Brenkert. 1995. Ecological and morphological diversification in fluvial cichlid fishes. Environ. Biol. Fishes 44:235–261.

Zelditch, M. L., D. L. Swiderski, H. D. Sheets, and W. L. Fink. 2004. Geometric morphometrics for biologists: a primer. Elsevier, San Diego.

Associate Editor: K. Schwenk