# Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika

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## Abstract

A recent phylogenetic analysis of mitochondrial DNA sequences from eretmodine cichlids from Lake Tanganyika indicated independent origins of strikingly similar trophic specializations, such as dentition characters. Because genetic lineages with similar trophic morphologies were not monophyletic, but instead were grouped with lineages with different trophic phenotypes, raises the question of whether trophic morphology covaries with additional morphological characters. Here, we quantified morphological variation in body shape and trophically associated traits among eretmodine cichlids using linear measurements, meristic counts and landmark-based geometric morphometrics. A canonical variates analysis (CVA) delineated groups consistent with dentition characters. Multivariate regression and partial least squares analyses indicated that body shape was significantly associated with trophic morphology. When the phylogenetic relationships among taxa were taken into account using comparative methods, the covariation of body shape and trophic morphology persisted, indicating that phylogenetic relationships were not wholly responsible for the observed pattern. We hypothesize that trophic ecology may be a key factor promoting morphological differentiation, and postulate that similar body shape and feeding structures have evolved multiple times in independent lineages, enabling taxa to invade similar adaptive zones.

## Introduction

The cichlid species flocks of the East African Great Lakes, Victoria, Malawi, and Tanganyika are unique examples of adaptive radiations (Greenwood, 1984). In each lake, highly specialized species that occupy a wide range of trophic niches are found, which are similar morphologically and behaviourally (Fryer & Iles, 1972). The similarities in trophic morphology between fishes from different lakes could result from common ancestry, followed by dispersal or vicariance. However, recent comparisons between morphological characters and molecular phylogenies have demonstrated multiple convergent events in trophic morphology between lakes (Kocher *et al*., 1993; Meyer, 1993) and even within a single lake (Rüber *et al*., 1999).

A recent phylogenetic analysis of mitochondrial DNA sequences indicated independent origins of strikingly similar trophic specializations, such as dentition characters, in the endemic Lake Tanganyika cichlid fishes of the tribe Eretmodini (Rüber *et al*., 1999; see also Fig. 1). This tribe comprises four nominal species currently assigned to three genera: *Eretmodus cyanostictus* Boulenger 1898, *Spathodus erythrodon* Boulenger 1900, *S. marlieri* Poll 1950, and *Tanganicodus irsacae* Poll 1950. Differences in dentition, and the shape and the number of oral teeth, are the main diagnostic characters that delineate these species (Poll, 1986). The teeth of *Eretmodus* are spatula-shaped with a slender neck region, those of *Spathodus* are cylindrical-shaped with a flattened and truncated crown,

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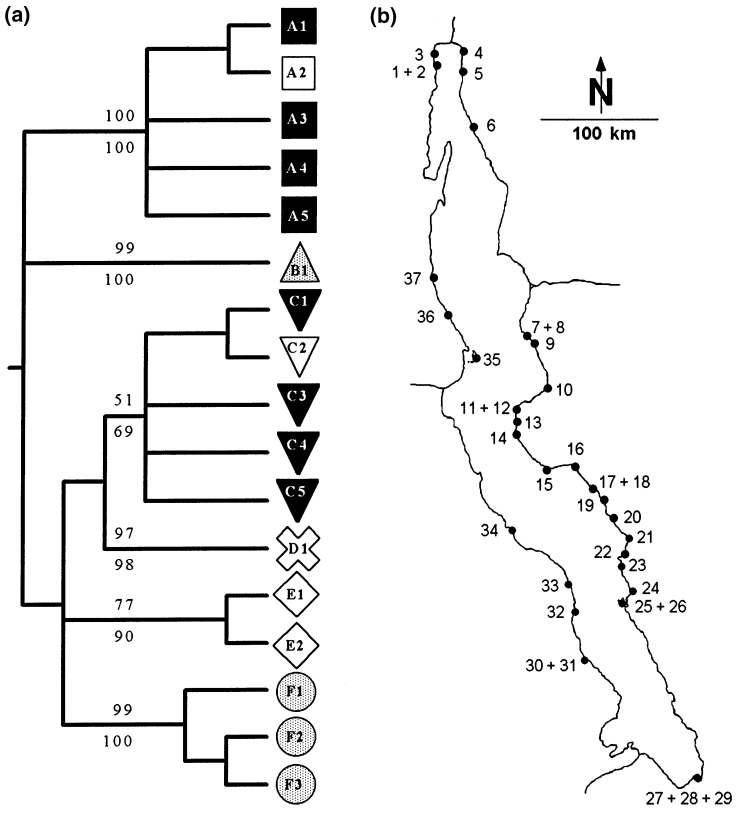



**Fig. 1** (a) Hypothesized phylogenetic relationship among the eretmodine populations used in this study, based on mitochondrial DNA sequences. The tree shown (modified from Rüber *et al.*, 1999) is a strict consensus tree from maximum parsimony (MP) and neighbour joining (NJ) analyses of partial cytochrome *b* and control region sequences. MP bootstrap support values for the six major lineages (A–F) are given above branches and those from NJ below branches. For further details on the molecular phylogeny of eretmodine cichlids see Rüber *et al.* (1999). The six phylogenetic lineages (A–F) are indicated by different symbols and the 17 distinct phylogenetic clades are labelled according to Table 1 (black = *Eretmodus*-, grey = *Spathodus*-, and white = *Tanganicodus*-like dentition). (b). Map of Lake Tanganyika showing the localities used in this study.

and those of *Tanganicodus* are slender and pointed (Fig. 2). Based on the molecular phylogeny six distinct lineages were identified; the genera *Eretmodus*, *Spathodus*, and *Tanganicodus* are considered nonmonophyletic and thus warrant taxonomic reassessment (Rüber *et al.*, 1999). Fishes with a particular tooth shape were not resolved monophyletically and it was suggested that parallel evolution of tooth shape resulted in independent origins of similar trophic specialization within this tribe. Such a repeated pattern of morphological divergence in oral tooth shape among eretmodine cichlids might indicate ecological processes as key factors in shaping their evolution (Rüber *et al.*, 1999).

The observation that similar tooth shapes have evolved more than once within the Eretmodini raises the question of whether differences in tooth shape are accompanied by additional morphological differences. The objective of our study was to test (1) whether there were detectable differences in body shape among different populations of eretmodine cichlids irrespective of their tooth shape; (2) whether body shape was correlated with morphological characters associated with trophic exploitation and finally (3) whether this pattern of body shape variation was consistent with phylogenetic relationships or with differences in oral tooth shape. Here, we employ geometric morphometrics to describe body shape variation in eretmodine cichlids in relation to their phylogenetic relationships and their respective trophic adaptation, as attested by differences in the shape of their oral jaw teeth. We discuss our findings in terms of phylogeny, convergence, and ecological specialization in this cichlid tribe.

## Materials and methods

### Data collection and quantification of body shape

We studied 412 specimens from 17 populations defined according to previous phylogenetic analyses (Rüber *et al.*, 1999; Fig. 1). Of the six well supported mtDNA lineages (A–F), lineages A and C contained fish with multiple dentition types, whereas lineages B, D, E and F contained specimens with one of the tooth types found in eretmodine cichlids. Lineages A, C, E and F were divided into phylogeographical clades as shown in Table 1 and Fig. 1.

Overall body shape was quantified using geometric morphometric (GM) methods (Bookstein, 1991; Rohlf & Marcus, 1993). GM methods generate shape variables from a set of homologous landmarks recorded on each specimen, after differences in specimen position, orientation, and size have been mathematically held constant (Rohlf & Slice, 1990). Unlike linear distance measurements, GM shape variables preserve the geometry of the anatomical structure throughout the analysis (Adams &

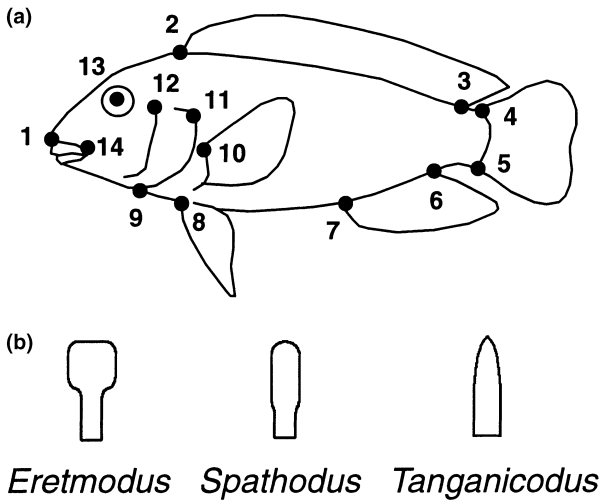



**Fig. 2** (a) Positions of the 14 landmarks used to define body shape of eretmodine cichlids. These landmarks include: (1) anterior tip of snout at upper jaw, (2) anterior insertion of dorsal fin, (3) posterior insertion of dorsal fin, (4) dorsal insertion of caudal fin, (5) ventral insertion of caudal fin, (6) posterior insertion of anal fin, (7) anterior insertion of anal fin, (8) anterior insertion of pelvic fin, (9) posterior border of branchiostegal membrane on ventral midline, (10) dorsal base of pectoral fin, (11) dorso-caudal margin of gill cover, (12) dorsal end of pre-opercular bones just below the pterotics, (13) centre of eye and (14) posterior border of upper lip. All landmarks except landmark 13 were pinned with small insect pins to aid in more precisely identifying these points. (b) The three tooth-shape types found in eretmodine cichlids (see Table 1).

Rohlf, 2000). Therefore, with GM shape variables, it is possible not only to perform statistical comparisons of shape, but also to generate graphical representations of mean forms to study trends in shape variation (e.g. Adams & Funk, 1997; Caldecutt & Adams, 1998; Adams & Rohlf, 2000).

From each adult specimen we recorded the *x, y* coordinates of 14 homologous landmarks chosen for their capacity to describe overall body shape (Fig. 2). Nonshape variation was removed using Generalized Procrustes superimposition (Rohlf & Slice, 1990), which translates all specimens to a common location, scales them to unit size, and rotates them so that their corresponding landmarks line up as closely as possible. Shape variables were then generated from the aligned specimens using the thin-plate spline equation (Bookstein, 1991) and the standard formula for the uniform component (Bookstein, 1996). All morphometric analyses were performed in TPSRELW (Rohlf, 1999b).

In addition to overall body shape, four trophic characters were scored for each specimen: two morphological measurements and two meristic characters. These variables are not included in the general description of body shape and do not *a priori* covary with it. The measures are gape width, measured across the posterior corners of the lips, and interorbital width, and the meristic characters are the oral tooth counts of all erupted teeth on the premaxillary and dental bones. These variables are commonly used to describe ecomorphological variation in fishes (e.g. Lavin & McPhail, 1985; Yamaoka *et al.*,

**Table 1** List of specimens, phylogenetic clades, tooth types, mean standard size ± SD per group, and sample sizes for eretmodine populations used in this study.

| Species | Phylogenetic clade* | Tooth type† | Mean standard length ± SD | Localities* | Sample size per locality | Sample size |
|---|---|---|---|---|---|---|
| *Eretmodus* cf. *cyanostictus* (A) | A1 | Er | 49.51 ± 7.78 | 3, 5, 6 | 7, 15, 8 | 30 |
| *Tanganicodus irsacae* | A2 | Ta | 45.65 ± 3.39 | 1, 2, 3 | 5, 2, 1 | 8 |
| *E.* cf. *cyanostictus* (A) | A3 | Er | 54.66 ± 7.98 | 11, 12, 13, 14 | 4, 1, 6, 1 | 12 |
| *E.* cf. *cyanostictus* (A) | A4 | Er | 51.57 ± 6.00 | 19, 20, 21, 23 | 2, 3, 4, 1 | 10 |
| *E.* cf. *cyanostictus* (A) | A5 | Er | 50.67 ± 7.17 | 35 | 14 | 14 |
| *Spathodus* cf. *erythrodon* (B) | B1 | Sp | 45.51 ± 5.47 | 4, 6 | 22, 7 | 29 |
| *E. cyanostictus* | C1 | Er | 51.35 ± 7.05 | 24, 25, 26 | 17, 6, 13 | 36 |
| *T.* cf. *irsacae* (C) | C2 | Ta | 50.94 ± 5.92 | 21, 22 | 4, 3 | 7 |
| *E. cyanostictus* | C3 | Er | 52.39 ± 4.62 | 30, 31 | 16, 14 | 30 |
| *E. cyanostictus* | C4 | Er | 50.38 ± 8.56 | 32, 34 | 20, 21 | 41 |
| *E. cyanostictus* | C5 | Er | 52.53 ± 7.87 | 27, 28, 29 | 6, 4, 22 | 32 |
| *T.* cf. *irsacae* (D) | D1 | Ta | 43.96 ± 4.00 | 30, 31, 32 | 24, 7, 17 | 48 |
| *T.* cf. *irsacae* (E) | E1 | Ta | 43.12 ± 4.20 | 35, 36, 37 | 7, 7, 10 | 24 |
| *T.* cf. *irsacae* (E) | E2 | Ta | 48.48 ± 4.43 | 7, 8, 9, 10, 11, 15, 16 | 4, 3, 3, 3, 6, 2, 1, 2 | 24 |
| *S. erythrodon* | F1 | Sp | 51.40 ± 5.02 | 34 | 24 | 24 |
| *S. erythrodon* | F2 | Sp | 54.65 ± 8.47 | 33 | 14 | 14 |
| *S. erythrodon* | F3 | Sp | 51.66 ± 5.54 | 17, 18, 19 | 14, 8, 7 | 29 |

* Phylogenetic clades and locality numbers as shown in Fig. 1.

† Follow the current taxonomic classification of eretmodine cichlids (Poll, 1986): Er = *Eretmodus*-, Sp = *Spathodus*- and Ta = *Tanganicodus*-like tooth shape.

1986; McDowall, 1998; Huysseune *et al*., 1999; Turgeon *et al*., 1999; Jónsson & Skúlason 2000). Because of their potential relevance in food exploitation (see Discussion) we hereafter refer to them as trophic characters and we are interested in examining whether they are correlated with body shape in eretmodine cichlids.

### Statistical analyses

We performed several statistical and graphical analyses to explore body shape variation among populations, and to determine whether body shape significantly covaried with oral tooth shapes and/or among phylogenetic clades. First, we performed a canonical variates analysis (CVA) to determine if populations differed significantly in body shape. Pairwise multiple comparisons among populations were calculated by transforming generalized distances into Hotelling's $T^2$ values, following standard techniques (see Marcus, 1993). To visualize body shape differences we generated thin-plate spline deformation grids along the first CV axis. Thin-plate spline deformation grids are similar to D'Arcy Thompson's transformation grids (Thompson, 1917), where the shape differences of one specimen relative to another are represented as a set of bent grid lines superimposed over the landmark co-ordinates of the specimen. Deformation grids were also generated for several representative group means, to further display the differences between them. All statistical analyses were performed in NTSYS-pc (Rohlf, 2000), and graphical depictions of shape deformations were generated in TPSRELW (Rohlf, 1999b).

We also determined whether body shape was statistically associated with the trophic characters, by performing a multivariate regression and a partial least squares analysis. Partial least squares analysis is a multivariate correlation technique that describes the covariation between two sets of variables (see e.g. Rohlf & Corti, 2000). The significance of this correlation was assessed using a randomization test. Deformation grids along the axis of body shape were generated to facilitate interpretation of the statistical results. Partial least squares analysis was performed in TPSPLS (Rohlf, 1999a).

Using multivariate regression and partial least squares analysis, we assessed whether or not overall body shape was significantly associated with the trophic characters. However, it is well known that shared evolutionary history can generate spurious correlations between character sets, because closely related taxa are typically more similar to one another than would otherwise be expected (Felsenstein, 1985; Harvey & Pagel, 1991). Therefore, it must be determined to what degree the observed association between body shape and trophic morphology can be explained simply by shared evolutionary history (i.e. phylogeny). If the association between body shape and trophic morphology disappears when phylogeny is taken into account, it can be concluded that shared evolutionary history was the most probable cause of the observed correlation. If, on the other hand, the association exists even after the phylogenetic relationships are taken into account, then an evolutionary explanation other than phylogeny (e.g. selection, convergence, etc.) can be postulated to explain the observed pattern of character association.

We performed a phylogenetic generalized least squares (PGLS) analysis (Martins & Hansen, 1997) to determine whether the relationship between body shape and trophic morphology existed after phylogeny was taken into account. PGLS is a phylogenetic regression method (Grafen, 1989), in which the covariance among specimens as a result of phylogeny is expressed in the regression error term, and is thus accounted for during the analysis (see Martins & Hansen, 1997). The most commonly used comparative method; Felsenstein's (1985) independent contrasts, yields identical statistical results to PGLS, and is thus a special case of PGLS (Garland & Ives, 2000; F. J. Rohlf, pers. comm.). PGLS is a more general technique however, in that it extends easily to multivariate data, and can be used unambiguously when polytomies are found in the phylogeny (F. J. Rohlf, pers. comm.). We used the strict consensus tree shown in Fig. 1 (see also Rüber *et al*., 1999) to represent the phylogenetic relationships among populations, and treated specimens within each population as a polytomy. PGLS analysis was performed in NTSYS-pc (Rohlf, 2000).

## Results

### Body shape variation among populations

CVA revealed significant differences among the 17 populations in overall body shape (Wilks' $\Lambda = 0.0081$, $P << 0.0001$). Forty-three of the 136 multiple comparisons among populations were also significant, although small sample sizes prohibited several statistical comparisons. Figure 3 illustrates the separation among the 17 groups as found from the CVA. The first CV axis separates the populations having the three different tooth types, and generally describes differences between deep bodied fishes with a deep and short skull and a ventrally orientated mouth and more fusiform fishes with a more elongated and pointed head. To characterize the differences in body shape between populations having different tooth types, we generated thin-plate spline deformations of a representative specimen from four different lineages (Fig. 4). The results indicated that populations with an *Eretmodus*-like tooth shape are deep bodied, with a ventrally orientated mouth. Groups with *Spathodus*-like teeth show a deepening of the head relative to the more posterior body and a more horizontally orientated snout. Finally, fishes with *Tanganicodus*–like teeth are more fusiform with a shallowing of the head relative to the more posterior body, a deep caudal peduncle, and an elongated head with a long pointed snout.

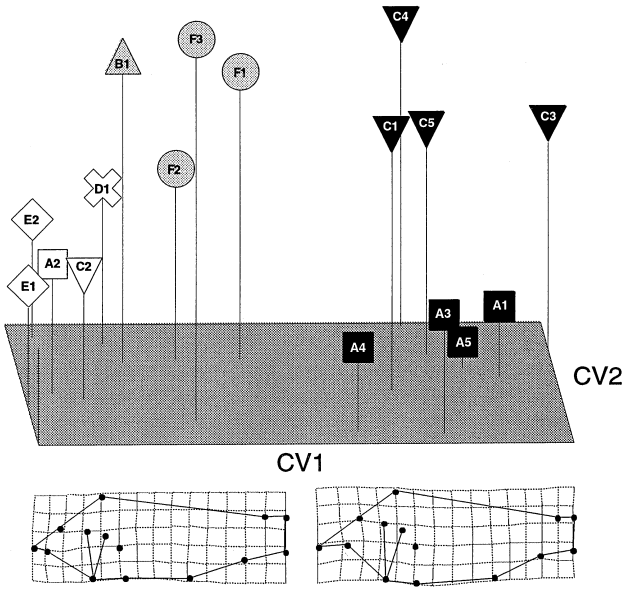



**Fig. 3** (a) CV ordination of group means for 17 populations of eretmodine cichlids, with deformation grids along the first CV axis. The first three axes explain 65% of the total variation. The six phylogenetic lineages (A–F) are indicated by different symbols and the 17 distinct phylogenetic clades are labelled according to Table 1 (black = *Eretmodus*-, grey = *Spathodus*-, and white = *Tanganicodus*-like dentition).

### Relationship between body shape and trophic morphology

Using multivariate regression we found a significant relationship between body shape and trophic morphology (Wilks' $\Lambda = 0.118$, $P << 0.0001$). Similarly, we found a significant positive relationship between trophic characters and body shape with partial least squares analysis ($r = 0.72$; $P = 0.001$). The relationship between body shape and trophic morphology is seen in Fig. 5, where body shape is represented as deformation grids along the first body shape axis. Negative deviations along this axis corresponded to specimens with a *Tanganicodus*-like tooth shape and the positive deviation to specimens with an *Eretmodus*-like tooth shape (see Fig. 4). Based on these linear combinations, we can describe the relationship between trophic characters and body shape as follows: specimens with low tooth counts and a small gape- and interorbital width have relatively elongated heads and a forward directed snout, whereas specimens with high tooth counts and a large gape- and interorbital width have deep heads and a ventrally directed snout. These findings are consistent with direct comparisons of tooth counts, where specimens with *Tanganicodus*-like tooth shape had the lowest number of teeth, and those with an *Eretmodus*-like tooth shapes had the highest number of teeth ($F = 171.2$; $P << 0.0001$). Specimens with a *Spathodus*-like tooth shape have an intermediate tooth number between the specimens characterized by an *Eretmodus*-like and a *Tanganicodus*-like tooth shape.

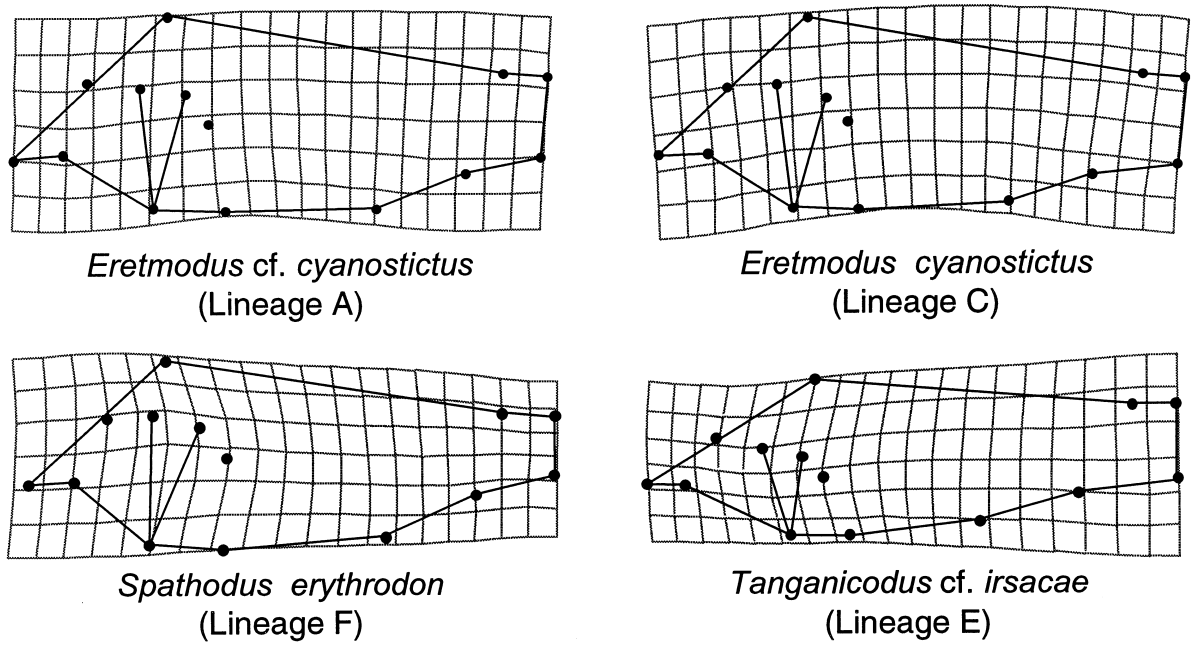



**Fig. 4** Thin-plate spline representations of group means from four representative populations emphasizing shape differences between populations having different tooth types.

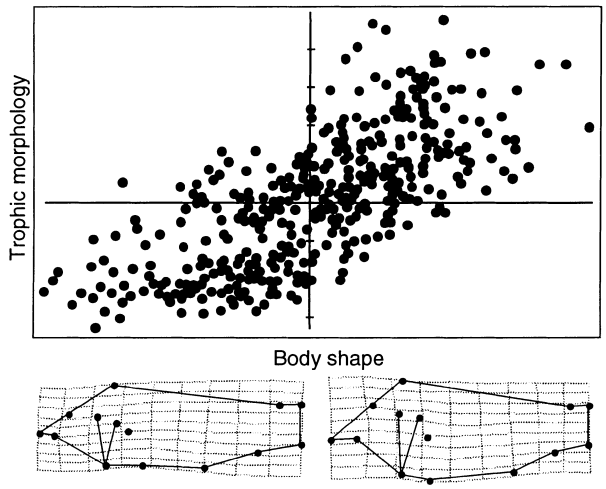



**Fig. 5** Representation of the relationship between body shape and trophic morphology as found through a partial least squares analysis performed using all individuals. Body shapes at the positive and negative extremes of the distribution are represented as deformation grids.

When the phylogenetic relationships among specimens were taken into consideration using PGLS, there was a significant association between overall body shape and trophic morphology (Wilks' $\Lambda = 0.368$, $P << 0.0001$). Thus, although shared evolutionary history may account for some of the covariance in body shape and trophic morphology, there is still a significant association between these two character sets in spite of phylogeny. Therefore, some evolutionary mechanism other than phylogeny is necessary to explain the observed relationship between body shape and trophic morphology.

## Discussion

### Covariation of body shape and trophic morphology

In this study, we examined variation in body shape and trophic morphology in several genetic lineages of eretmodine cichlids from Lake Tanganyika. Using CVA, we found significant differences in body shape among populations (Fig. 3), and the resulting ordination plot revealed that populations with different tooth types were well separated, particularly along the first CV axis. Specimens with an *Eretmodus*-like dentition were at the positive extreme of this axis and those with a *Tanganicodus*-like dentition at the negative extreme (fishes with a *Spathodus*-like tooth shape were intermediate). Further, specimens with an *Eretmodus*-like tooth shape from the genetically distinct A and C lineages were also well separated in the CV plot, corroborating results from other studies that found differences in dentition (Huysseune *et al.*, 1999) and feeding behaviour (Yamaoka, pers. comm.). We conclude that significant body shape variation exists in eretmodine cichlids, and that such variation seems to follow differences in oral tooth shape.

In addition to body shape, we quantified four trophic characters, and using multivariate regression and partial least squares analyses, we found that variation in trophic characters was significantly associated with variation in body shape. Specimens with low tooth counts and a small gape- and interorbital width had relatively elongated heads and a forward directed snout, while specimens with high tooth counts and a large gape- and interorbital width had deep heads and a ventrally directed snout. These results identify a significant body shape – trophic morphology relationship, which implies that characterization of eretmodine cichlids on the basis of body shape (Figs 3 & 4) also differentiates them for their suite of trophic characters (Fig. 5). Although this body shape – trophic character relationship is quite strong, what is not known is the potential cause of this association.

One obvious candidate that must be investigated is the influence of shared evolutionary history (phylogeny) on this body shape – trophic character association. We performed a PGLS analysis to account for covariation because of the phylogenetic relationships of the taxa. We found that the significant association of body shape and the trophic characters was still present even after the removal of phylogenetic signal from the data set. Therefore, some evolutionary mechanism other than phylogeny is required to explain the covariation between body shape and trophic characters in eretmodine cichlids.

### Evolutionary causes of morphological change

The results presented here reveal that variation in eretmodine cichlid body shape corresponds more closely to trophic morphology than to the phylogenetic relationships revealed by mtDNA sequences. Thus, there appears to be conflicting patterns of phenetic similarity and phylogenetic relatedness in this cichlid tribe. Two possible evolutionary scenarios could explain this. The first is that particular body shapes, and suites of trophic characters, have multiple independent origins, and that convergent evolution and parallelism of both character sets are prevalent in this group. The alternative explanation is that the phylogenetic relationships proposed by the mtDNA sequences do not represent the true branching pattern among taxa, because of molecular introgression and population hybridization. Although we cannot completely rule out this second possibility, we find it to be quite improbable.

For introgression to explain the observed morphological pattern, many independent introgression events would be required. For instance, lineages A2 and C2 each have *Tanganicodus* dentition and body shapes, but are found within genetic lineages characterized by *Eretmodus* dentition and body shape (A and C lineages, respectively). Because they are geographically close to

their sister clades, introgression is a possibility, but *two* independent introgression events would be required: one each for A2 and C2. There are other instances in the phylogeny however, where introgression is much less possible. For example, *Spathodus* and *Tanganicodus* are resolved in genetically clear distinct lineages (e.g. B and F; D and E, respectively). Because these populations do not have overlapping distributions, the opportunity for hybridization is nonexistent, and thus the possibility that introgression could occur and explain each of these instances is remote. Therefore, we feel that introgression is not a probable explanation of the observed pattern, and turn to some other evolutionary explanation.

Given that introgression is an improbable scenario, how can we explain the apparent convergent evolution of body shape and trophic morphology? We hypothesize that selection pressures imposed by similar ecological habitats has driven morphological evolution and trophic specialization multiple times, in independent lineages, in this group. Although this scenario requires a tight link between ecological specialization and habitat use, there is much support for this in eretmodine cichlids. Previous field studies have shown that *E.* cf. *cyanostictus* is specialized to feed on filamentous algae by scraping (Yamaoka *et al.*, 1986; Sturmbauer *et al.*, 1992; but see Liem, 1979). In contrast, *T. irsacae* with its acute dental arcade is an invertebrate picker (Yamaoka *et al.*, 1986). The diet of *S. erythrodon* is intermediate and contains algae but also a high proportion of ostracods, copepods, and insect larvae (H. H. Büscher, pers. comm.).

The dentitional differences found by Yamaoka *et al.* (1986) and Huysseune *et al.* (1999), and our analysis on body shape variation among eretmodine cichlids, allow us to draw some tentative conclusions about the functional correlates of these characters in terms of their feeding ecology. The arrangement of tooth groups, the large number of oral teeth and gape width as well as the stout body shape characteristic of *Eretmodus* (Fig. 4) may be indicators of scraping abilities: more teeth and a broad jaw as found in *Eretmodus* imply an increase in scraping surface. The shape of the oral jaw teeth on the other hand may be important in prey grasping, broad equally sized uniscupid teeth with a flattened crown as seen in *Eretmodus* being more useful for scraping filamentous algae. On the other extreme of the ecomorphological axis, less densely spaced pointed uniscupid teeth as seen in *Tanganicodus* may be more useful for the capture of mobile prey by picking. Invertebrate picking in *Tanganicodus* may be further fascilitated by the small interorbital width increasing the ability to visually select food items and the fusiform body shape allowing faster manoeuvre.

A striking feature of the distribution of eretmodine cichlids is the occurrence of sympatric species pairs along most of the coastline that differ in tooth shape. However, in different parts of the lake, the members of these species pairs belong to different genetic lineages (e.g. *Eretmodus* lineage A sympatric with *Tanganicodus* lineage E, *Eretmodus* lineage C sympatric with *Spathodus* lineage F; Fig. 1, Table 1; Rüber *et al.*, 1999). The highly significant relationship between tooth shape and body shape suggests parallel evolution of not only dental morphology, but also of body shape among genetically diverged lineages. The replicated evolution of morphologically divergent species pairs points to the presence of well defined trophic niches that have facilitated ecological segregation, and to the adaptive value of the observed morphological associations. It is probable that such covariation is produced by similar selective pressures on body shape and feeding morphology, rather than by developmental constraints, enabling the multiple independent invasions of the same adaptive zone.

Trophic resource partitioning and microhabitat segregation among sympatric eretmodine taxa has been indicated (Hori *et al.*, 1983; Hori, 1987); but further ecological data are required to better understand the morphological divergence of these cichlids. Trophic segregation may be an important factor promoting divergence within and between populations (Schluter & McPhail, 1993; Robinson & Wilson, 1994; Schluter, 1996). Therefore, the adaptation to different trophic niches through the modification of trophic morphology, body shape, and feeding behaviour as found in the Eretmodini may account for the formation and maintenance of the high degree of diversity found in lacustrine cichlid communities (Galis & Metz, 1998; Bouton *et al.*, 1999; Dieckmann & Doebeli, 1999). Our results seem to indicate that this ecological specialization and morphological divergence can occur rapidly, and independently of phylogeny even within a single cichlid tribe endemic to a single lake.

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