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Evolution

Replicated evolution of trophic specializations in an endemic cichlid fish lineage from Lake Tanganyika

(Eretmodini/phylogeny/adaptive radiation)

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ABSTRACT **The current phylogenetic hypothesis for the endemic Lake Tanganyika cichlid fishes of the tribe Eretmodini is based solely on morphology and suggests that more complex trophic morphologies derived only once from a less specialized ancestral condition. A molecular phylogeny of eretmodine cichlids based on partial mitochondrial DNA cytochrome *b* and control-region sequences was used to reconstruct the evolutionary sequence of trophic adaptations and to test alternative models of morphological divergence. The six mitochondrial lineages found disagree with the current taxonomy and the morphology-based phylogeny. Mitochondrial lineages with similar trophic morphologies are not grouped monophyletically but are typically more closely related to lineages with different trophic phenotypes currently assigned to other genera. Our results indicate multiple independent origins of similar trophic specializations in these cichlids. A pattern of repeated divergent morphological evolution becomes apparent when the phylogeography of the mitochondrial haplotypes is analyzed in the context of the geological and paleoclimatological history of Lake Tanganyika. In more than one instance within Lake Tanganyika, similar morphological divergence of dentitional traits occurred in sympatric species pairs. Possibly, resource-based divergent selective regimes led to resource partitioning and brought about similar trophic morphologies independently and repeatedly.**

Phylogenetic information about species that form adaptive radiations will increase knowledge about the patterns and processes that drive morphological diversification and speciation. The reconstruction of morphological diversification based on a molecular phylogeny may offer new insights into the causes of phenotypic differentiation and speciation and the role of determinism and internal constraints in the evolution of adaptive radiations (1–6). The endemic cichlid species flocks of the East African Great Lakes—Victoria, Malawi, and Tanganyika—provide outstanding examples for adaptive radiations and rapid speciation resulting in unparalleled species diversities of hundreds of endemic species in each of these three lakes (1, 7). Lake Tanganyika is the longest (650 km long), deepest (about 1.4 km deep), and oldest [9–12 million years (8)] and houses the genetically most diverse flock of cichlids (reviewed in ref. 1).

Cichlids of the tribe Eretmodini (9) are endemic to Lake Tanganyika. They encompass a high degree of diversity in oral tooth shapes and might therefore serve as a model system to investigate morphological differentiation among closely related species. This tribe comprises four nominal species currently assigned to three genera: *Eretmodus cyanostictus*, *Spathodus erythrodon*, *Spathodus marlieri*, and *Tanganicodus irsacae*. The shape of the oral jaw teeth is the main taxonomic character defining these species. The teeth of *Eretmodus* are spatula-shaped with a slender neck region, those of *Spathodus* are cylindrical with a flattened and truncated crown, and those of *Tanganicodus* are slender and pointed (9). These differences in dental morphology are correlated with dietary and behavioral differences ranging from invertebrate-picking in *T. irsacae* to algae-scraping in *E. cyanostictus* and *S. marlieri* and an intermediate diet in *S. erythrodon* (10, 11).

A morphology-based phylogeny derived from osteological features of the skull placed *Spathodus* and *Tanganicodus* as a derived sister group to *Eretmodus*, which shares features of the jaw apparatus with more generalized cichlids (12). However, a recent phylogenetic study of the tribe Eretmodini using partial mtDNA control region sequences indicated that mtDNA lineages within the Eretmodini do not agree with the current taxonomy (13, 14) and that the generic classification based mainly on dentition (the number and position of teeth) and tooth shape has to be reconsidered. This is in agreement with the observation that a single tooth-replacement pattern is responsible for the diversity in dention among eretmodine cichlids (15).

In this study, we reconstruct the evolution of trophic characters in eretmodine cichlids to shed light on morphological divergence within a phylogeographic and historic context. Given the high degree of intralacustrine endemism found in the identified eretmodine lineages, we considered it likely that the study of populations from parts of the lake that were previously not included would result in the discovery of new mtDNA lineages. We therefore sampled individuals from the entire Lake Tanganyika shoreline (Fig. 1*a*). We then tested whether certain trophic traits, such as tooth shape, evolved once or multiple times during the adaptive radiation of eretmodine cichlids.

MATERIALS AND METHODS

Species and DNA Methods. We used a total of 90 specimens, comprising all four currently recognized Eretmodini species, collected from 62 localities distributed along the entire Lake Tanganyika shoreline (Fig. 1*a*). Voucher specimens have been deposited in the Africa Museum in Tervuren, Belgium. DNA was extracted from muscle tissue by using standard proteinase K digestion and phenol/chloroform extraction (16) followed by

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Abbreviations: cyt *b*, cytochrome *b*; NJ, neighbor joining; MP, maximum parsimony.

Data deposition: The sequences reported in this paper have been deposited in the GenBank database. For accession numbers, see *Appendix*.

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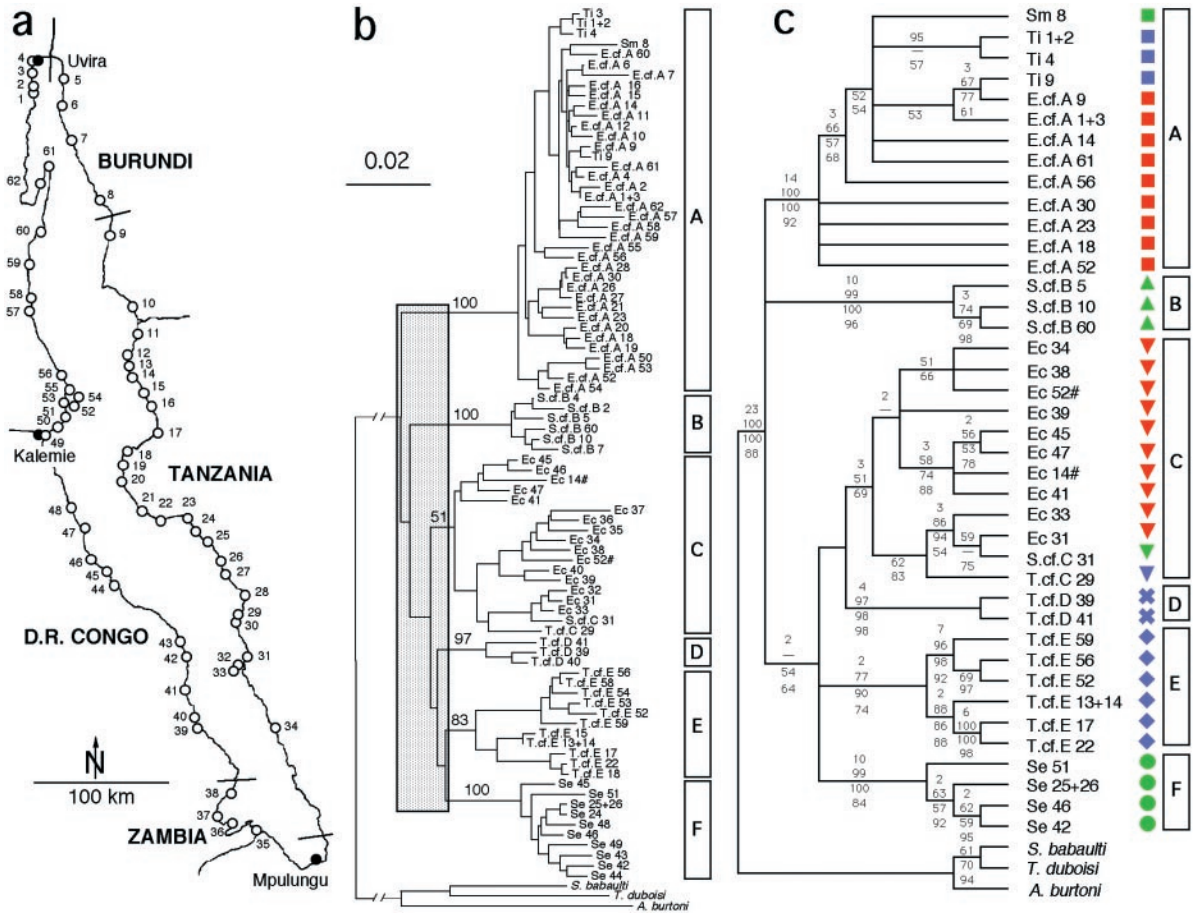

FIG. 1. (*a*) Map of Lake Tanganyika showing the localities studied. Circles in bold indicate type localities: Uvira, *T. irsacae* and *S. marlieri*; Mpulungu, *E. cyanostictus*; Kalemie, *S. erythrodon.* Fishes from lineages where the distribution does not include the type locality are referred to as: *genus name* cf. *species name.* (*b* and *c*) Phylogenetic analyses using a combined data set of partial cyt *b* and control region sequences. Locality numbers are given behind species names that are based on the current taxonomy (9). Ec, *E. cyanostictus*; E.cf.A., *E.* cf. *cyanostictus* (lineage A); Se, *S. erythrodon*, S.cf.B or C, *S.* cf. *erythrodon* (lineages B and C respectively); Sm, *S. marlieri*; Ti, *T. irsacae*; T.cf.C, D, or E, *T.*cf. *irsacae* (lineages C, D, or E, respectively). Ec (14)# and Ec (52)# indicate distinct taxa with an *Eretmodus*-like dentition than E.cf.A (14) and E.cf.A (52). They differ in coloration (33) and in the number of tooth groups and teeth per group (15). Published sequences (cyt *b*/control region) from *Tropheus duboisi* (Z12039/Z12080), *Simochromis babaulti* (Z12045/U40529), and *Astatotilapia burtoni* (Z21773/Z21751) were used as outgroups (34–36). The assignments to the six major lineages (A–F) are given in boxes. (*b*) NJ phylogram of the 90-taxa data set. Bootstrap values are shown only for the six major lineages (A–F). Shaded box highlights the time window in which the six eretmodine lineages originated. Bar scale indicates the inferred number of nucleotide substitutions. (*c*) Strict consensus tree of the MP and the NJ analyses using the 44-taxa data set. Bootstrap values ≥50% for the MP analysis and decay indices >1 are shown above branches. Bootstrap values ≥50% for the NJ analysis and quartet-puzzling support values are shown below branches. Different symbols follow the assignments to lineages A–F (red, *Eretmodus*-; green, *Spathodus*-; and blue, *Tanganicodus*-like dentition type).

PCR and direct sequencing of two mtDNA gene fragments by using standard methods (13). The two primer pairs used to amplify a portion of the cytochrome *b* (cyt *b*) gene and of the proline tRNA with a segment of the control region are given in refs. 17 and 18.

Phylogenetic Reconstruction and Hypotheses Testing. A total of 338 bp of the control region and 363 bp of the cyt *b* were aligned and combined for all further analyses. Gaps in the control region were treated as missing data. We conducted the analyses in two steps. First, we constructed a neighbor-joining (NJ; ref. 19) tree with all 90 specimens by using TREECON Version 1.3b (20). Second, we used a smaller data set with a representative subset of 44 specimens from 34 localities. This data set was analyzed with the maximum parsimony (MP; ref. 21) and NJ methods by using PAUP* Version 4.0d64 (21). Heuristic searches (TBR branch swapping, MULPARS option effective, and random stepwise addition of taxa with 10 replications) were used to find the most parsimonious trees. NJ was performed based on Kimura two-parameter corrected distances (22) as in the first step of the analysis. In addition, a heuristic maximum likelihood (23) tree search procedure was performed by using the quartet-puzzling algorithm in PUZZLE Version 3.1 (24) by using the default options with 1,000 puzzling steps.

Phylogenetic relationships were also examined by introducing different character-state weighting schemes for transitions and transversions in the MP analyses as well as by successive character reweighting based on the rescaled consistency index (25) by using the unweighted MP consensus tree as the starting tree. Robustness of the inferred MP and NJ trees was tested by using the bootstrap method (26) with 500 resamplings for the MP analysis and 500 and 1,000 resamplings for the NJ analyses of the 90 taxa and the 44 taxa data set, respectively. Decay indices (27) were calculated for the MP trees as an index of support (28) by using AUTODECAY Version 3.0.3 (29). Competing phylogenetic hypotheses were compared by using the Templeton (30) and Kishino-Hasegawa (31) tests as implemented in PAUP*. To examine the evolution of trophic specialization in eretmodine cichlids, we mapped tooth shapes (treated as unordered characters with three states) onto phylogenetic hypotheses by using MACCLADE Version 3.06 (32).

RESULTS

Sequence Variation. Of 158 variable sites (63 and 95 for the cyt *b* and the control region, respectively) identified among the 40 different haplotypes from the combined cyt *b* and control region data set (44 taxa), 119 (54 and 65) were informative under parsimony.

Phylogenetic Reconstruction. We identified six distinct mitochondrial lineages within the Eretmodini (labeled A–F); lineages A, B, and D–F were supported by bootstrap values >70% in the MP, NJ, and maximum likelihood analyses and lineage C by bootstrap values <70% in the MP and NJ analyses and <50% in the maximum-likelihood analysis (Fig. 1 *b* and *c*). The designation of the different lineages is based on the NJ and MP analyses (Fig. 1). Fig. 1*b* shows the NJ tree of the 90-taxa data set, and Fig. 1*c* shows the strict consensus tree of the NJ and MP analysis of the 44-taxa data set. In the NJ trees, lineage A represents the sister group to the remaining eretmodines. In the NJ tree of the 90-taxa data set, lineage C was placed as sister group to D, E, and F, whereas lineages C and D were placed as a sister group of E and F in the NJ tree of the 44 taxa data set. The MP analysis of the unweighted data set resulted in 12 most parsimonious trees (tree length = 464 steps; consistency index = 0.47; consistency index excluding uninformative characters = 0.39). In this analysis, lineage B was resolved as the sister group of the remaining eretmodines, and lineage F was resolved as sister group to C, D, and E. Various weighting schemes in the MP analysis for transitions and transversions in different gene segments only showed differences in basal relationships among lineages but did not result in topologies different from the strict consensus of the NJ and the unweighted MP analyses as shown in Fig. 1*c*. Successive character reweighting resulted in an increase in the number of most parsimonious trees, an uncommon outcome in phylogenetic reconstruction (37).

Evolution of Tooth Shape. Four (B, D–F) of the six mtDNA lineages include only specimens with one particular tooth morphology. Lineages A and C include cichlids of more than one trophic type. Specimens with an *Eretmodus*-like dentition are found in both lineages A and C. Individuals with a *Spathodus*-like dentition are assigned to mtDNA lineages A–C and F, and those with a *Tanganicodus*-like dentition are found in lineages A and C–E.

Individuals with similar tooth shape and hence identical taxonomic designations were not resolved monophyletically (Figs. 1 and 2). The hypothesis that all individuals with the same tooth shape belong to one mtDNA lineage was tested statistically (30, 31). MP analyses were used to search for the shortest trees under the constraint that a particular tooth shape is monophyletic, but these hypotheses were rejected (Table 1), indicating that species with the same tooth morphology do not form a monophyletic group and that at least one, perhaps all three, tooth-shape classes evolved more than once. Tracing the three different tooth shapes on all MP trees requires eight steps (Fig. 2). Alternative reconstructions exist because the topology of the NJ tree is not significantly different from the MP trees by using the Templeton (Wilcoxon's Ts = 108, n = 24, $P > 0.05$) and Kishino-Hasegawa (dt = 7, SD = 5.19, t = 1.347, $P > 0.05$) tests. However, in none of the alternative topologies did any of the tooth shapes evolves only once. Tracing tooth shape on the NJ tree requires one additional step.

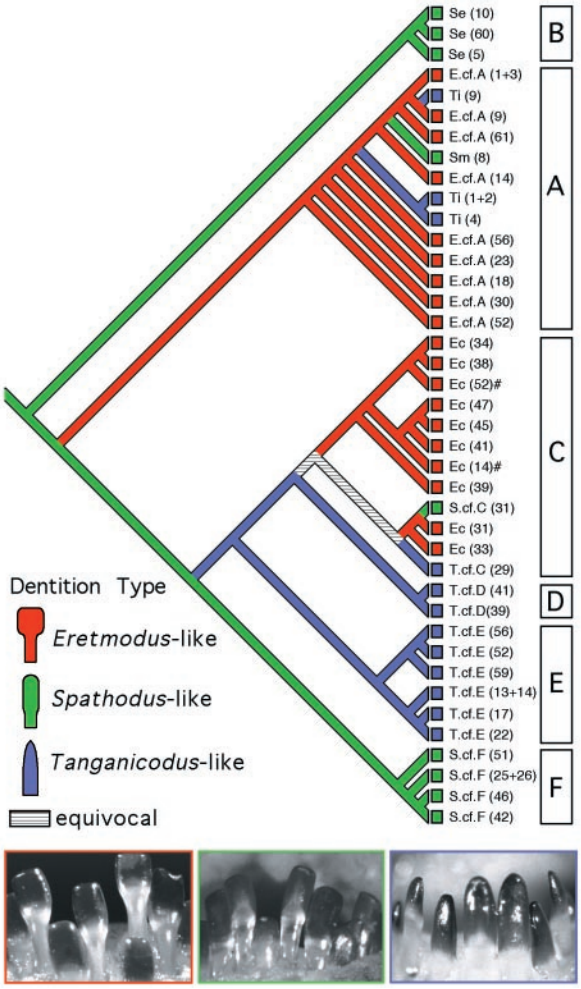

FIG. 2. Reconstruction of the evolution of tooth shape within the Eretmodini based on one of the 12 most parsimonious trees by using the combined mtDNA data set and no weight. Tracing tooth shape on different MP trees does not alter the reconstruction shown here because the 12 most parsimonious trees only differ in the relative position of the four basal taxa from lineage A [Ec.cf.A (18, 23, 30, and 52)] and in the relative position of Ec (34, 38, and 52#) from lineage C. Tooth shape was treated as an unordered character with three character states. The character reconstruction shown is just one possible reconstruction, because the ancestral state of tooth shape in eretmodine cichlids is tentative. However, alternative reconstructions also yield multiple instances of parallel evolution.

DISCUSSION

Molecular Phylogeny of Eretmodine Cichlids Indicates Parallel Evolution of Trophic Adaptations and Suggests the Recognition of Several New Species. mtDNA data of this and some previous studies show that the taxonomic diversity of cichlids from Lake Tanganyika is likely to be greater than currently appreciated (38). The molecular phylogenetic analysis of new populations from the Congo shores discovered an additional mtDNA lineage (lineage D) that was not seen in previous analyses (refs. 13 and 14; Fig. 1). The recognition of six genetically distinct lineages (Fig. 1*b*) indicates that specimens with identical tooth shapes from different lineages may constitute distinct species. Until this idea is tested, we prefer to use a terminology for eretmodine cichlids that provides information on phenotype as well as mtDNA type: *Eretmodus*-, *Spathodus*-, and *Tanganicodus*-like give reference to the currently used generic classification of eretmodine cichlids based on dentitional differences complemented with the name of the lineage (A–F) that connotes their phylogeographic assignment (Figs. 1 and 3).

We confirmed that morphologically similar individuals from a given locality belong to the same lineage by sequencing additional specimens not included in this analysis. For example, from locality 39 (Fig. 1*a*), 30 *E. cyanostictus* specimens showed lineage C haplotypes, whereas 25 *T.* cf. *irsacae* specimens from the same locality showed lineage D haplotypes.

Table 1. Hypotheses tested with the combined cyt *b* and control region DNA sequence data

			Templeton test			Kishino-Hasegawa test			
Hypothesis	NT	TL	T_S	*n*	*P* value	ΔTL	SE	*t*	*P* value
MP unconstraint	12	464							
MP constraint									
Eretmodus-like	210	507	68–178	41–50	<0.0001	43	8.5–9.4	4.5–5.0	<0.0001
Spathodus-like	288	504	40–159	41–51	<0.0001	40	6.6–8.2	4.7–6.1	<0.0001
Tanganicodus-like	1,440	502	157–367	48–59	<0.0004	38	7.6–9.2	4.0–4.9	≤0.0001

The number of trees (NT) and tree length (TL) for the unconstraint and the constraint hypothesis is given. T_S is the test statistic for the Wilcoxon signed-rank test. *n* is the number of characters that differed in the number of changes on the two trees compared. Difference in number of steps (ΔTL) ± SE is between the MP tree and the tree constraint to conform to the stated hypothesis. *t* is the Student's *t* test statistic. Because there were multiple most-conservative comparisons between the unconstrained and the constrained trees, the range of all pairwise comparisons is given. Significant results denote the rejection of the hypothesis that a particular tooth-shape class is monophyletic.

Lineages A and C are the only two lineages that contain individuals with different trophic morphologies. In lineage C, which is dominated by cichlids with an *Eretmodus*-like dentition, we found a *Tanganicodus*-like dentition at locality 29 (Fig. 1*a*) as well as a few kilometers north of that location (13, 14) and a *Spathodus*-like dentition at locality 31 (Fig. 1*a*). The *Eretmodus*-like-dominated lineage A contains the scarce species *S. marlieri*, which occurs in different, intermediate sand rock habitats and at greater depth than other eretmodine species (38), and *T. irsacae*, both of which show an aberrant tooth morphology for lineage A and are found only in the northernmost part of the lake (Fig. 3). From these specimens, new tissue samples were taken and resequenced to confirm their haplotypes.

The presence of multiple oral tooth shapes within a single mtDNA lineage as found in lineage A and C is not likely to result from phenotypic plasticity as a response to different habitat use. Although phenotypic plasticity in the lower pharyngeal jaws has been documented in cichlids (39–41), we are not aware of reported cases that involve the shape of oral jaw teeth. Moreover, fishes with different tooth shapes also differ concomitantly in body shape (L.R. and D. C. Adams, unpublished data), and tank-bred individuals kept on an identical diet retain their oral tooth shapes (L.R., unpublished data), indicating that oral tooth shape in eretmodine cichlids has a strong genetic component.

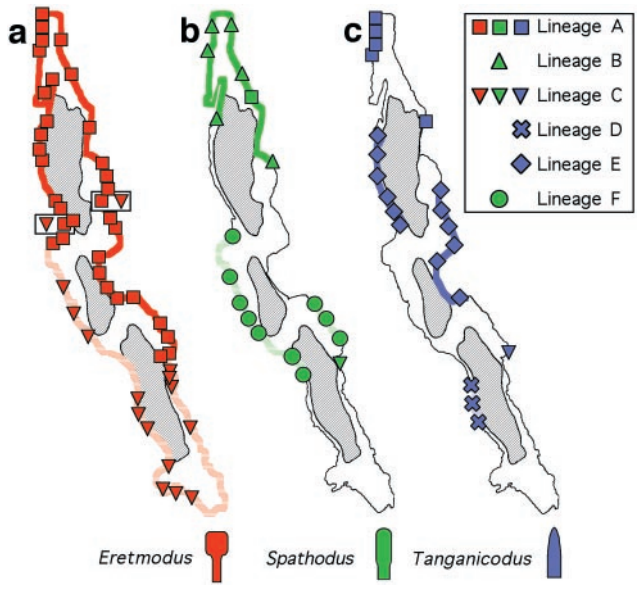

FIG. 3. Maps of Lake Tanganyika showing the haplotype distribution of the Eretmodini studied according to their tooth shape (3a, *Eretmodus*-; 3b, *Spathodus*-; and 3c, *Tanganicodus*-like). Different shadings distinguish the distribution of different mtDNA lineages with the same tooth shape (not shown for *T. irsacae*). The distribution ranges were inferred from field observations, specimen collections, and haplotypes. The symbols follow the assignments to lineages A–F as in Fig. 1 and are summarized in the box. The two localities where *E. cyanostictus* (lineage C) and *E.* cf. *cyanostictus* (lineage A) are found sympatric are indicated by a small box in *a*. The three isolated Pleistocene sub-basins are indicated in gray.

A second hypothesis to explain the occurrence of multiple oral tooth shapes within a single mtDNA lineage is hybridization. Experimentally produced hybrids between two Lake Malawi haplochromines that differ in trophic morphology showed a mosaic of parental, intermediate, and unique patterns of morphological expressions (42). All specimens from lineage A and C with either a *Spathodus*- or *Tanganicodus*-like tooth shape (Fig. 2) showed no morphological features of either a lineage A or C *Eretmodus*-like specimen. Therefore, it seems unlikely that recent hybridization or past introgression of mtDNA haplotypes into a clade with a different tooth morphology can explain these results. Although unlikely, this possibility needs to be addressed in future studies in which the morphology of hybrids is compared with that of parental species and nuclear markers are used to evaluate whether hybridization has had an impact on the observed pattern.

Our results allow us to statistically reject the traditional hypothesis (12) that specimens with identical trophic specializations, such as the shape of their oral jaw teeth, are derived from a single immediate common ancestor. None of the three tooth-shape types (*Eretmodus*-, *Spathodus*-, and *Tanganicodus*-like) was resolved monophyletically (Table 1), and at least eight evolutionary transitions between tooth shape types occurred (Fig. 2).

Phylogeographic Patterns, the Geological History of Lake Tanganyika, and Morphological Differentiation. Eretmodine cichlids are restricted along shallow rocky and pebble shores and are unable to disperse across open water. Each of the six eretmodine lineages shows a limited distribution within the lake (Figs. 1 and 3). The high degree of intralacustrine endemism and the pronounced phylogeographic structuring of eretmodines can be partly explained by the influence of major lake level fluctuations in the Pleistocene that are generally assumed to have had a strong influence on phylogeographic patterns and speciation of rock-dwelling cichlids (34, 43). During this time, the single lake basin of Lake Tanganyika split up into three isolated sub-basins (shown in gray in Fig. 3; refs. 44 and 45); this event is still reflected in the distribution of mtDNA lineages.

The northern and southern shorelines of each of these sub-lakes might have permitted dispersal and gene flow between cichlid populations from western to eastern coast lines or *vice versa.* The occurrence of some lineages on both opposite shores of the lake (e.g., lineage E and F; Fig. 3) can best be explained by this route of gene flow (43). The formation of the six distinct eretmodine lineages appears to have occurred within a brief period of time (Fig. 1*b*), probably before the onset of the lake level fluctuations in the Pleistocene.

In addition to the influence of lake level fluctuations on the geographic distribution of eretmodine mtDNA lineages, sev-

eral interesting patterns emerge when distributions are viewed in conjunction with the phenotypes that characterize certain lineages (Fig. 3). Eretmodine cichlids with identical trophic morphologies from different mtDNA lineages in general reveal a nonoverlapping distribution. Those with *Eretmodus*-like dentition (shown in red) from lineages A and C have a complementary lake-wide distribution (Fig. 3*a*). We found only two localities where these morphologically and genetically distinct *Eretmodus*-like specimens occur sympatrically (Fig. 1). Specimens with a *Spathodus*-like dentition (green) from lineages B and F show a strict complementary distribution. Only *S. marlieri* from lineage A is found within the distribution range of *S*. cf. *erythrodon* from lineage B (Fig. 3*b*). Specimens with a *Tanganicodus*-like dentition (blue) from lineages A and C–E also show complementary distributions (Fig. 3*c*).

In most parts of the lake, fish with two distinct tooth types from two different mtDNA lineages can be found sympatrically (Fig. 3). This is the case for the range covered by lineages D–F. Not considering the *Spathodus*- and *Tanganicodus*-like fishes from lineage A, this pattern would extend and include the distribution of lineage B. The allopatric distributions of *S.* cf. *erythrodon* (lineage B), *T.* cf. *irsacae* (lineage E), *S. erythrodon* (lineage F), and *T*. cf. *irsacae* (lineage D) are shown in Fig. 3 *b* and *c*. These lineages are found sympatrically with either *E.* cf. *cyanostictus* from lineage A or *E. cyanostictus* from lineage C. In the southernmost part of the lake (locality 33–39, Fig. 1*a*) *E. cyanostictus* is the only eretmodine found (33).

Ecological Causes of Recurrent Parallel Evolution and Adaptive Radiations. The phylogenetic analysis and the phylogeographic distribution of mtDNA lineages refutes the assumption that the presence of similar pairs of trophic specialists (*Eretmodus*-like with either *Spathodus*- or *Tanganicodus*-like dentition type) evolved only once and that subsequently they colonized other coastlines. The data support the hypothesis that lineages with identical trophic morphology evolved independently and concurrently in different parts of Lake Tanganyika. The multiple independent evolution of identical tooth shapes, as indicated in Fig. 2, suggests recurrent parallel evolution of ecologically important morphological traits between closely related species within the same lake basin and challenges the current approach of cichlid taxonomy, because it often relies, sometimes exclusively, on characters related to feeding, such as dentition and tooth morphology.

The phylogeographic distributions of the six mtDNA lineages and the phylogenetic mapping of the morphological traits reveal patterns that suggest that not just vicariance events, such as major lake-level fluctuations, have been responsible in shaping the intralacustrine distribution of eretmodine cichlids. Our data show a consistent pattern in morphological divergence in dentition of sympatric species pairs. The allopatric distribution of genetically distinct lineages that are characterized by similar trophic morphology strongly suggests that ecological processes, such as competitive exclusion, that can play a central role in structuring communities (46) between two species (different mtDNA lineages) with the same tooth morphology might be responsible for this pattern of species distributions. Moreover, over a wide range of the lake's shores, sympatrically occurring eretmodine species pairs are found. In general, a species pair contains members of two distinct mtDNA lineages, and in addition, the species of such a pair show consistent differences in oral tooth shape, with one species having an *Eretmodus*-like dentition and the other either a *Spathodus*- or *Tanganicodus*-like dentition. In different areas of the lake, however, these morphological species pairs belong to different mtDNA lineages (Fig. 3).

Differences in trophic morphology, such as tooth shape, in closely related fishes or ecomorphs of the same species are often correlated with tradeoffs for resource use (47, 48). The distinct tooth morphologies found in eretmodine cichlids are correlated with differences in diet (10, 11). The repeated formation of morphologically distinct pairs of species in different parts of Lake Tanganyika suggests that ecological diversification may be a major driving force behind morphological differentiation and evolutionary divergence in these fishes. Similar patterns have been found in postglacial fishes inhabiting lacustrine environments that have led to ecological speciation (2, 6). Further ecological studies might increase our understanding of the adaptive value of oral tooth shape in eretmodine cichlids (by evaluating how species with different tooth shapes differ in habitat use and in efficiencies of trophic resource exploitation) and how differentiation in trophic morphology might have facilitated the coexistence of lineages. These ecological data would also provide information on the possible role of either character displacement as a consequence of resource competition in sympatry, or alternatively, nonresource competition-driven character divergence under allopatric or sympatric conditions as a driving force in the recurrent and independent origin of trophically complementary species pairs.

The observation that extensive parallel evolution in morphological and ecological traits in cichlids can result in remarkably similar phenotypes has been previously reported for distantly related taxa from Lakes Malawi and Tanganyika (17, 49) and on a more restricted geographic scale in the *Pseudotropheus tropheops* species group from Lake Malawi at two localities (50). Our results indicate that parallel evolution can occur within a single lake between closely related species. Thus, it seems that morphological parallelism may be a common phenomenon in adaptive radiations of cichlid fishes and suggests that certain patterns of morphological adaptation and ecological divergence have occurred repeatedly in comparable lacustrine environments. Further ecological and molecular phylogenetic studies as well as comparative developmental work might shed light on the relative importance of ecological mechanisms such as niche partitioning and adaptive divergence on one hand and developmental and genetical constraints on the other in shaping the morphological diversification and speciation in the endemic cichlids of the East African Great Lakes.

Appendix

Accession numbers for sequences reported in this paper (cytochrome *b*/control region):

E.cf.A: 1, Z97471/Z97412; 2, Z97470/Z97413; 3, Z97472/Z97411; 4, Z97469/Z97410; 6, Z97488/X90610; 7, Z97489/X90611; 9, Z97490/X90612; 10, Z97491/X90631; 11, Z97492/X90613; 12, Z97494/X90614; 14, Z97496/X90632; 15, Z97493/X90616; 16, Z97495/X90617; 18, Z97486/X90618; 19, Z97487/X90633; 20, Z97503/X90619; 21, Z97482/X90620; 23, Z97498/X90621; 26, Z97499/X90635; 27, Z97500/X90622; 28, Z97501/X90623; 30, Z97502/X90624; 50, Z97504/Z97424; 52, Z97483/Z97425; 53, Z97485/Z97423; 54, Z97481/Z97422; 55, Z97479/Z97420; 56, Z97480/Z97421; 57, Z97477/Z97418; 58, Z97478/Z97419; 59, Z97476/Z97417; 60, Z97475/Z97416; 61, Z97474/Z97415; 62, Z97473/Z97414.

Ec: 14#, Z97497/X90615; 31, Z97511/X90634; 32, Z97512/X90625; 33, Z97513/Z97433; 34, Z97514/Z97438; 35, Z97516/Z97436; 36, Z97517/Z97434; 37, Z97515/Z97437; 38, Z97518/Z97435; 39, Z97510/Z97432; 40, Z97509/Z97431; 41, Z97508/Z97430; 45, Z97505/Z97428; 46, Z97507/Z97429; 47, Z97506/Z97427; 52#, Z97484/Z97426.

Sm: 8, Z97519/X90593.

S.cf.B: 2, Z97535/Z97446; 4, Z97536/Z97448; 5, Z97532/X90594; 7, Z97534/X90595; 10, Z97533/X90629; 60, Z97537/Z97447.

S.cf.C: 31, Z97520/X90609.

Se: 24, Z97523/X90604; 25, Z97524/X90605; 26, Z97525/X90607; 42, Z97530/Z97445; 43, Z97531/X90608; 44, Z97527/

Z97444; 45, Z97528/Z97442; 46, Z97529/Z97443; 48, Z97526/Z97441; 49, Z97522/Z97440; 51, Z97521/Z97439.

Ti: 1, Z97539/Z97450; 2, Z97540/Z97451; 3, Z97541/Z97452; 4, Z97542/Z97449; 9, Z97538/X90596.

T.cf.C: 29, Z97555/X90603.

T.cf.D: 39, Z97557/Z97459; 40, Z97556/Z97460; 41, Y15133/Y15134.

T.cf.E: 13, Z97549/X90597; 14, Z97550/X90598; 15, Z97551/X90628; 17, Z97552/X90599; 18, Z97553/X90600; 22, Z97554/X90601; 52, Z97546/Z97458; 53, Z97547/Z97456; 54, Z97548/Z97457; 56, Z97545/Z97455; 58, Z97544/Z97454; 59, Z97543/Z97453.

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