Report

Convergent Evolution within an Adaptive Radiation of Cichlid Fishes

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Summary

The recurrent evolution of convergent forms is a widespread phenomenon in adaptive radiations (e.g., [1–9]). For example, similar ecotypes of anoles lizards have evolved on different islands of the Caribbean [2, 6], benthic-limnetic species pairs of stickleback fish emerged repeatedly in postglacial lakes [1, 3], equivalent sets of spider ecomorphs have arisen on Hawaiian islands [7, 8], and a whole set of convergent species pairs of cichlid fishes evolved in East African Lakes Malawi and Tanganyika [10, 11]. In all these cases, convergent phenotypes originated in geographic isolation from each other. Recent theoretical models, however, predict that convergence should be common within species-rich communities [12, 13], such as species assemblages resulting from adaptive radiations. Here, we present the most extensive quantitative analysis to date of an adaptive radiation of cichlid fishes, discovering multiple instances of convergence in body and trophic morphology. Moreover, we show that convergent morphologies are associated with adaptations to specific habitats and resources and that Lake Tanganyika's cichlid communities are characterized by the sympatric occurrence of convergent forms. This prevalent coexistence of distantly related yet ecomorphologically similar species offers an explanation for the greatly elevated species numbers in cichlid species flocks.

Results and Discussion

Adaptive radiation, the rapid evolution of a multitude of species from a common ancestor as a consequence of their adaptation to various ecological niches, is thought to be responsible for much of the morphological and ecological diversity on earth [4, 9]. Interestingly, parallel adaptive radiations of the same group of organisms frequently produce convergent forms [1–9], which is commonly understood as the result of independent adaptations to similar ecological conditions [3, 4, 14, 15]. Convergence in morphology and behavior is typically observed between species that evolved in geographic isolation [2, 3, 7, 10]. Theoretical models, on the other hand, predict that convergence should also be common within species-rich communities [12, 13], thus challenging the standard ecological premises that closely related species should be ecologically similar [16, 17] and that two species cannot coexist in the same niche [18]. Such models suggest that there is an alternative strategy for enabling stable coexistence than to be sufficiently distinct: to be sufficiently similar. According to these models, convergent evolution actually appears to be characteristic in "species-saturated communities" [12] and to occur when the number of species exceeds the number of available niches [13], as is probably the case in the exceptionally diverse species flocks of cichlid fishes in the East African Great Lakes Victoria, Malawi, and Tanganyika.

Against this background we explore the cichlid fish assemblage of Lake Tanganyika (LT) (Figure 1A) and provide what is to date the most thorough examination of a cichlid adaptive radiation. Our integrative study combines molecular phylogenetic, geometric morphometric, and diet analyses in a data set of more than a thousand specimens from 71 species (see Table S1 available online and Experimental Procedures). Our morphological comparisons focus on two ecologically highly relevant characters, overall body shape and the shape of the lower pharyngeal jaw bone (LPJ). The LPJ is the central unit of the pharyngeal jaw apparatus, which is a second set of tooth-bearing jaws in the pharynx used to process food [11, 22] (Movie S1). Finally, we use carbon and nitrogen stable isotope ratios as proxy for trophic ecology—in combination with stomach and gut content analyses.

We first present a robust phylogenetic framework for the species flock (Figure 1B), which largely agrees with previous studies [19, 20]. When clustering the species according to body and LPJ shape, the phylogenetic structure vanishes (Figures 2A and 2C), indicating that the shape of these traits is largely uncoupled from the phylogenetic background of a species. All larger cichlid tribes are broken up into two or more body and LPJ shape clusters, and the different tribes overlap in morphospace (Figures S1A and S1B). A large fraction of the sister taxa are not each other's closest ally in the morphological cluster analyses, and the cluster trees based on shape data are incongruent with the molecular phylogeny (body shape: Δ -lnL = 2885.87; Δ tree length = 1059; $P_{SH} < 0.001$; $P_{KH} < 0.001$; LPJ shape: Δ -lnL = 3709.20; Δ tree length = 1484; $P_{SH} < 0.001$; $P_{KH} < 0.001$). Instead of correlating with phylogeny, species that are morphologically alike are, in general, more similar in trophic ecology (Figures 2 and S1). This integrated analysis leads to two main observations. First, species from distinct clades are grouped into the same morphoclusters, whereas sister-species are often quite distinct morphologically (Figure S2); this suggests prevalent convergence in body and LPJ shape within the cichlid species flock of LT. Second, there appears to be a strong link between (trophic) morphology and ecology in LT cichlids; this suggests that, just like in other cases of convergent evolution, natural selection is the driving force in the evolution of convergent forms [1, 5, 15, 23]. In the following, we provide examples for convergent species and quantify convergence in sympatry in the cichlid species flock of LT.

Perhaps the most striking case of convergent evolution within LT's cichlid assemblage involves *Neolamprologus prochilus* and the enigmatic *"Ctenochromis" benthicola* (Figure 3A and indicated in bold in Figures 1 and 2). Both species occur sympatrically and are similar to a degree that even local fishermen, who otherwise ably distinguish species, consider them as one. In line with this, geometric morphometric analyses cluster them together, they have similar stable isotope signatures (Figures 2 and S1), and they show the same

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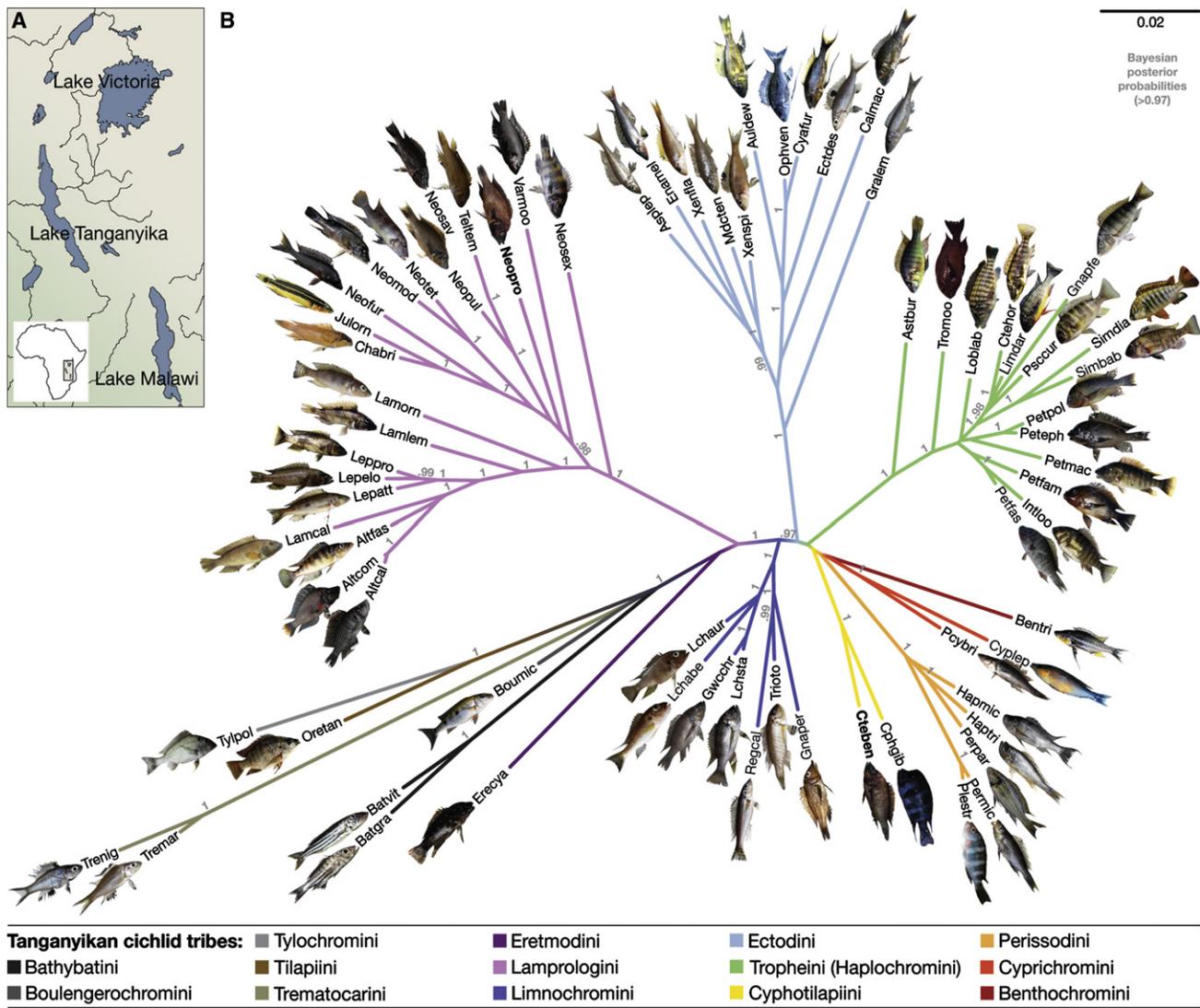
Figure 1. The Cichlid Species Flock of Lake Tanganyika

(A) Map of East Africa showing the three Great Lakes. Lake Tanganyika (LT) is the oldest lake in East Africa and, consequently, accommodates the genetically, morphologically, and ecologically most diverse cichlid species flock [11, 19].

(B) Maximum-likelihood phylogeny of the 71 Tanganyikan cichlid species in our core data set, based on two nuclear (*ednrb1*, *phpt1*) and one mitochondrial (ND2) marker (2,013 bp in total) and the GTR+G model of molecular evolution. Numbers above the branches depict Bayesian posterior probabilities >0.97. Full species names are given in Table S1; different colors denote the main cichlid lineages ("tribes"), some of which are likely to have undergone secondary subradiations [19–21]. Note that the cichlid adaptive radiations of Lakes Malawi and Victoria consist of one of these tribes only, the Haplochromini (the Tanganyikan representatives of which are often referred to as Tropheini) [21]. Our phylogeny confirms the monophyly of the tribes; at least seven genera are, however, paraphyletic, which already indicates convergence in traits used to classify them initially. For example, the putative haplochromine "*Ctenochromis*" *benthicola* (Cteben) emerges as a member of the Cyphotilapiini, whereas its congener, *C. horei* (Ctehor) remains within the Tropheini/Haplochromini. The other paraphyletic genera are *Gnathochromis* (Gna), *Lamprologus* (Lam), *Limnochromis* (Lch), *Neolamprologus* (Neo), *Perissodus* (Per), and *Petrochromis* (Pet). Images of the fishes were taken directly in the field.

stomach contents, namely remnants of the endemic shrimp *Limnocaridina* sp. (Figure 3A). Yet, whereas *N. prochilus* belongs to the Lamprologini, "*C.*" *benthicola*—formerly considered a Haplochromini and congener of *C. horei*—now emerges as a member of the Cyphotilapiini (Figure 1B). Pairwise genetic distances of 10.6% and 1.4% in the mitochondrial and nuclear DNA, respectively, suggest that the two species are separated by several million years of independent evolution, which lies in the range of the eye-catching convergent species pairs observed between Lakes Tanganyika and Malawi [10]. But cichlids do not only resemble other endemic cichlids. The rare *Baileychromis centropomoides*, for

example, is very similar in overall body shape to an endemic *Lates* sp. (Figures 3B and S3).

To quantify convergence in the LT cichlid species flock, we plotted relative morphological distance against phylogenetic distance for each pair of species and compared it to simulations of trait evolution (Figure 4A). Applying a conservative threshold (see Experimental Procedures), we identify 122 and 132 species pairs that are convergent in body and LPJ shape, respectively, which is about five times more than predicted by the models. Importantly, more than three quarters of these convergent species pairs overlap in habitat and depth distribution (Table S2), and they show a significantly greater
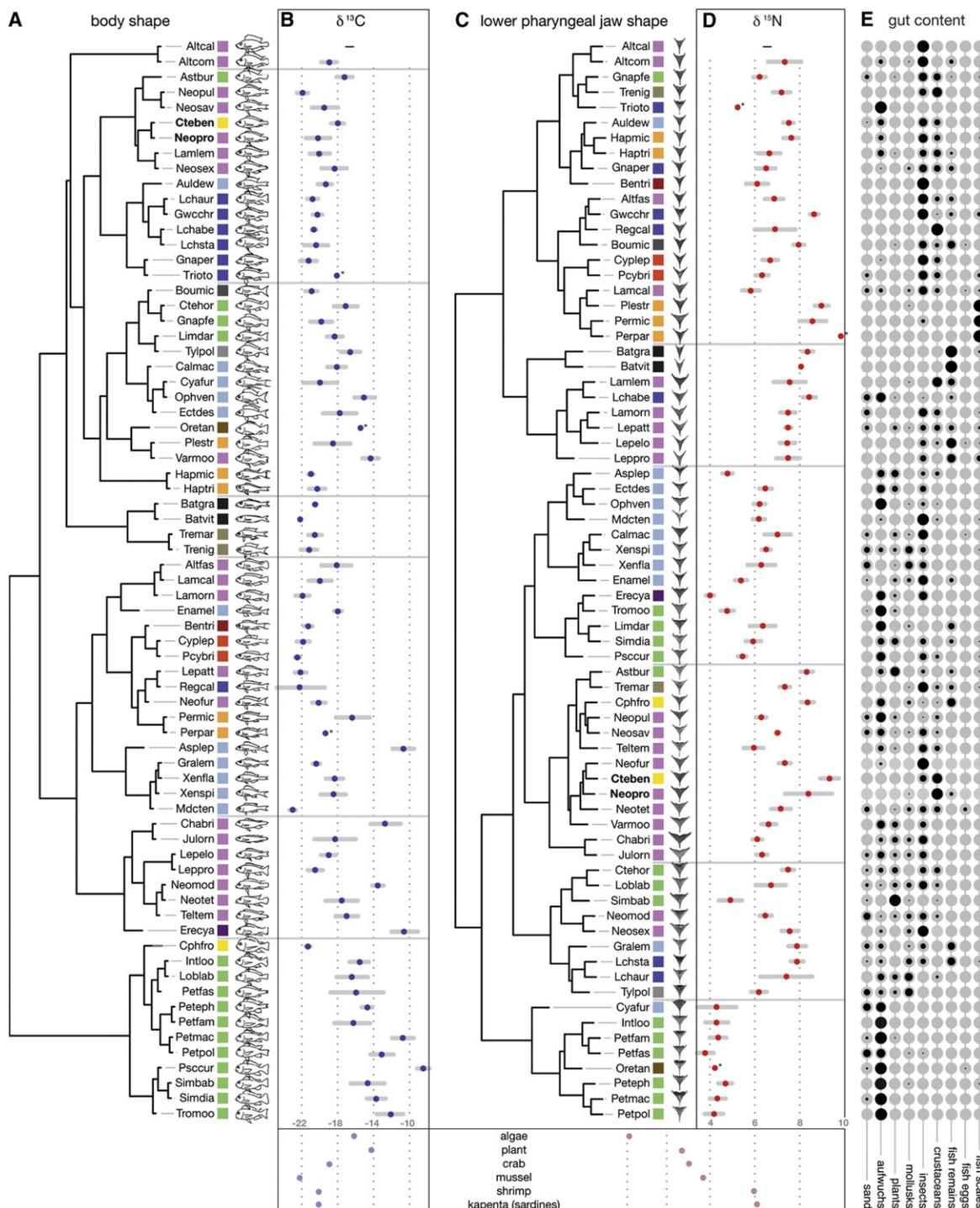
Figure 2. Ecomorphological Diversity in Cichlids from Lake Tanganyika

(A) Cluster analysis on the basis of 17 homologous landmarks on body shape.

(B) $\delta^{13}C$ stable isotope signatures.

(C) Cluster analysis on the basis of eight homologous and six sliding landmarks on the lower pharyngeal jaw bone.

(D) $\delta^{15}N$ stable isotope signatures.

(E) Results from the stomach and gut content analyses (in volume %).

Outlines in (A) are based on real photographs; images in (C) are taken from dissected LPJs (see Table S1 for details). The main morphoclusters are separated by gray lines, and the tribes are colored as in Figure 1. Colored dots in (B) and (D) represent average values; gray bars indicate 95% confidence limits of a t distribution. * marks species with too small a sample size, so that 95% confidence intervals were not calculated. The ratio between the rare isotope ^{13}C to ^{12}C (the $\delta^{13}C$ value) indicates the primary carbon source, which may vary between macrohabitats (e.g., benthic versus pelagic), whereas the $\delta^{15}N$ value (^{15}N to ^{14}N) serves as proxy for the relative trophic level of an organism. Accordingly, in LT cichlids, $\delta^{13}C$ values correlate with body shape clusters (F = 2.66, p < 0.005), whereas $\delta^{15}N$ values correlate with LPJ shape (F = 4.03, p < 0.005). Note that each trophic level is separated by approximately 3.4‰ in $\delta^{15}N$ from the one below. To facilitate comparisons, we also included average stable isotope values for some plant and animal species from LT (see box at the bottom).
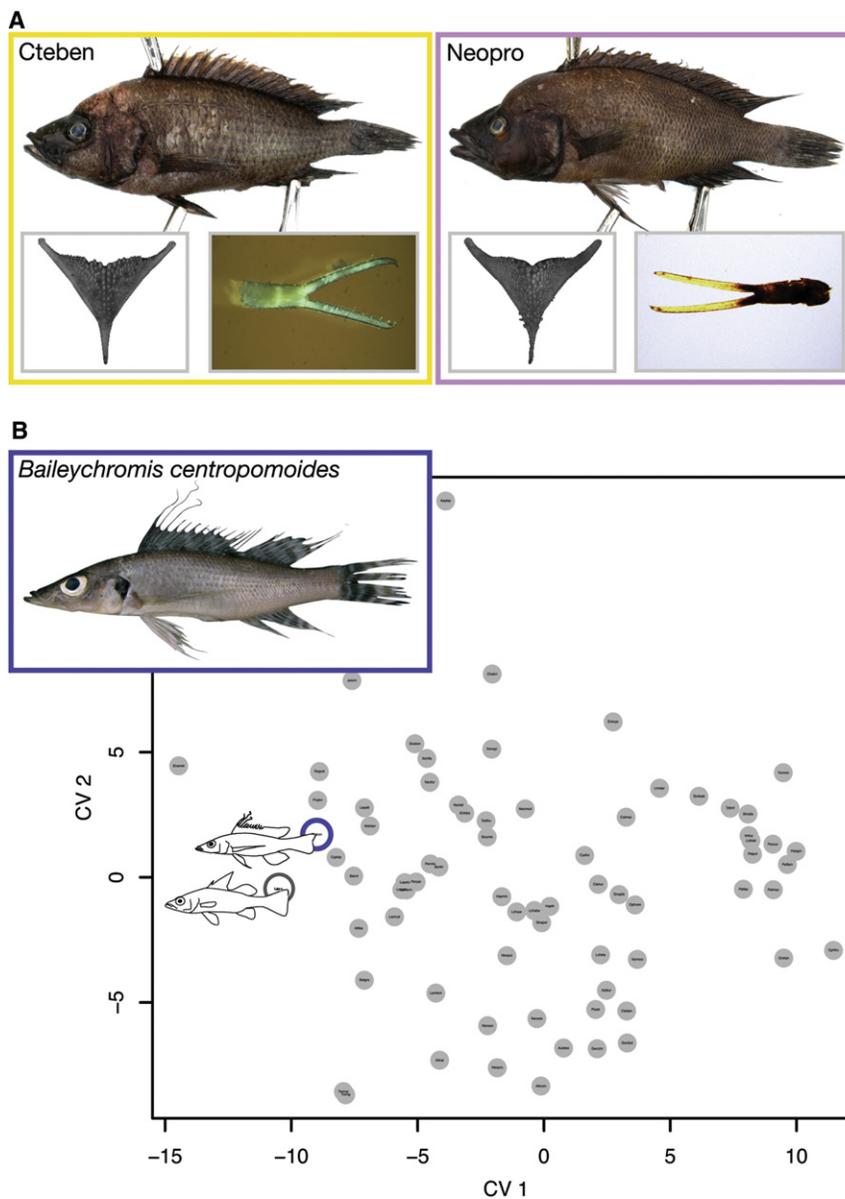
Figure 3. The Curious Cases of Convergent Evolution between "*Ctenochromis*" *benthicola* and *Neolamprologus prochilus* and between *Baileychromis centropomoides* and *Lates* sp.

(A) "*C.*" *benthicola* (Cteben) and *N. prochilus* (Neopro) are phylogenetically distinct (Figure 1) but show great similarities in morphology and in stable isotope signatures (Figure 2). For each species, the LPJ and a pincer of the freshwater shrimp *Limnocaridina* sp. (found in the stomach of the respective specimen) is shown.

(B) Canonical variates analysis showing that *B. centropomoides* is morphologically similar to *Lates* sp. endemic to LT (*B. centropomoides* shows the by far smallest Procrustes distance to *Lates*; see Figure S3). Each dot represents a species. Note that *Lates* used to be classified in the family Centropomidae until recently, which is where the species name for *Baileychromis* is derived from.

A large proportion of phenotypic differentiation in LT's cichlid assemblage occurred along only a few principal axes in morphospace (Figure 4C), which reflect adaptations to specific habitats and feeding regimes. For body shape, we detect divergence and convergence in the relative body height, which generally correlates with a pelagic or benthic lifestyle, respectively; the relative sizes of the head and trunk; the sizes of mouth and eye; and the position of the mouth. The divergent and convergent features of the LPJ involve its relative length and width (affecting lever ratios), the relative size and position of the posterior horns (important muscle attachment sites), and the shape of the toothed area. Interestingly, the DTT trajectory for LPJ shape largely coincides with the trajectory of the stable isotope data (Figure 4B), underpinning synchronized differentiation in both an important trophic character (the pharyngeal jaw apparatus) and the trophic niche (as approximated by stable isotopes). This once more confirms a strong link between morphology and ecology in LT cichlids.

In comparison with other renowned examples of adaptive radiation, the situation in LT is unique in its richness of convergent forms that evolved in situ and that coexist in the same habitats (Figures 2, 3, and 4). But what has triggered convergent evolution within the species flock of cichlids in LT? One possibility is that convergent evolution is a feature of advanced adaptive radiations, such as the LT cichlid species flock, which constitutes the relatively oldest cichlid radiation of the East African lakes. Representatives of distant lineages that independently adapt to the same habitat and the resources therein later in the radiation might then already be sufficiently distinct in certain life-history traits to enable coexistence. In the convergent species pair *N. prochilus* and "*C.*" *benthicola* (Figure 3), for example, the former is a substrate spawner, whereas the latter is a mouthbrooder. Convergence

overlap in diet compared to random species pairs (p < 0.05 for body shape; p < 0.0001 for LPJ shape). These results demonstrate that cichlid communities within LT are characterized by the sympatric occurrence of convergent forms and that convergence is particularly prevalent in trophic morphology.
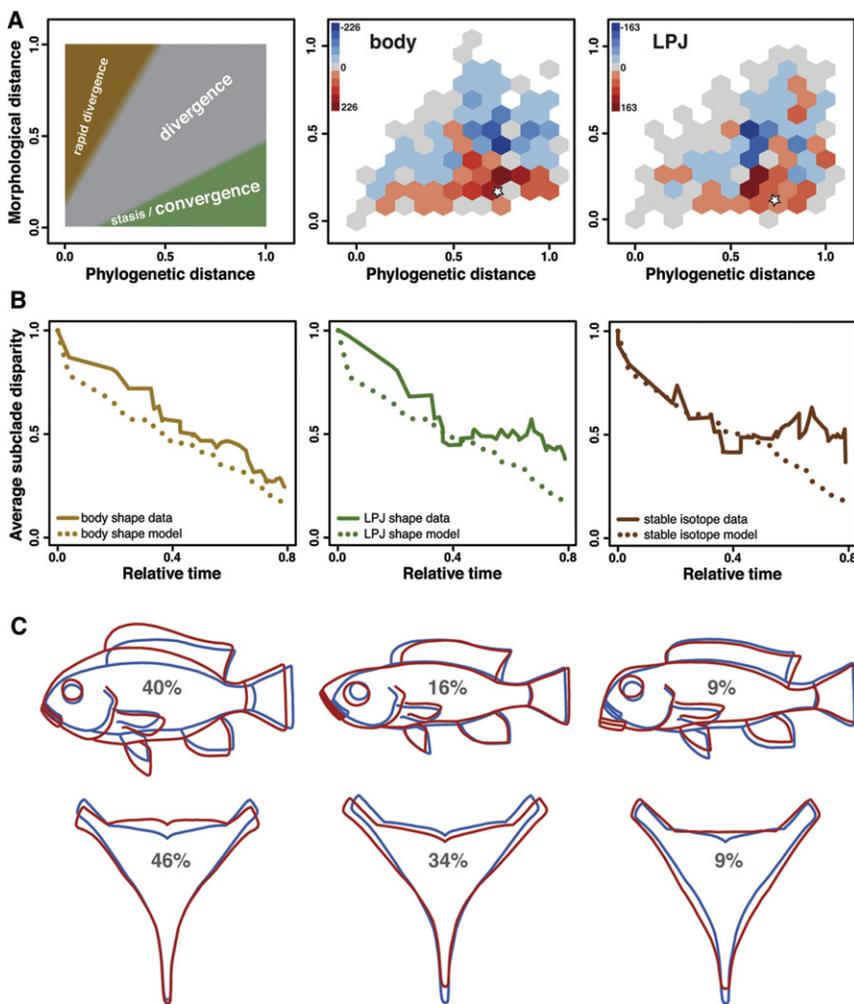
We then performed disparity-through-time (DTT) analyses to reconstruct convergent evolution along the evolutionary history of the species flock. The DTT analysis uncovers a large overlap in body morphology between the subclades emerging in the progress of the radiation (Figure 4B). The DTT plots on the basis of LPJ shape reveal that phases of larger subclade overlap are punctuated by a phase of neutral-like disparity. Overall, there is a strong signal of convergent evolution, which is unlikely to be explained by varying rates of speciation or of morphological evolution, because both have been shown to be rather constant in the cichlid adaptive radiation of LT [20, 25] (Figure S4). The DTT analyses thus suggest that convergent evolution in body and LPJ shape occurred throughout the time course of the radiation.

Figure 4. Convergence and Adaptive Disparity in the Cichlid Species Flock in Lake Tanganyika

(A) Pairwise distance-contrast plots showing the correlation between phylogenetic versus morphological distance. The expectation from neutral trait evolution ("divergence") is a correlation between morphological and phylogenetic distance. Species pairs with small morphological yet large phylogenetic distance are indicative of stasis (in cases where there are no intermediate species with distinct morphologies) or convergent evolution [24]. To assess the prevalence of convergent evolution in body and jaw shape, we contrasted the positions occupied by all pairwise comparisons (n = 2,485) with those resulting from a Brownian motion model of trait evolution. We binned the data points into hexagons, the colors of which reflect the differential abundance of observed versus model comparisons. Different shades of blue indicate that our data contained fewer comparisons than expected from the model, whereas shades of red indicate that there were more pairwise comparisons in the data. The latter are predominant in the area indicative for convergence. The white asterisk marks the convergent species pair "*Ctenochromis*" *benthicola* and *Neolamprologus prochilus* (see Figure 3).

(B) Disparity-through-time (DTT) plots showing the average disparity retained in subclades (for body shape and LPJ shape and stable isotopes). Here, DTT plots inform about the time course of ecomorphological evolution. Moving along the phylogeny (from the root to the tips), the relative disparity of subclades is calculated at each internal node, averaged, and plotted against evolutionary time. The observed data is compared to a scenario of trait evolution estimated under a Brownian motion model (dotted line) on the same phylogeny. In order to avoid the effects of "tip overdispersion" due to missing terminal taxa, the most recent 20% of the plots were omitted.

(C) Shape changes along axes, which account for most of the divergence in the LT cichlid radiation. Axes are derived from evolutionary principal component analyses for body (first, second, and fourth axis) and LPJ shape (first, second, and third axis). The relative variance explained by each axis is given in percent.

(and niche overlap) would then be the product of secondary subradiations within the main Tanganyikan tribes [19, 20] superimposed upon each other—a stage that other adaptive radiations might not yet have reached. This scenario seems unlikely, though, given that our DTT analyses reveal a signal of convergence that is constantly high throughout the radiation (Figure 4B). Also, empirical studies comparing various adaptive radiations [26] and theoretical work [27] revealed that diversity appears to be greatest in radiations of intermediate ages and to actually decrease toward later stages. A second possibility is that convergent species initially emerged in isolation—e.g., when LT was temporarily split into separate basins during extremely low lake stands [28]—and only became admixed at a later stage of their evolution. Again, this does not seem to be compatible with our DTT and LTT analyses, which revealed that the signal of divergence and convergence is rather constant throughout the radiation and not restricted to certain periods—e.g., of lake level low stands—only.

That morphological differentiation resulted in convergence in LT might better be explained by the limited number of niches and, hence, adaptive zones (compared to the number of species) that cichlids can invade within the lake [29].

Alternatively, there might be a limit in the number of possible morphologies that cichlids can produce, due to some sort of developmental or genetic constraint [14]. The main morphoclusters in body and LPJ shape (Figure 2) might reflect such constraints. Perhaps it is also a combination of the finite number of niches and morphologies that explains convergence within the adaptive radiation of LT cichlids.

In any case, convergence in ecologically relevant traits within a single radiation is compatible with predictions made by current population ecology theory [12, 13]. It seems that self-organized similarity does not only play an important role in the maintenance of diversity, for example of plankton [30], but also in the rapid formation of organismal diversity via convergent evolution. Because resources are jointly used by several ecomorphologically similar and co-occurring cichlid species from distinct clades in LT, species numbers are maximized without increasing overall disparity. A key to the cichlid problem (i.e., why are there so many species?) might thus lie in the frequent occurrence of convergent evolution—not only between lakes but especially within a single lake and in adaptively relevant traits such as the LPJ. The question is now whether divergence via convergence is a more general pattern of diversification in species-rich communities. It would thus be

of great interest to extend the kind of integrative analysis implemented in this study to other adaptive radiations and, especially, to the cichlid adaptive radiations in Lakes Malawi and Victoria. Even more so, because a recent comparison across 46 cichlid adaptive radiations [31] suggests that the LT radiation is an outlier from an otherwise more general trend in cichlid radiations, which appear to be triggered by both ecological opportunity and sexual selection.

Experimental Procedures

Sampling
Sampling was performed under permission from the Department of Fisheries, Lake Tanganyika Research Unit, Mpulungu, Zambia. In total, we sampled more than 1,000 specimens for this study (see Supplemental Experimental Procedures and Table S1 for further details).

Phylogenetic Analyses
We analyzed one mitochondrial (ND2) and two nuclear (*ednrb1*, *phpt*) markers (see Supplemental Experimental Procedures and Table S1 for GenBank accession numbers used in this study). We relied on maximum likelihood and Bayesian methods for phylogenetic analysis using PAUP*, MRBAYES, and the BEAST package. The appropriate model of molecular evolution for the heuristic tree searches in PAUP* was determined with JMODELTEST; MRBAYES was run for ten million generations with a burn-in of 10%; data were partitioned in BEAST. We first analyzed our core data set combining the mitochondrial and nuclear DNA sequences in 71 taxa, then the core data set including *Baileychromis centropomoides*, and, finally, a mitochondrial data set including the ND2 sequences of 180 taxa (i.e., ca. 90% of all Tanganyika species). Trees derived from the latter analysis were used for lineage-through-time plots. For incongruence testing, we applied the Kishino-Hasegawa (KH) and the Shimodaira-Hasegawa (SH) test implemented in PAUP*.

Geometric Morphometric and Morphological Analyses
We assessed the body shape of 1,049 individuals using landmark-based geometric morphometrics. xy coordinates of 17 landmarks, distributed across the whole fish body (see Figure S5A), and the scale of each picture were recorded using TPSDIG [32]. Aligned Procrustes coordinates were used for a pooled-within-species regression of shape against centroid size in MORPHOJ 1.02d [33]. Species averages were then used for principal component analysis (PCA), for disparity-through-time analyses, and for the calculation of pairwise distances between species. For LPJ assessment we recorded coordinates of eight true landmarks and 20 semilandmarks describing the outline of the bone (Figure S5B). We then clustered the species according to similarity in body and LPJ shape, using agglomerative hierarchical clustering in R.

Stomach and Gut Content Analyses
Contents were removed from the intestinal tracts of 506 specimens and separated up into one or more of the following categories: sand, aufwuchs (algae), plant material, mollusks, insects (imagines and larvae), crustaceans, fish (remains), fish eggs, and fish scales. We determined volume (in %) and weight (in μg) of each category.

Stable Isotope Analysis
White muscle tissue from 727 specimens (see Table S1) was dried, pulverized, and analyzed on an elemental analyzer (Thermo Finnigan) coupled to a Finnigan Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS).

Pairwise Distance-Contrast Plots
To estimate the extent of convergence, we compared the phylogenetic distance to the morphological distance of each species pair [24]. The morphological distance was calculated as Euclidean distance from the pooled-within-species regressions of shape against centroid size using R's dist() function. In total, we had 2,485 species comparisons; therefore, we used hexagonal binning (x = 10 bins) to overcome overplotting. We also simulated neutral trait evolution on the phylogeny, using Brownian motion and Ornstein-Uhlenbeck models. Species comparisons that we derived from these simulations were then compared to our actual data by subtracting the binning counts of the simulations from those of the data. We tested for statistical significance of the difference of pointwise means

between simulations and data (each 1/10 of the x axis) by bootstrapping (1,000 replications).

Disparity-through-Time Analysis
DTT analyses were performed according to Harmon et al. [34], comparing the observed data to a scenario of trait evolution estimated under a Brownian motion model. Positive deviations of the data from the simulations indicate a higher overlap in morphospace among subclades than would be expected under neutral evolution.

Evolutionary PCA
We estimated the ancestral character states for body and LPJ shape at each node in the phylogeny and calculated the extent and the direction of shape change along each branch. These branchwise estimates were then subjected to PCA to find the axes of greatest evolutionary divergence. All evolutionary PCAs were performed in MORPHOJ.

Supplemental Information

Supplemental Information includes five figures, two tables, Supplemental Experimental Procedures, and one movie and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.10.048.

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