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Multifaceted impacts of an innovation on dental diversity in an adaptive radiation of cichlid fishes

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Evolutionary innovations bring species into new ecological zones by opening ecological opportunity. However, innovations can have varied effects on morphology, which is determined by both intrinsic properties of the innovation and extrinsic properties of the adaptive zone. Here, we show that the evolution of complex teeth with multiple cusps—a vertebrate innovation—has mixed effects on the trajectory of dental evolution in an adaptive radiation of cichlid fishes. Complex teeth first evolved outside Lake Tanganyika and facilitated a secondary incursion of riverine lineages into the lake through herbivorous niches. Complex dentitions are more restricted and segregate along multiple axes of dental diversity. This dental novelty generated by the evolution of complex teeth was probably spurred by adaptive evolution pulling traits towards distinct optima. By accelerating the diversification of tooth cusps, complex teeth unlocked a new axis of dental diversity, leading to diversification within but not between ecological niches. These patterns are probably driven by the functional demands of herbivory. Our results show that innovations can shape the tempo and mode of morphological change through both intrinsic and extrinsic effects. Because the consequence of innovation is often varied, our results highlight the need consider these effects jointly to better understand the macroevolutionary diversity of innovations and their outcomes.

1. Introduction

Evolutionary innovations are thought to generate significant increases in biodiversity. While often resulting in rapid cladogenesis, the evolution of these traits can also shape the tempo and mode of morphological change [1]. Innovations bring lineages into new adaptive zones by conferring gains in organismal performance [2,3]. However, the range of downstream phenotypic diversity outcomes is varied [4]. Powered flight, which required major modification of the limbs and sternum, led to the diverse radiation of modern birds and extensive diversification of the flight apparatus. Other innovations may introduce species to a new but restricted adaptive landscape. The unique feeding mechanism of the sling-jaw wrasse (*Epibulus*) facilitates extreme performance in jaw protrusion [5], but there are only two species of *Epibulus*, and this novelty has not diversified further. While innovations frequently open up opportunities for further diversification, they may also support impressive gains in performance with little or no subsequent expansion.

What determines these evolutionary paths? The myriad of potential outcomes stems largely from the accessibility of ecological opportunity within the newly invaded adaptive zone and the potential for substantial reorganization of organismal structures. Innovations that open up rich adaptive zones with ample ecological opportunity could drive rapid diversification [6–9]. Intrinsic innovations (e.g. increasing skeletal complexity) could accelerate morphological diversification along novel axes by allowing expansion into new or previously unreachable phenotypic or performance space [10–15]. Expanding the range of achievable morphologies could have downstream effects on phenotypic, functional and ecological diversification [16,17]. In contrast, the biomechanical or physiological construction of the innovation may itself limit the potential for subsequent modification, or the adaptive landscape around the innovation may be flat, lacking ecological opportunity [4,18–20]. The timing of innovation can also have significant consequences. Because ecological opportunity is expected to decline through time in evolutionary radiations [21], innovations that facilitate novel ecological roles could break barriers of competitive exclusion and biotic filtering creating opportunities for secondary colonization events [22–24]. Competitive pressure from incumbent taxa might inhibit the diversification of secondary colonizers in spatially restricted systems, despite lacking the same innovation [24,25]. The interaction of these intrinsic and extrinsic factors determines the range of morphological outcomes following the evolution of an innovation.

Here, we explore the macroevolutionary outcome of an innovation—complex teeth with multiple cusps [26–28]—for dental diversity within the radiation of cichlid fishes in Lake Tanganyika (LT). Teeth are a major component of the fish feeding system, and variation in the arrangement and shape of teeth has important functional implications for prey detachment, capture and processing [29–33]. We first ask in what context complex teeth arose in this radiation and then explore the dynamics of dental evolution among lineages that differ in tooth complexity. The cichlid fishes of LT are a compelling system for studies of dental innovation because the radiation includes a secondary colonization event and multiple independent origins of complex teeth [34,35]. The evolution of complex teeth in LT contrasts with other rift lakes [28] in that diverse lineages with simple teeth comprise the majority of endemic species. Moreover, the addition of tooth cusps inherently changes the complexity of teeth [30], which may have an intrinsic effect on dental diversification. This combination of features allows us to interpret how both intrinsic and extrinsic factors determine the impact of this innovation on feeding morphology during the adaptive radiation of LT cichlids. We quantified dental diversity along three distinct axes—the overall dentition, attributes of individual teeth and the shape of tooth cusps—and evaluated whether the trajectory and pace of dental diversification shift following the evolution of complex teeth. By considering the ecological context in which complex teeth evolved in LT cichlids, we reveal the multifaceted impact this innovation had on the dental system.

2. Methods

We quantified dental diversity from 352 specimens representing 150 species (1–6 specimens per species) of cichlid fishes from LT. Specimens were acquired through the aquarium trade or from museum collections (electronic supplementary material, table S3). Our sampling includes representatives from all 12 tribes and all but two genera, both monotypic (*Baileychromis* and *Tangachromis*), and encompasses 60% of endemic species in the radiation. We also included *Astatotilapia burtoni*, a haplochromine species widespread in LT's marginal habitats.

3. Data collection

To characterize aspects of the overall dentition, we counted the number of outer row teeth and number of inner tooth rows for each specimen, separately for the premaxilla and dentary. We computed the variance in tooth height (see below) per jaw, per specimen, as a proxy for heterodonty and homodonty [31]. We refer to this dataset as 'dentition'. We define simple teeth as those having a single tooth cusp, and complex teeth as those having two or more tooth cusps following Peoples *et al.* [28] (figure 1*a*).

To quantify functional aspects of individual teeth, we extracted the first 5 outer row teeth on the premaxilla and dentary, beginning at the symphysis and moving posteriorly. Extracted teeth were photographed under a compound microscope in both lateral and labial views. We excluded teeth that were broken or had clear signs of significant wear. We measured and computed 7 morphological traits with functional significance (electronic supplementary material, table S1) including tooth height, tooth curvature, tooth base length, cusp height, cusp cross-section aspect ratio, enameloid ratio and cusp taper using the software ToupView (ToupTek Photonics, Inc.) (electronic supplementary material, figure S1a,b). To account for effects of size, we converted measurements to log-shape ratios [36] by dividing each by the geometric mean of (standard length [SL] × premaxilla length × jaw width [JW]) for premaxillary teeth and by the geometric mean of (SL × dentary length × JW) for dentary teeth, then using a log-transformation. Ratios generated from linear measurements were log-transformed without size correction. Because ratios may not account for allometric trends, we also retained the residuals of a log–log regression of each ratio against SL as an alternative method that removes effects of size. We found that values from both approaches were highly correlated ($R^2 = 0.978$–0.998) (electronic supplementary material, figure S2) and used log-ratios in all analyses. Our final dataset included 3231 extracted teeth across the premaxilla and dentary. We refer to this dataset as 'linear morphometrics'. To obtain species-level information for phylogenetic comparative analyses, we first quantified the mean value of each trait per specimen, then the mean values per specimen to get species mean values. Each species' mean value was thus based on measurements from 5 to 15 teeth. Teeth from the premaxilla and dentary were analysed separately; results in the main text represent dentary teeth. Patterns of dental diversity did not vary between jaws.

Finally, we used geometric morphometrics to quantify the shape of individual tooth cusps. To reduce noise and non-biological variation, we chose a single tooth from each specimen ($n = 352$ teeth for each jaw). We used a combination of fixed landmarks and sliding semi-landmarks, which can accurately capture variation in cusp morphology without introducing non-biological variation [37,38]. We placed two landmarks at the enameloid–dentine junction, and a third at the tip of the major cusp; for

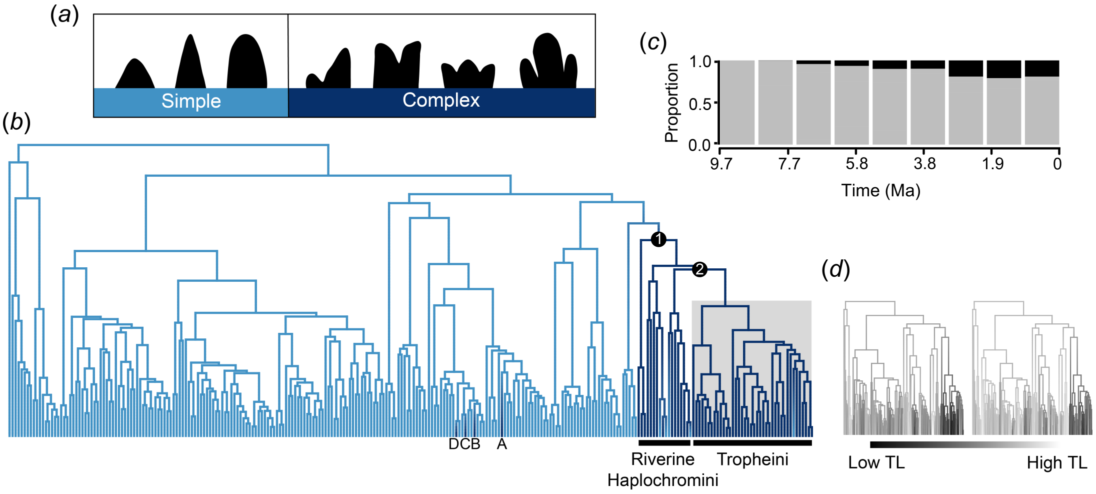

Figure 1. The evolution of complex teeth and trophic diversity in LT cichlids. (*a*) Silhouettes depicting a range of simple and complex tooth shapes found in LT cichlids. (*b*) Ancestral state reconstruction of complex teeth (dark blue) in the LT radiation and riverine outgroups. The Tropheini are highlighted in grey shading. Black points correspond to (1) the riverine origin of complex teeth and (2) the split between Haplochromini and Tropheini. Four intralacustrine origins of complex teeth in A *Asprotilapia leptura*, B *Ophthalmotilapia boops*, C *Cunningtonia longiventralis* and D *Cyathopharynx foae*. (*c*) The proportion of herbivorous and omnivorous lineages (black) through time in approximately 1 MY intervals. Grey bars include zoobenthivores, zooplanktivores, piscivores and lepidophages. (*d*) Ancestral state estimation of δ^{15}N (nitrogen, left) and δ^{13}C (carbon, right) stable isotope signatures, a proxy for trophic level (TL), across the LT radiation ($n = 232$ species).

simple teeth, this was simply the tip of the tooth (electronic supplementary material, figure S1c). We then placed 40 sliding semi-landmarks around two curves (n = 20 landmarks each) traced around the lateral edge of the cusp using tpsDig2 v.1.1. We aligned and scaled all landmarks using a generalized Procrustes analysis (GPA) in 'geomorph' [39], sliding semilandmarks based on minimizing bending energy. We computed species means of Procrustes-aligned coordinates; species means were used for all further analyses.

(a) Disparity and morphospace occupation

We used the time-calibrated phylogeny of Ronco *et al.* [34], pruned to include the 150 species in our study, for all phylogenetic comparative analyses of dental diversity. This timetree was built using 547 cichlid genomes and includes both cichlid and other teleost fossil calibrations. All analyses were replicated across the three datasets (dentition, linear morphometrics and geometric morphometrics).

To visualize the major axes of dental variation, we performed principal component analyses (PCA) on the correlation matrix of the dentition and linear morphometrics dataset using 'prcomp' in the 'stats' R package (R Core Team) and on the covariance matrix of the geometric morphometrics dataset using the 'gm.prcomp' function in 'geomorph [39]'. To compare dental diversity between species with simple and complex teeth, as well as betweeen herbivores and non-herbivores, we calculated disparity for each group using 'morphol.disparity' in 'geomorph' [39,40], using the size-corrected values for the dentition and linear morphometric datasets and Procrustes coordinates for the geometric morphometric dataset as inputs. We employed two methods to test for differences in morphospace occupation between species with simple and complex teeth. First, we used phylogenetic multivariate analysis of variance (p-MANOVA) under a Brownian motion model in the R package 'geiger' [41]; we also used this approach to compare dental traits between herbivores and non-herbivores. To compare the degree of morphospace overlap and uniqueness between groups, we created n-dimensional hypervolumes for our dentition (n = 3, 100% variance), linear morphometrics (n = 7; 100% variance) and geometric morphometrics (n = 5; 94.5% variance) datasets using the first three, seven and five principal component (PC) axes, respectively, with the R package 'hypervolume' v.3.1.4 [42,43]. The first five PC axes of the geometric morphometrics dataset were chosen through visual examination of scree plots. We created a sample of 100 permuted hypervolumes for each group, generated a null distribution of overlap statistics under the null hypothesis that the two groups occupy the same volumes, estimated the fraction of space unique to each group as well as Jaccard and Sørensen similarity, and calculated the p-values for the observed statistics with respect to the generated null distributions.

We visualized how the accumulation of disparity through time differed from that expected under a null Brownian model with the 'dtt' function in the R package 'geiger' [41,44]. For each dataset, we estimated the morphological disparity index (MDI), which quantifies the average difference in the disparity of a clade compared with a null Brownian model. Positive values indicate that disparity is distributed within rather than among subclades, suggesting that species within each subclade are exploring a greater range of dental space than expected under Brownian motion (BM).

(b) Integration

We compared the strength of evolutionary phenotypic integration between species with simple and complex teeth. For each pairwise trait combination, we estimated the strength of morphological integration (r-pls) separately for simple and complex species with the 'phylo.integration' function (10 000 permutations) in 'geomorph'. We used the first five PC axes from the geometric morphometric analysis of cusp shape. We assessed significance with the 'compare.pls' function in 'geomorph'. We used analysis of variance (ANOVA) tests to compare the distribution of *r-pls* values between simple and complex species across all comparisons ($n = 95$) and for only those trait comparisons that differ significantly in their strength of integration between groups ($n = 19$).

(c) Rates of evolution

We used four approaches to estimate multivariate rates of trait evolution across our three datasets: (i) a single, constant-rate Brownian (BM) rate for each group, (ii) state-dependent BM rates, (iii) branch-specific BM rates, and (iv) multivariate rates under an Ornstein–Uhlenbeck (OU) model. For all three datasets, we compared multivariate Brownian rates of evolution between simple and complex lineages, as well as between herbivores and non-herbivores, using the 'compare.evol.rates' function in 'geomorph [39]', with 10 000 permutations to assess significance. However, this simple model attributes all rate variation to the observed groups, even when variation in rate is independent of the group identity. To account for this background rate variation, we employed the (ii) MuSSCRat model implemented in RevBayes [45,46]. This expanded Brownian model jointly estimates the evolution of the discrete and continuous characters, separating the effect of the discrete character from other sources of rate variation. We modelled background rate variation using an uncorrelated log-normal (UCLN) clock, which places an independent rate parameter on each branch, and set a prior of 20 discrete character transitions. The Markov chain Monte Carlo (MCMC) was run for 200 000 generations with 10% burn-in and convergence checked with Tracer 1.7.2 ([47]; see also [3]). To estimate branch-specific and species-specific rates (i.e. tip rates), we used a relaxed-clock multivariate Brownian model implemented in RevBayes following Burress *et al.* [48], with a prior of 20 rate shifts. The MCMC was run for 500 000 generations with 10% burn-in, and convergence was checked with Tracer 1.7.2. We plotted these rates through time using a custom R script that summarizes the rate across branches of the phylogeny in user-specified time slices. Finally, to evaluate whether the evolution of dental traits is subject to unique selective regimes between simple and complex lineages (represented by an OU model of evolution), we fit several multivariate BM and OU models with the R package 'mvMORPH' [49]. We fit these models separately for each dataset. We included OU models that had single (OU1) or multiple (OUM) selective regimes, and BM models with either a single rate (*BM1*) or separate rates for each group (*BMM*). We fitted each model 100 times over a distribution of 100 stochastic character maps to account for uncertainty in the ancestral history of complex teeth and compared models using the mean Akaike information criterion (AIC) of 100 fitted models. For the best-fit OU model, we averaged all fits by their Akaike weights to evaluate the adaptive values (theta; θ) of each trait.

(d) Evolution of complex teeth and diet

To investigate whether the origin of complex teeth occurred within LT or in surrounding riverine lineages, we used the tooth complexity classifications of Peoples *et al.* [28] and the full phylogeny ($n = 265$ species) of Ronco *et al.* [34], which includes both endemic LT species and Haplochromine outgroups, to generate an ancestral state reconstruction of tooth complexity using stochastic character mapping. We compared the fit of an equal rates (ER) and unequal rates (ARD) character evolution model, fitted with the fitMk function in phytools [50], using AIC. We then generated 100 stochastic character maps with 'make.simmap', with the root state fixed to simple teeth. We summarized all 100 simmaps using 'densitymap' to plot the posterior probability of complex teeth on each branch.

To quantify the proportion of lineages occupying different diet categories through time, we used the diet classifications of Peoples *et al.* [28], pruned to match the 150 species in our study. We generated 100 stochastic character maps under an ARD model and summarized the proportions of each diet through time in equal-time-length bins averaged across all 100 simmaps. Using the same diet classifications, we grouped species as herbivores and non-herbivores in the principal component (PC) biplots of the three dental diversity datasets to visualize how dental diversity reflects diet (electronic supplementary material, figure S3b–d). To supplement our discrete diet classifications, we used the stable isotope data from Ronco *et al.* [34] as a continuous proxy for trophic level. We calculated species mean δ^{15}N and δ^{13}C values and visualized the log-transformed phylogenetic distribution of these values through time with the contMap function in phytools [50].

4. Results

(a) Riverine origins and ecological consequences of complex teeth

The adaptive radiation of cichlid fishes in LT occurred in two stages. After the initial radiation, multiple lineages dispersed out of LT [35]. Riverine lineages then re-entered the lake approximately 5–7 Ma, resulting in a successful secondary colonization event and subsequent diversification of the Tropheini (approx. 40 species) in parallel to an established radiation [34,35,51]. Ancestral state reconstructions show that complex teeth first evolved outside LT in riverine lineages ancestral to the modern Haplochromines and were absent from the initial radiating lineages within LT (figure 1*b*). This indicates that the re-entry into LT by riverine species and subsequent radiation of the Tropheini in rocky littoral habitats were accomplished by lineages with complex teeth, probably under intense competition with established species [34,35,51]. Within the lake, there are four independent origins (in *Asprotilapia leptura*, *Ophthalmotilapia boops*, *Cunningtonia longiventralis* and *Cyathopharynx foae*) and a single reversion in *Ctenochromis horei* (figure 1*b*) (ARD; ΔAIC = −0.89, AICω = 0.61; electronic supplementary material, table S2), contrasting with the exceptional lability of tooth complexity seen in Lakes Malawi and Victoria [28]. The evolution of complex teeth and herbivory is a coupled process in cichlids [28]. Ancestral state reconstructions of diet, δ^{15}N and δ^{13}C reveal that herbivorous niches were not occupied by cichlids at the onset of the radiation and only began being filled after the increase in lineages with complex teeth (figure 1c,d; electronic supplementary material, figure S3a). Collectively, these results suggest that the riverine origin of complex teeth played a role in the successful incursion of riverine species into LT and subsequent *in situ* radiation of the Tropheini by increasing ecological opportunity through low trophic level niches, despite the presence of considerable ecological and morphological diversity [34].

(b) Morphospace occupation

Species with simple and complex teeth segregate in dental morphospace across all three morphological axes, and there is high dental diversity across the LT cichlid radiation (figure 2*a*–c). Among dentitions (tooth number, row number, variance in tooth height), the primary axis of variation (PC1, 46.3%) separates morphologically homodont dentitions of few teeth in a single row (low PC1, e.g. *Perissodus*) from heterodont dentitions comprising many teeth in multiple rows (high PC1, e.g. *Lepidiolamprologus*) (figure 1*a*). Species with simple teeth have 2.45 × greater disparity ($p < 0.01$) (figure 3*a*) and occupy different morphospace regions (phylogenetic MANOVA; $p < 0.05$) that are largely unique from area occupied by complex species, despite the appearance of significant overlap in two dimensions (Jaccard similarity [JS] = 0.069, $p < 0.0001$; fraction of unique morphospace [F_{simple}] = 0.915, $p < 0.0001$). Species with simple teeth occupy extreme morphospace regions, while species with complex teeth are restricted to central regions with a lower proportion of unique occupation ($F_{\text{complex}} = 0.724$) (figure 2*a*). These patterns show that species with simple teeth occupy a greater amount and have explored more extreme regions of morphospace, while complex-toothed species have similar numbers of teeth and tooth rows and largely homodont dentitions. Functional aspects of individual teeth, captured with seven linear measurements, vary considerably across species. While simple teeth show great diversity and range from short cones (low PC1, e.g. *Trematocara*) to stout and highly recurved in scale-eaters (high PC1, e.g. *Plecodus*), complex teeth are more limited in morphology despite having similar amounts of disparity (figures 2b and 3a). Complex teeth are larger, with bases elongated along the antero-posterior axis, and have broad cusps with higher cross-sectional aspect ratios (figure 2*b*). This combination of functional traits is largely unique to complex lineages ($F_{\text{complex}} = 0.85$) with little overlap between simple lineages (JS = 0.012, $p < 0.0001$; $F_{\text{simple}} = 0.987$) (figure 2*b*). Complex teeth are thus largely distinct from but more limited than simple teeth, even without *a priori* classification of their complexity. Through the addition of cusps, complex teeth may be able to intrinsically generate a greater diversity of cusp shapes because of their increased complexity. We find that complex species, which can have teeth with two or three cusps, have 3.7× greater disparity in the shapes of tooth cusps than simple species ($p < 0.001$) (figures 2c and 3a). The cusp shapes of complex teeth have nearly no overlap with simple cusps (JS = 0.0038, $p < 0.0001$) and occupy an almost entirely distinct multidimensional shape space ($F_{\text{complex}} = 0.996$, $p < 0.0001$) (figure 2*c*). While simple teeth are largely restricted to cone shapes, the addition of tooth cusps generates a remarkable range of cusp shapes.

Comparing the dental diversity of herbivores with that of non-herbivores yielded largely similar results. Herbivores have different dental characteristics from non-herbivores across all three axes of dental diversity (phylogenetic MANOVA; $P_{\text{dentition}} < 0.01$, $P_{\text{linear}} < 0.001$, $P_{\text{geometric}} < 0.005$) and they occupy a similar region of morphospace to species with complex teeth (electronic supplementary material, figure S3b–d). Disparity followed a similar pattern; herbivores have greater disparity for the geometric morphometric (3.38×, $p < 0.001$) and linear morphometric (1.16×, $p = 0.5$) datasets, but non-herbivores have greater disparity of dentition traits (1.6×, $p = 0.069$).

Disparity-through-time (DTT) analyses indicate positive but non-significant morphological disparity index (MDI) values and an increase in disparity above the expectations under Brownian motion (above 95% CI) beginning approximately 3 Ma for all three axes of dental diversity ($\text{MDI}_{\text{dentition}} = 0.056$, $\text{MDI}_{\text{linear}} = 0.161$, $p = 0.997$; $p = 0.691$; $\text{MDI}_{\text{geometric}} = 0.074$, $p = 0.867$) (figure 2*d*–f). However, we acknowledge that these increases in disparity near the present could also be caused by measurement error or incomplete sampling. This rise coincides with the proportional increase of complex lineages, herbivores and lower trophic level feeding in the lake (figure 1*b*–*d*). During this time, the principal clades with complex teeth (*Tropheus* and *Petrochromis*) experienced rapid speciation and parallel evolution of ecomorphologies [34,52]. These results suggest that the rise of lineages with complex teeth may have been a significant generator of dental novelty compared with when the radiation contained primarily species with simple teeth.

(c) The tempo of dental evolution

We employed multiple approaches, including branch-specific [53], state-dependent [46] and OU [54] models, to characterize differences in the tempo and mode of multivariate dental evolution between species with simple and complex teeth. Lineages with complex teeth have faster rates of morphological evolution across all three axes of dental diversity, a congruent trend across models (figure 3*a*). Under a single-rate BM model, evolutionary rates are 1.04× (dentition, $p = 0.8$), 1.57× (linear morphometrics, $p < 0.05$) and 4.8× (geometric morphometrics, $p < 0.001$) faster for lineages with complex teeth. When including only linear morphometrics of tooth cusps, we find that species with complex teeth have 1.55× faster rates of cusp shape evolution ($p < 0.05$), which agrees with our geometric morphometric analysis of cusp shape. We find a similar pattern when comparing herbivores with non-herbivores: rates are 1.34× (linear morphometrics, $p < 0.001$), 1.33× (dentition, $p = 0.09$) and 3.35× (geometric morphometrics, $p < 0.001$) faster for herbivorous species. Tip rates, which are estimated under a model that allows for rate variation both across branches and through time, are 1.32× (dentition, phylogenetic analysis of variance [p-ANOVA]; $p = 0.2$), 1.28× (linear morphometrics, p-ANOVA; $p = 0.6$) and 4.91× (geometric morphometrics, p-ANOVA; $p < 0.001$) faster for

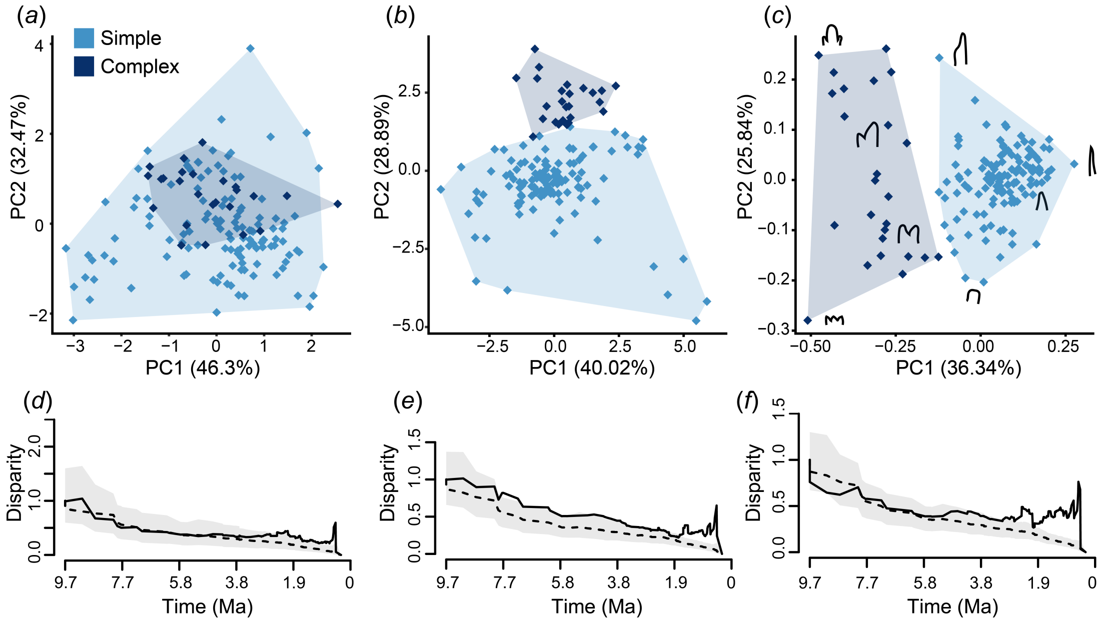

Figure 2. The dental diversity of LT cichlids. Principal component biplots of the (*a*) dentition, (*b*) linear morphometricand (*c*) geometric morphometric datasets. Representative cusp shapes are included in (*c*). Species with simple teeth are light blue and species with complex teeth are dark blue. Morphological disparity-through-time (DTT) plots for the (*d*) dentition, (*e*) linear morphometric, and (*f*) geometric morphometric datasets. The grey areas represent the 95% confidence intervals, the dotted lines the expectations under Brownian motion and the solid black lines the observed data.

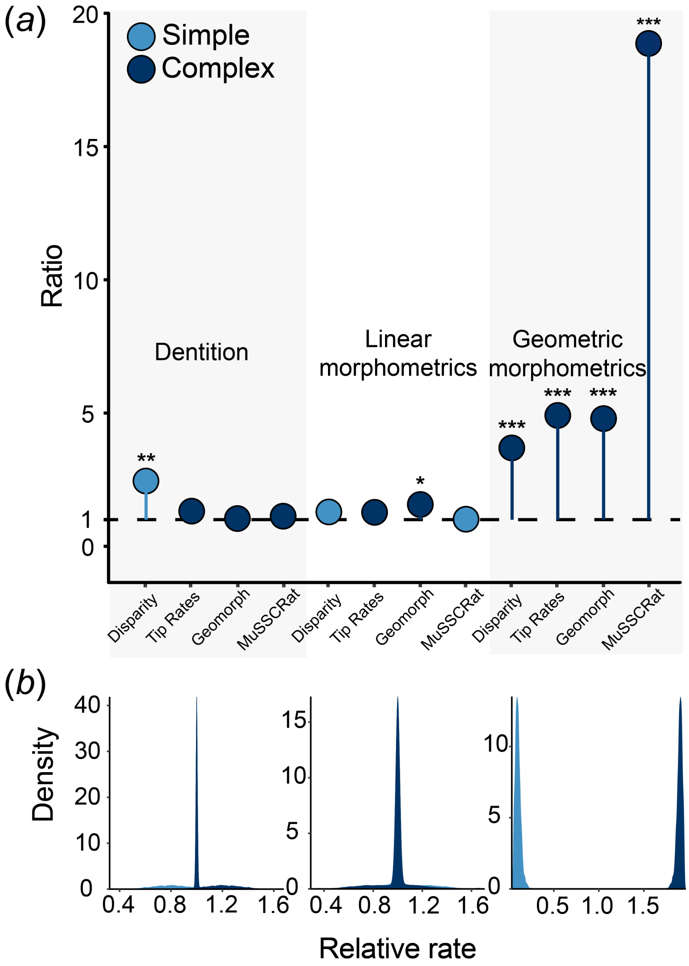

Figure 3. The tempo and mode of dental evolution in cichlid species with simple and complex teeth. (*a*) Ratios of morphological disparity and rates between species with simple (light blue) and complex (dark blue) teeth, for each dataset (dentition, linear morphometrics, geometric morphometrics). For each comparison, the group with a ratio >1 is shown. (*b*) Posterior distribution of multivariate relative rates estimated using the MuSSCRat model in RevBayes between species with simple and complex teeth for the dentition (left), linear morphometric (middle) and geometric morphometric (right) datasets. Relative rates for the dentition and linear morphometric datasets almost completely overlap. Significance levels: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

lineages with complex teeth (figure 3*a*). When accounting for rate variation independent of the observed character using the multiple state-specific rates of continuous character evolution (MuSSCRat) [46] model in RevBayes, we found that only rates of geometric cusp shape evolution are state-dependent (posterior probability [PP] = 1), with complex lineages having 18.8× higher relative rates (figure 3*a,b*). Rates of evolution of dentition (PP = 0.311) and linear morphometric traits (PP = 0.263) are not state-dependent, and estimated relative rates largely overlap (figure 3*b*), indicating that the evolution of many aspects of the dental system does not depend strictly on whether teeth are simple or complex under a BM model. Branches with transitions to complex teeth were often associated with high rates of evolution, including at the base of the Tropheini and leading to all four independent origins within LT, and rates across the tree increase following the rise of complex lineages in the lake at approximately 3 Ma (electronic supplementary material, figure S4).

We fit and compared several OU models of adaptive evolution in the R package mvMorph [49,54] to test whether the dental systems of simple and complex species are evolving towards distinct adaptive peaks. OU models with separate adaptive optima (θ) for lineages with simple and complex teeth had strong support when fit to the dentition (OUM; ΔAIC = 18.66; table 1) and linear morphometrics (OUM; ΔAIC = 82.08; table 2) datasets, but a BM model with distinct rates for simple and complex lineages best describes the evolution of geometric cusp shapes (BMM; ΔAIC = 16.24; table 3). We estimated trait optima for OUM models, averaged across 100 fitted models by their Akaike weights. Optimal complex dentitions comprised more equally sized teeth, reflecting homodonty, and many inner tooth rows (figure 4*a*). Teeth are taller, with more elongated bases, and have cusps that are broad and blunt, with a higher cross-sectional aspect ratio and a lower amount of enameloid-covered surface (figure 4*b*). These evolutionary optima are similar to the observed trait values of *Tropheus*. Optimal values for tooth number and curvature are similar between groups (figure 4*a,b*). These results indicate that lineages with simple and complex teeth are evolving towards distinct evolutionary optima for many traits within their dental system, which may reflect adaptive evolution of the dental system in response to ecological pressures.

(d) Integration

Directional morphological change may result from selection driving strong evolutionary integration between traits [55,56]. We evaluated the levels of evolutionary covariation within the dental system between simple and complex species by quantifying the strength of evolutionary integration between dental traits. The strength of covariation between traits varied greatly within both simple and complex species. While the range of *r-pls* values was similar between groups ($\text{range}_{\text{complex}} = 0.8224$, $\text{range}_{\text{simple}} = 0.8072$), the highest values were found in complex species, and the mean strength of integration between all pairwise trait combinations ($n = 95$) is 1.5× greater within species with complex teeth (ANOVA: $F = 12.6$, $p < 0.0005$) (figure 4*c*). Mean *r-pls* values were 0.295 for species with complex teeth and 0.196 for species with simple teeth. When only considering trait combinations for which there is a significant difference in the strength of integration between groups (pairwise p-value<0.05, $n = 19$ comparisons), integration was 1.8× greater within species with complex teeth ($r\text{-}pls_{\text{complex}} = 0.419$, $r\text{-}pls_{\text{simple}} = 0.229$; ANOVA: $F = 8.017$, $p < 0.01$) (figure 4*c*).

5. Discussion

Evolutionary innovations are often seen to promote expansion into new ecological niches or habitats [1,2]. By doing so, innovations can have varied effects on the evolution of form and function by subjecting species to novel ecological and evolutionary forces associated with ecological opportunity [6,10–12,18,57]. Here, we highlight the myriad of effects that the evolution of complex teeth has on the fish dental system, driven by both intrinsic properties of the innovation and extrinsic properties of the environment. Complex teeth facilitated the successful secondary colonization of and subsequent radiation within LT by the Tropheini by opening opportunity in low trophic level niches. Using a comprehensive toolkit of phylogenetic comparative methods, we show that complex teeth brought species into novel but restricted morphospace regions while accelerating diversification along a new axis. These novel diversification patterns, imposed by the functional demands of herbivory, probably broke barriers of competitive exclusion to facilitate diversification within herbivory but not beyond it. Our results suggest that innovations can be an important catalyst of morphological change, but their effect is determined by both intrinsic properties, such as how the innovation is accommodated within the functional system, and the extrinsic ecological context.

(a) The ecological context of Lake Tanganyika

Adaptive radiations may often unfold in stages, a pattern that leads to depleted ecological opportunity through time [34,58,59]. This could establish barriers to secondary colonization by requiring adaptive traits for unexploited resources. Our results show that during the initial radiation in LT, lineages lacked an ecologically versatile dental innovation that enables diet transitions to herbivory and omnivory [28]. As a result, higher trophic level niches were occupied first (figure 1*b,c*; electronic supplementary material, figure S3a), which left opportunity available at low trophic levels. Moreover, there are few non-cichlid herbivores in LT, which are largely limited to river mouths (e.g. *Labeo*) [60]. Following the evolution of complex teeth in rivers, this novelty was introduced to LT with the arrival of the Tropheini and rapidly increased in frequency as this lineage expanded (figure 1*b*) to become the dominant lineage in shallow-water environments. Our findings suggest that complex teeth allowed lineages to overcome barriers of competitive exclusion and biotic filtering [22–24], as these species overlap little with incumbent lineages in morphospace (figure 2*a*–c). In contrast, species with simple teeth repeatedly evolved dentitions with more extreme tooth sizes,

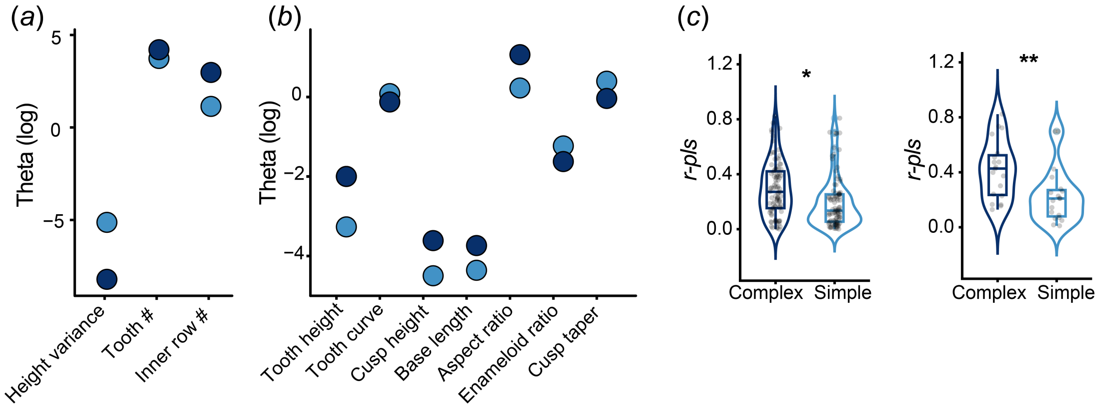

Figure 4. Coordinated directional evolution of lineages with complex teeth. Optimal trait values (theta) for (*a*) dentition and (*b*) linear morphometric traits estimated under an OUM model in mvMorph. All traits were log-transformed before estimation. Colours represent simple (light blue) and complex (dark blue) species. (*c*) Violin plots comparing the strength of integration (*r-pls*) between species with simple and complex teeth for all pairwise trait combinations ($n = 95$, left) and only comparisons for which the difference in integration between groups was significant ($n = 19$, right). Significance levels: $p < 0.05$ (*), $p < 0.01$ (**).

Table 1. Comparison of mvMorph trait evolution models fit to the dentition dataset. The AIC range reports the lower and upper limits of the range. The proportion preferred reports the proportion of stochastic character maps for which that model had the lowest AIC.

model	parameters	AIC	AIC range	ΔAIC	proportion preferred
BM1	single σ^2	799.8123	NA	39.2632	—
BMM	multiple σ^2	795.6558	787.8328, 804.1055	35.1067	—
OU1	single θ	779.2126	NA	18.6635	—
OUM	multiple θ	760.5491	755.806, 767.1262	0	1.0

Table 2. Comparison of mvMorph trait evolution models fit to the linear morphometrics dataset. The AIC range reports the lower and upper limits of the range. The proportion preferred reports the proportion of stochastic character maps for which that model had the lowest AIC.

model	parameters	AIC	AIC range	ΔAIC	proportion preferred
BM1	single σ^2	−1050.681	NA	212.941	–
BMM	multiple σ^2	−1113.692	−1228.355, −1020.606	149.93	0.04
OU1	single θ	−1181.544	NA	82.078	–
OUM	multiple θ	−1263.622	−1272.119, −1211.329	0	0.96

Table 3. Comparison of mvMorph trait evolution models fit to the geometric morphometrics dataset. The AIC range reports the lower and upper limits of the range. The proportion preferred reports the proportion of stochastic character maps for which that model had the lowest AIC.

model	parameters	AIC	AIC range	ΔAIC	proportion preferred
BM1	single σ^2	−895.5905	NA	261.7735	–
BMM	multiple σ^2	−1157.364	−1186.088, −975.9417	0	0.64
OU1	single θ	−956.5445	NA	200.8195	–
OUM	multiple θ	−1141.126	−1157.489, −1080.739	16.238	0.36

numbers or variation in tooth size (figure 2*a*,*b*) that meet the demands of other ecological niches (e.g. large slender fangs in *Bathybates*, a piscivore). These specialized morphologies for non-herbivorous niches, which probably existed during the early diversification of the Tropheini, may have limited further ecological diversification of complex lineages despite complex teeth being ecologically versatile.

The ancestors of the Tropheini are not the only secondary colonizers of LT with complex teeth. *Oreochromis tanganicae* (Oreochromini) and *Coptodon rendalli* (Coptodonini) are two herbivorous tilapiine cichlids that secondarily colonized LT, while *O. niloticus* maintains a small population in marginal habitats but has not colonized the lacustrine zone [34,61,62]. Despite these species having complex teeth, their young age suggests considerable overlap with the established Tropheini, which dominate shallow-water herbivorous niches and probably stymied intralacustrine diversification. These contrasting diversification patterns highlight the importance of ecological context in determining the outcome of innovation.

(b) Complex teeth and herbivory

Complex teeth with multiple cusps are an adaptation for herbivory across vertebrates [26–28]. In fishes, the multiple-angled cusps of complex teeth may be beneficial when cropping or scraping algae or removing loose food items from an algal matrix. Herbivory was an open niche during the early history of LT, and the majority of current herbivores are found within the Tropheini (figure 1*b*,*c*). Herbivores occupy similar dental morphospace to species with complex teeth (figure 2*a*–c; electronic supplementary material, figure S3b–d) and comparisons of disparity, dental traits and evolutionary rates between herbivores and non-herbivores mirror comparisons between species with simple and complex teeth. Moreover, 84% (21/15 species) of species with complex teeth in our study are herbivorous, indicating a tight association between complex teeth and herbivory in LT. Herbivorous fishes may be under strong selection owing to the constraints and requirements to feed on plant material. These functional demands have led to herbivores evolving similar morphologies, such as larger teeth and shorter, more robust jaws, which often occupy novel morphospace regions [63–68]. Our results show that species with complex teeth have a more integrated dental system (figure 4*c*), occupy unique, often extreme regions of dental morphospace (figure 2*b*,*c*) and are evolving towards distinct optimal trait values (figure 4*a*,*b*). High integration is known to generate more extreme trait combinations as a result of strong selection for ecological performance, promoting expansion into unexplored regions of morphospace [69]. Together, these results suggest that the functional demands of herbivory drive coordinated change in the dental system in fishes [63] (electronic supplementary material, figure S3b–d). Although herbivores have a restricted niche breadth, they often have the highest rates of morphological evolution [70,71], a pattern supported by our results. By enabling transitions to available low trophic level niches, complex teeth subjected the dental system to new demands, leading to coordinated and accelerated change (figures 1*c*,*d*, 2*a-c* and 4*a*,*b*).

Our results suggest that tooth complexity alone is not sufficient for specialized herbivory. Indeed, many adaptive changes in feeding morphology coincide with macroevolutionary transitions to herbivory in fishes [68,72,73]. In the dental system, a change in the aspect ratio of the cusp and height of teeth, an increase in the number of inner tooth rows and a reduction in the variance in tooth height are also necessary when transitioning to a primarily herbivorous diet (figure 4*a*,*b*). Complex lineages that are not herbivorous are omnivorous or have evolved further feeding adaptations while retaining a complex dentition (e.g. hypertrophied lips in *Lobochilotes labiatus*). Given its functional demands and specialized morphology, herbivory may often be absent during the onset of radiations [67,71], leaving ecological opportunity open in low-level niches for new lineages to exploit.

(c) Innovations shape phenotypic evolution.

The occupation of new ecological zones is fundamental to understanding how innovations influence macroevolution [1–3]. By introducing new functional demands associated with niche performance or increasing the amount of accessible phenotypic space, innovations can shape the trajectory and pace of morphological change [16,17]. Our results demonstrate that the trajectory of dental diversification following the evolution of complex teeth was shaped by both intrinsic and extrinsic factors. Complex teeth brought cichlids into herbivorous niches, which placed new functional demands on their dental system that accelerated evolution to unique morphospace regions (figures 2*a*–c; 3*a*). However, the limited ecological opportunity outside herbivory probably restricted further diversification of morphology and ecology. By opening a new axis to diversify along through the addition of tooth cusps, complex teeth could generate more diverse interactions with food items [30]. These diverse cusp shapes probably increased opportunities for niche partitioning within herbivory, enabling diversification within but not between ecological niches [74–76]. These varied outcomes highlight the interplay of intrinsic and extrinsic factors operating on the dental system following the evolution of complex teeth.

Appraising whether innovations have largely intrinsic or extrinsic effects can provide insight into their expected impacts on morphology. Intrinsic innovations expand the achievable phenotypic space by promoting major structural or mechanical reorganization [16], which often triggers pulses of accelerated change. For example, change to melanosome morphology in African starlings (Sturnidae) [10], modification to chromatin structure in eukaryotes [13,77], the intramandibular joint and mobile premaxilla of coral reef fish [4,11,14,78] and the latch-spring mechanism of trap-jaw ants [15] all enabled diversification of new forms. When combined with sufficient ecological opportunity and a broad adaptive landscape, these intrinsic innovations may promote diversification of the organismal system in which they are contained. Alternatively, other innovations primarily bring lineages into new ecological zones where extrinsic factors determine the trajectory of morphological change, and the innovation itself does not diversify. Antifreeze proteins allowed icefishes (Notothenioidei) to move into extreme thermal environments [79,80], but high ecological opportunity promoted their diversification [81,82]. Adhesive toepads limit morphological diversification in lizards because arboreal habitats introduce new constraints on morphology [83–85]; the secondary loss of toepads accelerates diversification of locomotory traits [19]. These innovations subject existing functional systems to new demands and may only function in a narrow range of parameter space. In these cases, extrinsic niche requirements or environmental conditions determine how morphology diversifies further. Distinguishing between the intrinsic and extrinsic effects of innovations, while appreciating the interaction between them, should be an emphasis for future studies that address how innovations have shaped morphological diversification across phylogenetic scales.

6. Conclusion

Our results suggest that by exposing lineages to new evolutionary and ecological pressures associated with herbivory, the evolution of complex teeth drove diversification of the cichlid dental system to novel but restricted regions of morphospace. The complex evolutionary dynamics of the dental system following the evolution of complex teeth was thus shaped by both intrinsic and extrinsic factors. Despite these varied impacts on morphology, complex teeth were a crucial innovation for the secondary incursion of riverine lineages into LT and subsequent diversification of the Tropheini in shallow-water, algal-rich habitats by breaking barriers of competitive exclusion. Innovations can have profound effects on the trajectory and pace of morphological change, the directionality of which is determined by properties of both the innovation and the new ecological zone. Understanding the interaction of these factors provides insight into why the outcome of innovation is varied and highlights the macroevolutionary diversity of innovations themselves.

Ethics. Euthanasia of specimens acquired from the aquarium trade was carried out in accordance with the University of California, Davis Institutional Animal Care and Use Committee, protocol numbers 22206 and 23818.

Data accessibility. Data generated during this study can be accessed on Dryad [86].

Supplementary material is available online [87].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors’ contributions. N.P.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; P.C.W.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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