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Cite this article: Avery TM, Dial TR, Matthews DG. 2026 Phenotypic plasticity drives local adaptation by disrupting a genetically integrated jaw apparatus in Trinidadian guppies. *Proc. R. Soc. B* **293**: 20252590.
https://doi.org/10.1098/rspb.2025.2590

Received: 7 October 2025
Accepted: 3 February 2026

Subject Category:
Evolution

Subject Areas:
evolution, biomechanics, ecology

Keywords:
integration, modularity, morphology, trophic adaptation, craniofacial, benthic-limnetic, Trinidadian guppies, fish

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8342197.

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Phenotypic plasticity drives local adaptation by disrupting a genetically integrated jaw apparatus in Trinidadian guppies

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Consistently across clades, researchers find a high degree of covariation in the shape of disparate elements within the same individual, a pattern known as morphological integration. Although integration can help to maintain functionality of multi-component systems, it can also constrain long-term evolution. On shorter time scales, morphology is often shaped by plastic environmental responses; however, it remains an open question whether plasticity is constrained by the same forces that shape patterns of morphological integration over longer evolutionary time scales. Here, we ask whether an incipient adaptive trophic divergence among Trinidadian guppies displays similar patterns of covariation between benthic and limnetic populations that are either reared in a common lab environment or sampled from wild populations. We perform geometric morphometric analysis (n = 83) on the premaxilla, dentary, anguloarticular and lower pharyngeal jaw, and find that morphology correlates with trophic niche in both lab-reared and wild-caught fish. Furthermore, we find that integration among these bones is significantly stronger in lab-reared fish (absence of environmental differences), while their shapes vary independently in wild-caught individuals. This suggests that phenotypic plasticity may allow organisms to explore novel morphospace as they locally adapt but does so at the expense of maintaining a highly integrated feeding apparatus.

1. Introduction

The development and evolution of organismal form are the result of a complex interplay between genetics and the environment [1]. Morphology is guided by a genetic blueprint, but ultimately phenotype is tied to the environmental context in which it is expressed through phenotypic plasticity. Among functional traits, these forces need to balance such that each trait can continue to perform its role [2], particularly when there are multiple elements comprising a larger functional unit. This is particularly true in the early stages of adaptive evolution, such as the morphological response in feeding structures when a population encounters a new trophic niche (as in [3–5]). As certain morphological elements respond to the new functional demands, first through plasticity (phenotypic response to environment) and then through adaptive evolution (genetic changes), it is imperative that the rest of the organism changes accordingly to maintain both feeding- and non-feeding-related functions.

One way that adaptation can be achieved while maintaining functionality is by organizing individual elements into modules: sets of components

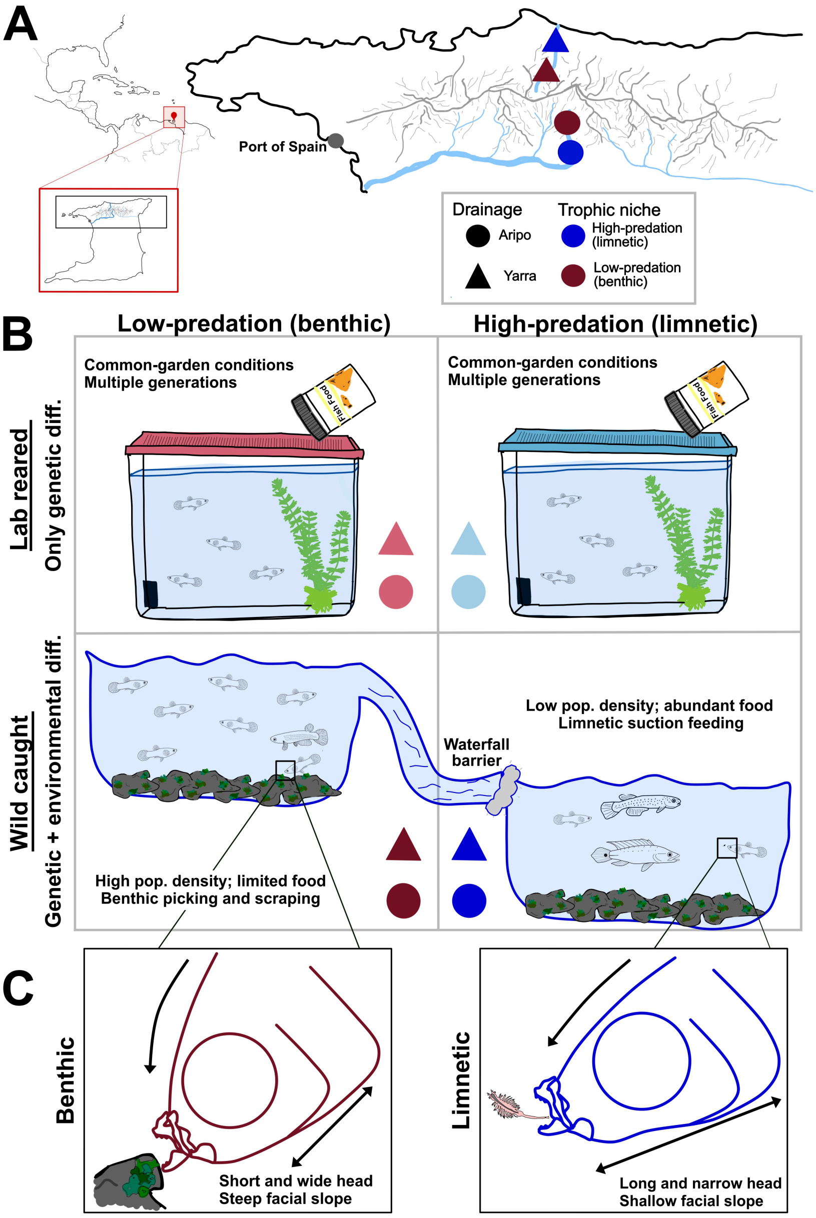

Figure 1. Guppies were collected from high-predation (limnetic) environments (blue) and low-predation (benthic) environments (red) within the Aripo (circles) and Yarra (triangles) rivers in Trinidad. (A) A map of the mountains in northern Trinidad showing the collection sites for specimens used in this study. (B) Juvenile guppies in high-predation environments are preyed upon by several species of fishes, resulting in low guppy population densities and allowing the remaining fish to feed limnetically on high-quality invertebrate prey from the open water column. Low-predation populations in the wild are only subject to predation pressures from the killifish (*Rivulus*) during the juvenile stage, resulting in high population densities and low food availability. Therefore, low-predation guppies have benthic diets consisting primarily of detritus and algae that they must scrape and pick from the bottom. This study utilizes a 2 × 2 experimental design in which fish from both limnetic (blue) and benthic (red) populations are raised either in a common-garden environment (light palette) or in the wild (dark palette). (C) Guppies feeding on the benthos have evolved shorter, wider and steeper heads, while those feeding in a limnetic manner have longer, narrower heads with a more shallow facial profile [44].

that are more phenotypically integrated (covaried) with each other than with other surrounding elements [6,7]. This can be achieved through several mechanisms including overlapping genetic control of elements, shared plastic responses to the same environmental stimulus or through common responses to selection over evolutionary time [6,8]. Each of these results in a measurable covariance structure across disparate morphological elements; by measuring this covariance in the context of a specific experimental design, we can then differentiate between the potential mechanisms [7]. For instance, hybrid crosses between two species that are raised in a common environment are unlikely to show covariation networks attributable to selection or plasticity, so any patterns found therein are likely due to genetically derived commonalities [9].

Regardless of the mechanism, if one part of a functional unit undergoes morphological evolution, then it is more likely to maintain or improve its function if it is integrated with the other elements in the unit [10–14]. For example, the function of mammalian jaws relies on the precise integration of upper and lower teeth for effective occlusion and mastication [15]. Indeed, morphological integration has been shown to be a pervasive and important facet of evolution across the animal kingdom, from the aforementioned mammal jaws, to fish pectoral fins [16], to the powerful raptorial appendages of mantis shrimp [17]. Yet this very blessing can also act as a curse, as morphological integration constrains evolutionary lability within a given module by limiting the available morphospace that a clade can explore [18–30]. While this is not always the case, examples of morphological integration driving novelty remain relatively rare and generally occur over longer evolutionary time scales or across phenotypic modules [24,31–34].

Even when integration acts as a constraint, phenotypic plasticity in response to environmental changes might not face the same constraints and therefore might represent an opportunity to escape this constraint. Yet for plastic responses to have evolutionary relevance, they must have a genetic basis and ultimately become canalized in development [35–40]. Indeed, there is evidence that DNA methylation, gene expression and the loci controlling craniofacial morphology change when animals are raised in a different environment [41–43]. Therefore, if the underlying genetic architecture of a functional unit is responsible for evolutionary constraint due to integration, plasticity driven by a different genomic region might not face the same constraints.

To investigate morphological integration as well as potential constraints in plastically and genetically derived morphological variation, we turn to a model system that exhibits repeatable and parallel patterns of local adaptation to divergent trophic and synecological environments [44]. Populations of Trinidadian guppies (*Poecilia reticulata*) were first established across several river drainages in the northern mountain range of Trinidad about 10 000 years ago [45] (figure 1A). As the guppies expanded in their new range, some populations were able to cross natural barriers in the streams such as waterfalls, partially isolating these populations of upstream guppies from their progenitor downstream populations. Predators such as the pike cichlid (*Crenicichla alta*) and wolfish (*Hoplias malabaricus*) were unable to establish populations above the barriers, leading to the formation of two distinct environments with highly divergent selective pressures: upstream (low-predation) environments compared with those downstream (high-predation) [45–52]. Guppies in these two trophic niches have since diverged in a wide range of traits including coloration, body size, gestation period, clutch size and other life-history traits [51,53–59].

In addition to these changes in the guppies themselves, the entire ecology of the streams has been affected by this difference in predation levels [60,61] (figure 1B,C). Due to high population densities in the absence of predators, the low-predation guppies have caused a crash in the populations of their primary food source, aquatic invertebrates [62–64]. This then has the effect of increasing trophic competition between these guppies and forcing them to diversify their diets to include benthic algae and detritus [46,57]. These differences in diet mirror the well-studied benthic-limnetic adaptive divergence seen in other species of fish (e.g. [65–68]) since low-predation guppies scrape attached algae and detritus off the benthos, while high-predation guppies primarily forage on unattached limnetic prey [46]. The differences in the mechanical demands for each of these feeding methods have then driven divergent evolution of craniofacial morphology between these populations [44] (figure 1C). Specifically, overall head shape has repeatedly shifted from more elongate and narrow in limnetic (high-predation) populations to more steep, wide and shortened craniofacial profiles in benthic (low-predation) populations. Head shape differences are due to both genetic and environmental disparity, with the plastic response accentuating the divergence genetically encoded in the base developmental plan. But what of the individual elements that make up the skull; are they able to acclimate and evolve independently or is their adaptive response governed by patterns of covariation across the skull?

We expand on Trinidadian guppies as a model system to investigate patterns of evolution and morphological integration among several highly functionally relevant bones in their feeding apparatus. Through geometric morphometric analysis of the oral and pharyngeal jaws of lab-reared guppies descended from both benthic and limnetic populations, we first ask whether these elements have undergone genetic evolution in response to the novel trophic environment experienced by benthic (upstream) guppies. These lab-reared guppies are raised under the same conditions, meaning that any observed morphological differences between populations are attributable to the genetic portion of development. We then compare these results to morphometric data from wild-caught fish that were raised in their respective natural environments where their development was additionally shaped by local phenotypic plasticity. Finally, to understand the interplay of integration and plasticity, we ask whether bones in lab-reared fish show different patterns of integration compared with wild-caught specimens. We hypothesize that: (i) jaw morphology among lab-reared individuals will show signatures of adaptation to the respective benthic and limnetic environments (genetic influence), (ii) morphological divergence between benthic and limnetic populations will be greater among the wild-caught fish who are subject to natural selection and divergent environments (both genetic and plastic influence), and (iii) the influence of plasticity will increase the degree of morphological covariation among wild-caught guppies compared with lab-reared ones due to shared functional demands within each environment. By comparing morphological divergence and integration within the two rearing conditions, lab-reared (differences attributed to genetic divergence) and wild-caught (disparities due to both genetics and environmentally induced plasticity), we are able to gain novel insights into the developmental covariation networks that constrain or allow adaptive evolution in new environments.

2. Methods

(a) Specimen collection, husbandry and micro-computer tomography (CT) scanning

We collected adult guppies from two independent river drainage systems in the mountains of northern Trinidad in spring 2013 and spring 2014. Guppy specimens were collected along the southern slope from the Aripo river drainage and along the northern slope in the Yarra river drainage (figure 1A). These two drainages are commonly used as evolutionary replicates in guppy studies, where the same adaptive patterns occur despite minor ecological differences [69]. Within each drainage we collected both limnetic and benthic guppy specimens (figure 1B,C). Some of the fish were immediately sacrificed to represent the wild-caught morphology (n = 33 Aripo and n = 18 Yarra). We exported the rest of the live fish with the permission of the Fisheries Division of the Ministry of Agriculture, Land and Fisheries, Republic of Trinidad and Tobago. These fish were brought into the United States with a valid U.S. Fish and Wildlife Service Declaration of Importation permit (USFWS Form 3-177) and housed at Brown University in a manner approved by the Institutional Animal Care and Use Committee at Brown University

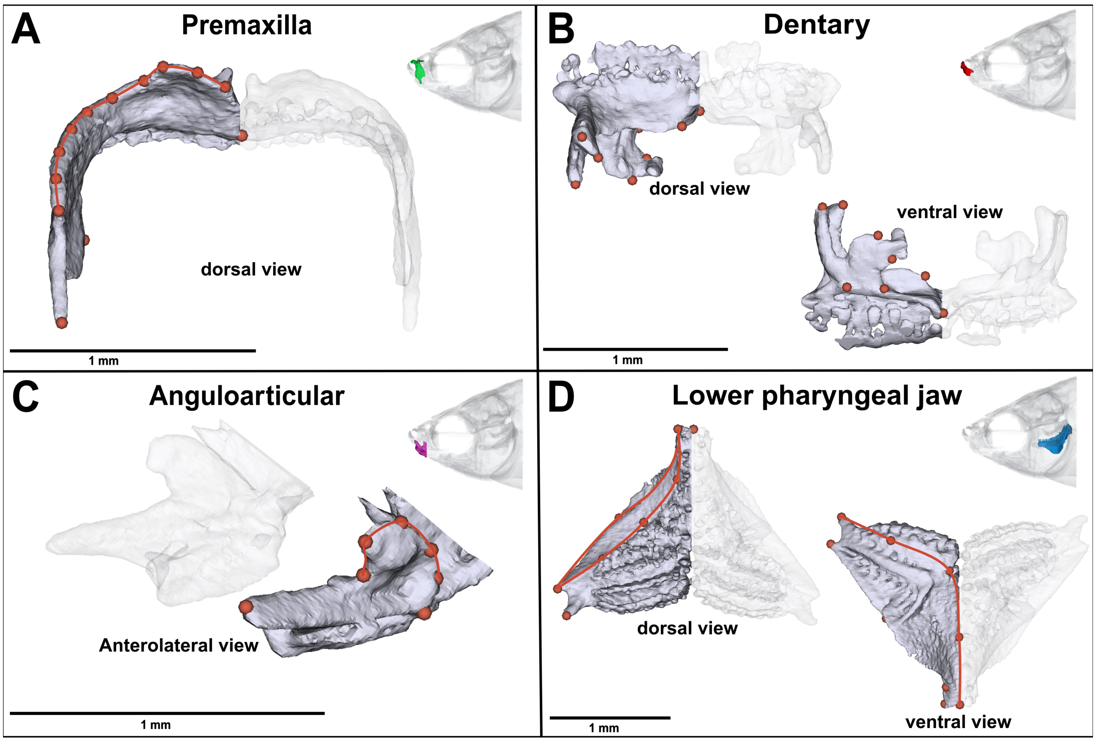

Figure 2. Fixed landmarks and semilandmarks used for each of the bones in this study. Standalone landmarks and those at the ends of lines are fixed landmarks, all other points lying along the line are semilandmarks. We placed a total of (A) 13 landmarks on each premaxilla (five fixed landmarks and eight sliding semilandmarks), (B) 10 landmarks on the dentary, all of which were fixed landmarks, (C) seven landmarks on the anguloarticular (four fixed landmarks and three sliding semilandmarks and (D) 12 landmarks on the lower pharyngeal jaw (five fixed landmarks and seven sliding semilandmarks).

(protocol: 1211035 to E.L. Brainerd). These fish were reared for at least two generations in identical conditions with all groups of lab-reared fish being fed the same mixed diet (newly hatched Artemia, Repashy Community Crave gel, Omega one flakes, Daphnia and Daro worms; figure 1B). After two generations, any morphological divergence between these groups of lab-reared guppies will therefore be the result of genetic differences between populations and not due to different environmental effects. Further details about collection and rearing conditions are available in Matthews *et al*. (2024) [44] as the same specimens are used in each study.

After sacrificing the lab-reared fish (n = 32), we used micro-computed tomography (micro-CT) (Bruker SkyScan 1173, Kontich, Belgium) to scan each individual (n = 83 total specimens), rendering images with isotropic resolution ranging from 6.8 to 9.0 μm. We reconstructed these X-ray images into image stacks using NRecon (Brucker, Kontich, Belgium).

(b) Segmentation and landmarking

We loaded CT scan image stacks into Mimics (v. 22.0, Materialise NV, Leuven, Belgium) to isolate each individual specimen from the scan. Each specimen was then further segmented to extract three-dimensional models of the lower pharyngeal jaw as well as three bones in the oral jaws: the premaxilla, dentary and anguloarticular (electronic supplementary material, figure S1). Although the dentary and anguloarticular are both parts of the mandible and are often fused in fish, we separate them in this study because they are articulated in guppies at the intramandibular joint and are therefore functionally independent of one another. To characterize the shapes of the oral and pharyngeal jaw bones, we placed both fixed landmarks and sliding semilandmarks on the three-dimensional models of the jaw bones using the three-dimensional Slicer software (v. 5.2.2) [70] (figure 2). We based the location of these landmarks off similar analyses of feeding morphology of cichlids [9,71], modified to best suit the available homologous points in guppies. To avoid capturing asymmetries within individuals, we only digitized the left side and the midline of the bones. However, in cases where the left side was distorted or otherwise damaged, we placed landmarks on the right side of the head and mirrored the points to achieve comparable landmarks.

(c) Geometric morphometrics and data analysis

We performed a geometric morphometric analysis on these landmarks to compare bone shapes between different trophic niches (limnetic versus benthic), river drainages (Aripo versus Yarra) and rearing conditions (wild caught versus lab reared). We separately analysed lab-reared and wild-caught specimens, where differences in lab-reared fish are assumed to be genetic and any additional divergence among wild-caught specimens is plastic. First, we conducted a generalized procrustes analysis using bending energy on each population in the R package geomorph (v. 4.0.4) [72,73]. Bending energy does not assume the independence of points but simultaneously deforms points in close proximity when calculating the mean shape of the group [74–76]. Next, we corrected the shape data for allometry using the residuals of shape regressed on centroid size, a measure of how much size scaling was done in the procrustes analysis that is used as a proxy for fish size [77,78]. This allometric correction allowed us to remove the variation in shape attributable to size for all the oral jaw bones (premaxilla, dentary and anguloarticular). Although there was an effect of size on the shape of the lower pharyngeal jaw, there were different allometric slopes depending on trophic niche. Therefore, for this analysis we do not correct for allometry in the lower pharyngeal jaw dataset and instead include centroid size as a covariate in the relevant statistical and shape results.

In order to understand the evolutionary factors influencing bone morphology, we regressed shape against trophic niche, drainage and the interaction between the two. The interaction effect was included for all models because drainage has a significant impact on the direction of trophic evolution in these fish [44]. We then grouped these results based on the rearing environment (lab reared versus wild caught) so we could determine the genetic and the genetic-plus-plastic effects, respectively. We used a principal component analysis (PCA) to visualize the shape variation in each bone from each rearing environment. Enclosed areas for each group (trophic niche and drainage) were created by circumscribing the most divergent data points from each population, representing the portion of morphospace that we observe this population occupying. For each bone, we created warped meshes using the function warpRefMesh (geomorph) of the theoretical shapes that correspond to the maximum and minimum values observed along principal component axis 1 and principal component axis 2 using the function picknplot.shape in geomorph. In figure 3, we note that the x-axis is mirrored in the premaxilla plot to better align with wild-caught shape space. We further display shape changes between ecologically divergent populations by calculating the mean shape of a given bone among Yarra benthic individuals, creating a warped mesh representing this shape using the warpRefMesh function in geomorph, and overlaying it on the same bone representing the mean shape among Yarra limnetic individuals. Within this plot, shape differences were magnified by two times to aid in visualizing the relevant shape variation.

To investigate the role of genetics and plasticity on the shape of jaw bones, we tested the morphological integration of individual jaw elements to each other using the 'integration.test' function in geomorph [72,73,79]. In order to include the lower pharyngeal jaw in the integration test, we corrected for its allometric effect using centroid size, population (limnetic versus benthic) and the interaction between the two. This interaction effect was included in the allometric model because size had a different effect on shape among limnetic and benthic populations. We first compared patterns of integration between lab-reared and wild-caught fish. Then, to test whether integration among lab-reared fish was driven by one genetic background more than the other, we compared patterns of integration between lab-reared fish descended from limnetic populations and lab-reared fish descended from benthic populations. In order to understand the degree of integration for each element, we calculated and visualized the average degree of integration (z-score) across all pairwise comparisons for each bone.

3. Results

(a) Lab-reared morphology

Due to the common-garden rearing of our lab-reared specimens, any observed morphological differences are likely due to genetic divergence. With this in mind, we found a significant effect (defined as $p < 0.05$) of trophic niche on the dentary shape, and marginally significant effect of trophic niche on premaxilla shape (defined as $p < 0.10$ to indicate compelling results that may not be fully supported due to the relatively small sample size within each population; table 1). However, there was not a significant effect of trophic niche on shape in the lower pharyngeal jaw or the anguloarticular. Instead, we found that the factor which explained the most variation in shape among lab-reared fish was the drainage, the river that a population was collected from (table 1). Specifically, the premaxilla, anguloarticular and lower pharyngeal jaw were all significantly different between drainages, and the dentary showed marginally significant differences between drainages. Within the dentary and the lower pharyngeal jaw, we also found that the effect of trophic niche on bone shape was dependent on the drainage that the fish were originally collected from. Altogether this suggests that trophic niche is driving genetic evolution within prey acquisition bones (premaxilla and dentary), but it does not appear to be the only force driving trophic evolution in these fish.

These results obtained through multivariate linear modelling can be more intuitively understood using PCA, which allows us to visualize the variation in the shapes of oral and pharyngeal jaw bones. The distance between any two points on the PCA graphs represents the degree of divergence in shape; nearby points have similar shapes, while more distant points are more dissimilar. It is also important to note that these graphical representations only display the two PC axes, which explain the most variation in shape. However, the statistical models account for all the variation across a higher-dimensional space, and therefore, it is possible for populations to be further diverged than they appear in the PCA plots.

Among lab-reared fish, we found that the shape of the dentary in benthic fish tended to be rostrocaudally shorter and more shallow along the dorsoventral axis compared with limnetic fish, though they are both similar in mediolateral width (figure 3). Limnetic dentaries were also slightly more mediolaterally concave compared with benthic bones. Conversely, premaxillae among benthic populations tend to be wider mediolaterally and longer rostrocaudally compared with limnetic specimens (figure 3). The degrees to which each of these trends holds was in part dependent on the drainage from which fish were sampled, but the direction of divergence in shape space was consistent between drainages.

(b) Wild-caught morphology

Wild-caught fish showed morphological divergence attributable to trophic niche in the shape of nearly all bones examined in this study (table 2). Interestingly, only the anguloarticular fails to show a strong, significant difference based on trophic niche. Drainage is still an important factor affecting the shape of these bones in wild-caught fish, being associated with shape changes

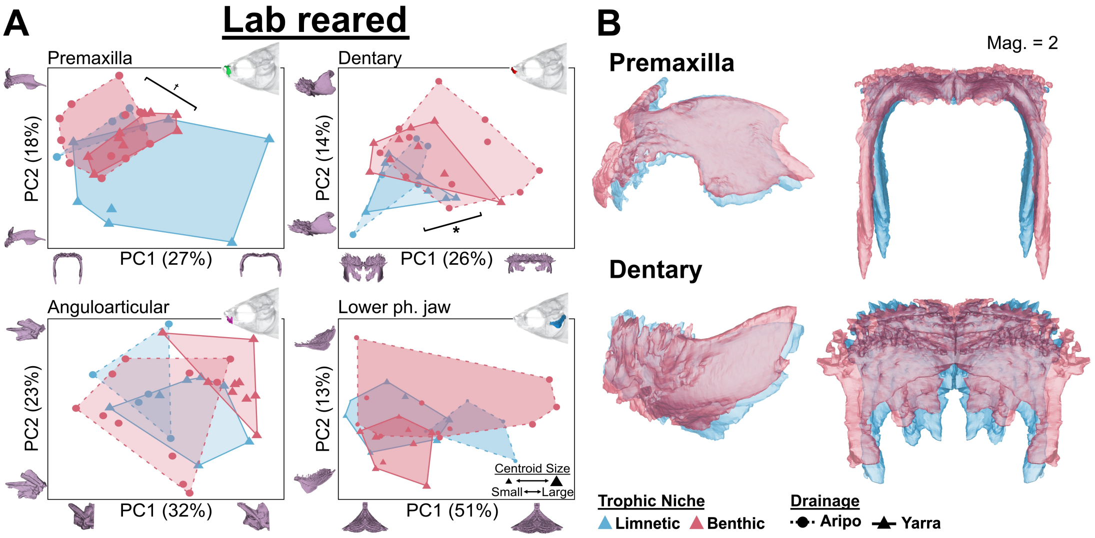

Figure 3. The premaxilla and the dentary displayed significant morphological divergence between fish descended from benthic and limnetic populations, even after being raised in an identical lab environment for several generations. (A) Principal component analysis reveals morphological divergences among lab-reared fish (n = 32) attributable to both drainage and trophic niche. The relative portion of total shape variance explained by each principal component (PC) axis is indicated on the axis in parentheses. Lower pharyngeal jaw shape was not corrected for allometry, so centroid size is indicated with the size of the data point. Models on the positive end of each axis represent the theoretical shape of a specimen that has the maximum score on that axis, and a score of zero on all other PC axes. (B) Blue bones are the theoretical mean shapes for lab-reared, benthic guppies whose ancestors were collected from the Yarra river drainage. Red bones are conversely the mean shape of lab-reared, limnetic fish descending from populations in the Yarra river drainage. Each bone is shown from a lateral (left) and a dorsoventral (right) view and a magnification of two is used to highlight shape differences. p-values are based on the statistical models presented in table 1. *$p < 0.05$, †$p < 0.10$.

Table 1. Statistical results of linear models explaining oral and pharyngeal jaw bone shape in lab-reared specimens. Models for each of the oral jaw bones are run on allometrically corrected data. Bold values are p-values less than 0.1.

lab-reared (n = 32)	trophic niche		drainage		drainage × trophic niche		centroid size		trophic niche × centroid size	
	z	p	z	p	z	p	z	p	z	p
premaxilla	1.47	**0.074**	1.85	**0.036**	1.25	0.105	—	—	—	—
dentary	2.04	**0.025**	1.58	**0.059**	1.68	**0.054**	—	—	—	—
anguloarticular	0.04	0.496	3.36	**<0.001**	0.62	0.282	—	—	—	—
lower pharyngeal jaw	0.47	0.322	3.45	**<0.001**	2.52	**0.003**	2.60	**0.006**	1.75	**0.047**

in the dentary, anguloarticular and lower pharyngeal jaw. Generally, the effect of trophic niche was not affected by drainage, with the possible exception of the lower pharyngeal jaw.

Mean premaxilla shape of benthic fish is mediolaterally narrow, rostrocaudally short and dorsoventrally shallow compared with limnetic fish (figure 4). The dentaries from wild-caught specimens also show a significant shape difference between limnetic and benthic populations. The average shape of the dentary in the benthic population is more mediolaterally wide and long along the rostrocaudal axis (figure 4). From a lateral view, benthic dentaries also show more dorsal curvature than limnetic ones. Finally, we found that trophic niche affected the shape of the lower pharyngeal jaws. This is mostly reflected in the fact that the lower pharyngeal jaws from benthic individuals are laterally narrower, rostrocaudally longer and less concave dorsoventrally (figure 4).

There was not a significant difference between the shape of the anguloarticular of a fish from a limnetic environment and a benthic environment, as evidenced by the nearly completely overlapping regions of shape space occupied by the two groups (figure 4A). We therefore do not present the mean anguloarticular shape of fish from each predation environment.

(c) Integration across the jaws

Every pairwise comparison of bones among lab-reared fish was found to be at least marginally significantly integrated ($p < 0.10$, table 3), despite the modest sample size of n = 32 lab-reared fish. Notably, all the strongest patterns of covariation are found in pairings with the anguloarticular, suggesting that this is driving much of the integration among lab-raised fish and that the other bones are less integrated with each other (table 3, figure 5, electronic supplementary material, table S1). Conversely, among wild-caught fish, the shape of each bone appears to vary more independently of the other bones. Within these fish, the only marginally significantly integrated pairs are the premaxilla-anguloarticular and the lower pharyngeal jaw-anguloarticular (table 3, figure 5, electronic supplementary material, table S1). All other comparisons show no signs of integration. Altogether, we find that there is a much lower degree of morphological integration among wild-caught fish than there is among lab-reared ones.

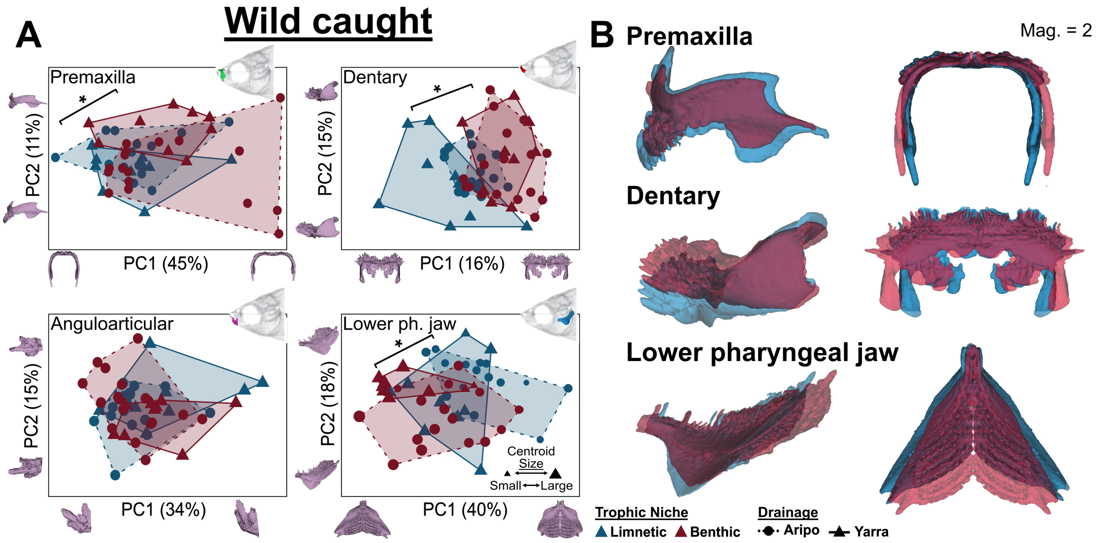

Figure 4. The premaxilla, dentary and the lower pharyngeal jaw displayed significant morphological divergence between fish collected from wild benthic and limnetic populations. (A) Principal component analysis reveals morphological divergences among wild-caught guppies ($n = 51$) attributable to both drainage and trophic niche. The relative portion of total shape variance explained by each principal component (PC) axis is indicated on the axis in parentheses. Lower pharyngeal jaw shape was not corrected for allometry, so centroid size is indicated with the size of the data point. Models on the positive end of each axis represent the theoretical shape of a specimen that has the maximum score on that axis, and a score of zero on all other PC axes. (B) Blue bones are the theoretical mean shapes for wild-caught, benthic fish collected from the Yarra river drainage. Red bones are conversely the mean shape of wild-caught, limnetic fish from the Yarra river drainage. Each bone is shown from a lateral (left) and a dorsoventral (right) view and a magnification of two is used to highlight shape differences. *p*-values are based on the statistical models presented in table 2. $^*p < 0.05$.

Table 2. Statistical results of linear models explaining oral and pharyngeal jaw bone shape in wild-caught specimens. Models for each of the oral jaw bones are run on allometrically corrected data. Bold values are *p*-values less than 0.1.

wild-caught ($n = 51$)	trophic niche		drainage		drainage × trophic niche		centroid size		trophic niche × centroid size	
	z	*p*	*z*	*p*	*z*	*p*	*z*	*p*	*z*	*p*
premaxilla	2.53	**0.006**	0.88	0.200	1.32	0.105	—	—	—	—
dentary	4.26	**<0.001**	3.00	**<0.001**	1.08	0.141	—	—	—	—
anguloarticular	−0.33	0.638	2.32	**0.012**	0.58	0.270	—	—	—	—
lower pharyngeal jaw	3.10	**0.002**	2.47	**0.005**	1.52	**0.072**	3.84	**0.002**	1.76	**0.044**

Finally, we found that lab-reared fish displayed some degree of integration within limnetically derived and benthically derived populations (electronic supplementary material, tables S2 and S3). However, neither population alone showed as strong integration as when they were combined. Therefore, the integration observed in lab-raised fish is not driven primarily by any one population group alone, but is rather tied to their rearing environment.

4. Discussion

In this study, we expand on the recent finding that Trinidadian guppies are undergoing an adaptive divergence in craniofacial morphology in response to ecosystem-wide changes in upstream, benthic environments [44]. We find that there is variation in the shape of individual bones in the feeding apparatus of these fish and that this variation has both a genetic and a plastic component. Importantly, much of this variation is attributable to trophic divergence (benthic versus limentic) between the populations. This is particularly true among the wild-caught fish where adult morphological divergence is the result of both genetic and environmental differences, as compared with those reared in a common-garden lab environment where there are only genetic differences between populations. We then show that these lab-reared fish have highly integrated oral and pharyngeal jaw morphology, despite there being significant variation in the shape of these bones. Finally, we show that wild-caught fish that naturally utilize different food sources display greatly reduced integration among the jaw bones. Together, these results show that the jaws of guppies are actively undergoing evolution, and they suggest that plasticity may help overcome evolutionary constraints as populations adapt to novel environments.

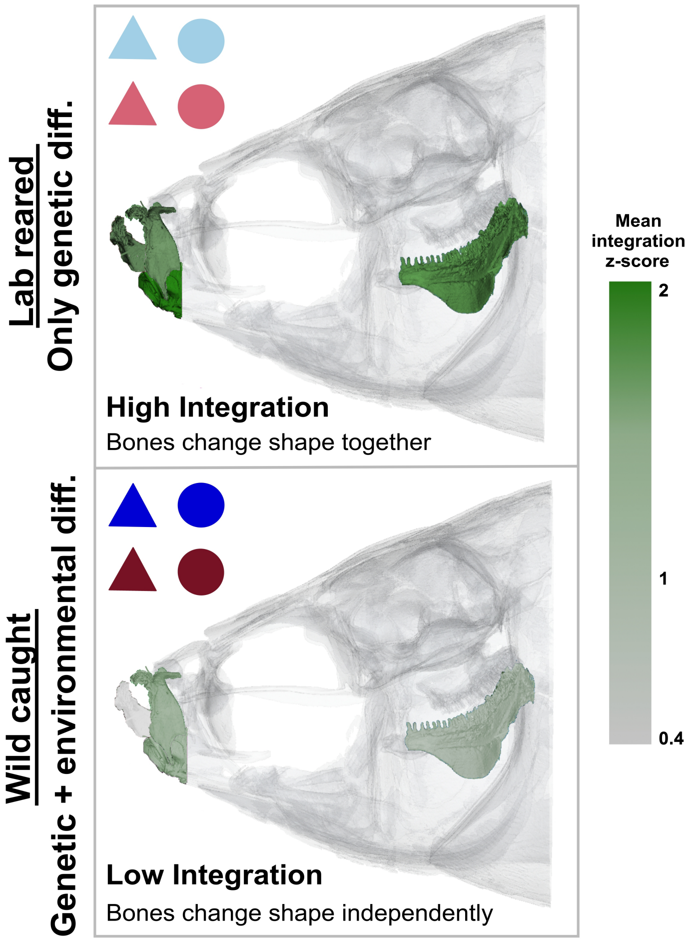

Figure 5. The average degree of integration between all the bones used in this study was higher in lab-reared specimens (only genetic differences) compared with wild-caught specimens (genetic and environmental differences), suggesting that plasticity reduces covariation across the skull. The colour of each bone represents the average integration test *z*-score across all pairwise comparisons with the other bones in the study (table 3). Darker green is associated with higher average *z*-scores, indicating a higher degree of integration of that bone with other prey capture and food processing structures.

Table 3. Integration test results. *p*-values for pairwise comparisons of integration from 'integration.test', geomorph. Strength of correlations is presented as the r-value from a two-block partial least squares analysis (r-PLS). Bold values are *p*-values less than 0.1.

	lab reared			wild caught		
	r-PLS	*z*	*p*	r-PLS	*z*	*p*
premaxilla—dentary	0.73	1.61	**0.053**	0.59	0.96	0.18
premaxilla—lower pharyngeal jaw	0.69	1.46	**0.067**	0.43	0.33	0.37
premaxilla—anguloarticular	0.68	1.87	**0.033**	0.57	2.13	**0.015**
dentary—lower pharyngeal jaw	0.71	1.44	**0.081**	0.58	0.47	0.31
dentary—anguloarticular	0.69	1.81	**0.034**	0.53	−0.17	0.57
lower pharyngeal jaw—anguloarticular	0.70	2.39	**0.005**	0.54	1.59	**0.066**
total pairs ($p < 0.10$)	—	—	**6/6**	—	—	**2/6**

(a) Jaw shape evolves in response to divergent trophic niches

As members of the Order Cyprinodontiformes, guppies and their relatives are specialized feeders with particular morphological adaptations that facilitate picking and scraping [80]. The genus Poecilia possess extreme morphological specializations, such as a protrusible premaxilla and novel ligamentous and muscular connections between the dentary and premaxilla, to further facilitate targeted benthic feeding [80,81]. Within the Trinidadian guppy system, limnetic food acquisition is consistent with the plesiomorphic condition of picking invertebrates out of the water column and off substrates [46,82]. When the guppies move to upstream predator-free environments and decimate invertebrate populations, they create a highly food-limited environment and are newly subject to strong selective pressure for benthic food acquisition [52,61,82]. Accordingly, previous work found that benthic guppies exhibit a derived condition characterized by a rostrocaudally compressed, laterally deeper and dorsoventrally steeper head shape compared with limnetic fish [44]. The results presented here are consistent with these past findings, most prominently that wild-caught premaxilla and dentary are shorter and wider in benthic fishes compared with limnetic suction feeders, possibly providing a competitive advantage in the novel benthic environment.

The most direct evidence of evolution in our study comes from fish that were reared in a common environment in the lab. While we hypothesized that trophic niche would be the primary driver of evolution in these fish, genetically driven differences are most evident when we compare fish from different drainages. Specifically, the shape of all four bones differed between the two river systems, the Aripo and Yarra drainages (table 1). We do not know whether this is simply the result of genetic drift between isolated populations, or if it is attributable to adaptive evolution caused by differences in the local environment of each drainage. However, the fact that the dentary and the premaxilla differ significantly between limnetic and benthic populations suggests that at least some of this evolution may be adaptive (table 1). We also see that there is an interaction between trophic niche and drainage in the shape of the dentary, indicating that this adaptive response might be sensitive to differences in the microhabitats between drainages.

Based on other examples of fish trophic adaptation, we would expect guppies competing over limited resources within the benthic environment to evolve shorter, wider, more robust jaws [3,71,83–86]. This stout form has two primary advantages; it creates a wider aperture, which allows the fish to take larger bites from the substrate, and it allows for greater force transmission during jaw abduction [87,88]. The second role is particularly important in the lower jaw, where the ratio of the articular process length to lower jaw length is often used as a proxy for a fish's biting ability [83,88]. Indeed, we find that the dentaries of lab-reared guppies descended from benthic populations are shorter and wider than the dentaries of fish descended from limnetic populations (figure 3). Unlike the lower jaw, the length of the premaxilla is not directly associated with bite force transmission. Accordingly, the premaxilla is wider and longer in benthic populations (figure 3B). Together, these results suggest that the genetic bases of dentary and premaxilla shape in the benthic environment are in fact adaptive as they both conform to the functional demands that they are exposed to in this derived environment.

(b) Plasticity further specializes oral jaw elements

Consistent with our original hypothesis that plasticity increases morphological differences, more bones diverge due to trophic niche in wild-caught fish as compared with the lab-reared fish. Specifically, we see significant shape change related to trophic niche in the three individual bones that directly contact the substrate during food acquisition or processing (premaxilla, dentary and lower pharyngeal jaw; table 1). We see no significant shape change as a function of trophic niche in the proximal lower jaw bone (anguloarticular), which predominantly acts as a hinge about which the dentary rotates during lower jaw extension/flexion in limnetic and benthic guppies alike [55,81,89]. Among the jaw bones that do diverge, we find that the change in morphology associated with benthic environments is consistent with what we would functionally expect in a substrate feeder [83,88]. Specifically, benthic guppies possess wider and shorter oral jaw elements than their limnetic counterparts (figure 4B).

Interestingly, among the bones that show the greatest divergence based on trophic niche (premaxilla and dentary), we find that the primary axes of divergence reflect similar morphological changes across lab-reared and wild-caught specimens (figures 3A and 4A). This means that the variation that arises is similar, no matter whether it is attributed to environmental or genetic effects, and may suggest similar underlying processes driving the plastic and the adaptive (genetic) effects. However, it is only in the dentary that we see similar divergence between benthic and limnetic fish in both rearing conditions (figures 3B and 4B). Specifically, the mean shape of the dentary is wider and shorter in benthic fish compared with limnetic fish in both rearing conditions. Conversely, rearing condition affects the shape differences between trophic niche of the premaxilla as the benthic premaxilla is longer than the limnetic premaxilla in lab-reared fish, but shorter in wild-caught fish. This suggests that plasticity in the premaxilla can substantially alter trophic morphology independently of the genetic effects.

(c) Plasticity disrupts integration during local adaptation

We predicted that shared functional demands would drive a coordinated plastic response, which would increase morphological integration between jaw bones in wild-caught fish. Contrary to this expectation, most pairs of bones in wild-caught fish showed very little covariation (figure 5, table 3, electronic supplementary material, table S1). Instead, we found the strongest evidence of integration in lab-reared individuals. It is unlikely that this pattern arises simply due to a lack of variation among these fish since there are significant divergences between drainages and to some level between trophic niches. This indicates that there is a strong integration of the genetic developmental plan underlying jaw morphology. Additionally, we found that the anguloarticular was both the least trophically divergent bone (figure 3A, table 1) and was also the most integrated bone within these fish (figure 5, table 3, electronic supplementary material, table S1). We therefore suggest that the anguloarticular may act as a linchpin of jaw evolution, maintaining holistic function across the jaw while allowing each individual element more developmental leeway than if they were all tightly integrated with one another. And although we do not know the genetic basis of these patterns of integration, there is evidence that similar patterns can be driven by shared developmental genetic architecture [9].

Importantly, when we examine guppies reared in their natural environment, we start to see strong signs of local trophic adaptation among the jaw bones (table 2, figure 4). With this putatively adaptive morphological response comes a decrease in the amount of integration among the bones of the jaws (table 3, figure 5). Whereas all bones show significant integration within lab-reared individuals (high genetic integration), only minor integration can be observed between pairs of bones within wild-caught individuals. Interestingly, it is also among wild-caught fish that we observe morphological differences most consistent with the functional expectations accompanying each environment. Therefore, functional optimization in this incipient adaptive divergence seems to occur primarily through plastic responses that are less constrained by morphological integration.

Altogether we hypothesize that plasticity drives local adaptation by disrupting a genetically integrated feeding apparatus, and suggest that this could be an important mechanism through which complex functional systems explore new morphospace without losing functionality. By maintaining genetic integration among the underlying developmental blueprint, an animal can ensure that they start life with a functionally viable phenotype. Then as they grow, their morphology can respond to the environment in a way that is unconstrained by the underlying mechanisms of integration. Since plasticity impacts elements based on their usage [84,90–92], it often pushes them towards a functional portion of morphospace [1,40,93–95]. If a population is then able to canalize these plastic changes so that they are a part of the base developmental programme, this population would have adaptively evolved without needing to blindly explore morphospace. Our results stand as initial evidence of this hypothesis, but more work will be needed to fully explore the mechanism.

Ethics. All procedures used in this study were approved by the Institutional Animal Care and Use Committees at Brown University (Protocol 1211035 to E.L. Brainerd) and at Harvard University (Protocol 20-03-2 to G.V. Lauder).

Data accessibility. Data and code used in this study are available in Dryad [96]. Supplementary material is available online [97].

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

Authors' contributions. T.M.A.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review and editing; T.R.D.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing—original draft, writing—review and editing; D.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review and editing.

All 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.

Funding. This work was funded by the National Science Foundation under grant nos. DGE1745303 to D.G.M. and IOS1601377 to T.R.D.

Acknowledgements. We thank David Reznick and Yuridia Reynoso for their help in acquiring and rearing specimens, Elizabeth Brainerd and George Lauder for the use of materials and facilities, and the Ramlal family for the accommodations in Trinidad. We also thank two anonymous reviewers for their constructive and professional critiques of the manuscript.

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