

# Rates of piscivory predict pharyngeal jaw morphology in a piscivorous lineage of cichlid fishes

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**Abstract** – The pharyngeal jaw apparatus is a key innovation hypothesised to increase foraging efficiency and facilitate utilisation of novel resources among teleost fishes. Here, we tested whether dietary characteristics could predict pharyngeal jaw morphology among eight species of Neotropical *Crenicichla*. Additionally, we tested the hypothesis that pharyngeal jaws may impose a functional constraint on piscivory via pharyngeal gape. We quantified the shape of the lower pharyngeal jaw (LPJ) using linear and geometric morphometrics and quantified diet using the relative volumetric proportions of prey items. We used principal component analysis to describe major axes of variation in LPJ shape and dietary patterns. The major axis of dietary variation significantly predicted LPJ morphology, which was driven by a significant relationship between LPJ shape and rates of piscivory. We also found that rates of piscivory predicted size-corrected LPJ depth. Size-corrected pharyngeal gape also significantly predicted rates of piscivory such that pharyngeal jaws may constrain piscivory by limiting pharyngeal gape. Strong form-to-function linkage between pharyngeal morphology and trophic patterns suggests an adaptive quality of the pharyngeal apparatus but may also impose functional constraints when consumers must switch prey or when prey availability is temporally or spatially unpredictable.

**Key words:** adaptive; functional constraint; *Crenicichla*; evolution; geometric morphometrics

## Introduction

The pharyngeal jaw apparatus of cichlid fishes represents a key innovation associated with an improved ability to process resources, increased foraging efficiency and facilitated the utilisation of novel resources (Liem 1973; Wainwright et al. 2012; Burress 2015). The pharyngeal jaws are the major site of food processing (Liem 1973) and exhibit myriad adaptations for crushing, tearing and grasping prey (Burress 2015). Although many bony fishes possess gill arches that are somewhat modified to assist with prey processing (Liem 1973; Wainwright 1989), the pharyngeal jaw of cichlids exhibits several unique qualities: (i) articulation of the upper pharyngeal jaw bones directly against the neurocranium, (ii) muscular slings that raise the lower pharyngeal jaw (LPJ) and

(iii) suturing that unites the two LPJ bones into a single structure (Liem 1973; Hulsey 2006; Wainwright et al. 2012). Pharyngognathly has evolved independently in several lineages including cichlids and wrasses, among others (Wainwright et al. 2012). This innovation may represent a key factor for the emergence of diversity that is unparalleled among vertebrates (Liem 1973; Hulsey et al. 2006; Salzburger 2009; Burress 2015).

Among piscivores, the pharyngeal jaws are often elongate, and less robust than other trophic guilds (Liem 1973; Barel et al. 1977; Burress et al. 2013a). The LPJ particularly is specialised for grasping, transporting and positioning prey, which is generally consumed whole by Neotropical piscivores (Winemiller 1989). The associated musculature is often poorly developed (Liem 1973; Barel 1983), and dentition is

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often sharp and recurved, sometimes appearing serrated or bearing accessory cusps (Casciotta & Arratia 1993). Despite these generalities, little is known about the pharyngeal jaw form-to-function linkage, particularly across ecological gradients. For example, many dietary patterns occur along continuums, such as consumers in which fishes constitute tertiary, secondary, or primary prey items (i.e., low to high rates of piscivory). In such cases, there may be predictable correlations between gradients of phenotypic modification (or specialisation) and ecological functions. For example, species often exhibit ontogenetic shifts to piscivory such that organisms proceed through successive stages in which they consume invertebrate prey early in development and gradually transition to fishes (Winemiller 1989; Mittelbach & Persson 1998). Pharyngeal jaw morphology may exhibit ontogenetic changes associated with the degree of piscivory (van Oijen 1989; Hellig et al. 2010). Likewise, among species, highly piscivorous species often exhibit the aforementioned characteristics to the extreme such as highly reduced morphology, elongate and slender lateral processes and exclusively recurved dentition (Burruss 2015).

Here, we investigate pharyngeal jaw form-to-function linkages among Neotropical cichlid fishes (Cichlidae: Cichlinae: *Crenicichla*). *Crenicichla* is the most speciose genus of cichlid with over 90 valid species (Kullander et al. 2010; Piálek et al. 2012). They occupy a unique region of the adaptive landscape associated with the elongate ram-feeding adaptive peak (López-Fernández et al. 2013; Arbour & López-Fernández 2014), are generally mesopredators and exhibit a wide range of degrees of piscivory (Burruss et al. 2013b,c). Piscivory is ubiquitous among *Crenicichla* and likely represents an ancestral condition; however, some species exhibit unique trophic roles, including specialisation on macrocrustaceans, benthic insects and molluscs (Montaña & Winemiller 2009; López-Fernández et al. 2012; Burruss et al. 2013a). Additionally, trophic diversification may have played a key role in their proliferation such that LPJ morphology varies predictably based on species diet (Burruss et al. 2013a). Thus, pharyngeal jaw morphology and diet may be co-evolved among *Crenicichla*. We tested whether dietary characteristics (e.g., principal components and rates of piscivory) could predict LPJ shape and depth among eight *Crenicichla* species from subtropical South America. Secondly, we tested the hypothesis that *Crenicichla* offset some functional constraints associated with piscivory by reducing gape limitation incurred by having pharyngeal jaws. Here, we predict that pharyngeal gape will predict rates of piscivory and that these two traits will have a negative relationship.

## Methods

### Sampling

Specimens used in this study were collected in Uruguay in 2010, 2012 and 2013 (see Burruss et al. 2013a,b,c for details) and are accessioned in the Auburn University Museum of Natural History (Auburn, U.S.) and Museo Nacional de Historia Natural (Montevideo, Uruguay). Some specimens of *Crenicichla missioneira*, *Crenicichla minuano* and *Crenicichla tendybaguassu* were also measured that are accessioned in the Museo de Ciencias e Tecnologia (Rio Grande do Sul, Brazil). Specimens were injected with and preserved in 10% formalin in the field and later stored in 70% ethanol.

### Geometric morphometrics

We dissected the LPJ from accessioned specimens: *Crenicichla celidochilus* ( $N = 11$ ;  $14.3 \pm 1.9$  cm), *Crenicichla lepidota* ( $N = 9$ ;  $12.2 \pm 1.7$  cm), *C. minuano* ( $N = 12$ ;  $10.8 \pm 2.1$  cm), *C. missioneira* ( $N = 11$ ;  $14.5 \pm 2.8$  cm), *Crenicichla punctata* ( $N = 8$ ;  $16.2 \pm 0.6$  cm), *Crenicichla scottii* ( $N = 5$ ;  $17.2 \pm 2.4$  cm), *C. tendybaguassu* ( $N = 5$ ;  $12.8 \pm 1.8$  cm) and *Crenicichla vittata* ( $N = 9$ ;  $18.9 \pm 3.4$  cm). Only specimens that represent adult (i.e., maximally piscivorous) size classes were used to avoid confounding effects of ontogeny (i.e., Burruss et al. 2013c). The LPJ was cleaned and photographed in dorsal aspect using a mounted Nikon D5100 digital camera (Nikon Corporation, Tokyo, Japan). We used four homologous and 18 sliding landmarks (Fig. 1a) that describe the shape of the LPJ. Sliding landmarks are not associated with a homologous structure, but are used to quantify the curvature between two homologous landmarks. All analyses were performed with the tps programs suite. Photographs were digitised and landmarked using tpsUtil (Rohlf 2004) and tpsDIG2 (Rohlf 2006) respectively. Landmarks were superimposed, aligned and relative warps (RWs) were generated using tpsrelw (Rohlf 2007). Relative warps are principal components of shape variation. Size was removed from the analysis during superimposition and generation of the Procrustes fit.

### Linear morphometrics

To quantify the relative depth of the LPJ, we measured the linear distance between the dorsal plane of the dentigerous area and the ventral edge of the keel (Fig. 1b). Pharyngeal gape was measured as described by Wainwright & Richards (1995). Wooden rods of increasing diameter were inserted through the upper and LPJs. The diameter of the

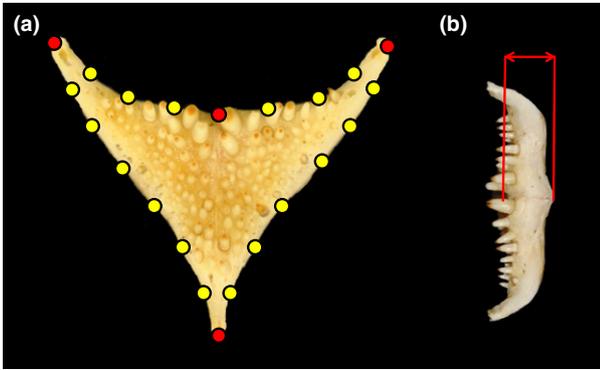


Fig. 1. Landmark scheme used for geometric morphometrics (a) and the linear distance reflecting the depth of the lower pharyngeal jaw (LPJ) (b). Red and yellow dots represent homologous and sliding landmarks respectively. Images depict the LPJ of *Crenicichla scottii* in dorsal and posterior views.

largest rod that would fit firmly among the pharyngeal jaw bones and into the oesophagus was considered the pharyngeal gape. To account for size in these measurements, we used the residuals from the linear regression with standard length. Measurements were made using digital callipers to the nearest 0.1 cm.

#### Stomach content analysis

We quantified the relative proportions of prey items as described by Winemiller (1989). Briefly, the contents of the anterior half of the digestive tract were removed, sorted, identified and measured in appropriately sized graduated cylinders. For small items, sorted material was spread onto glass slides and its area compared to that of a substance of a known volume. We analysed the diets of two novel species (e.g., *C. vittata* and *C. punctata*) as well as utilised existing literature that followed the same methodology (i.e., Burress 2012; Burress et al. 2013a). Sample sizes are presented in Table 1. Prey items were pooled into five general categories: fishes, insects, crustaceans, molluscs and plants. We then used principal component analysis to describe major variation in the diet among *Crenicichla* species. Principal components were generated using the princomp function in R. The first relative warp and first principal component were used as indices that describe the most important variation in LPJ shape and diet respectively.

#### Statistical analyses

We tested whether dietary variables (PCs) could predict LPJ morphology (RWs and LPJ depth) using the lm function in R. Based on the dietary PCA results, we also tested for relationships between the proportion of fishes consumed (%) and morphologi-

Table 1. Data matrix used to generate dietary principal components. Values represent the volumetric proportion (%) of each prey item. Values are rounded to the nearest 0.5. Species are listed in order of decreasing rates of piscivory. The detailed taxonomic-based gut contents reported in Burress (2012) and Burress et al. (2013a) were generalised into broad functional groups.

| Species                          | N  | Prey item |        |            |         |            |
|----------------------------------|----|-----------|--------|------------|---------|------------|
|                                  |    | Fish      | Insect | Crustacean | Mollusc | Vegetation |
| <i>Crenicichla vittata</i>       | 11 | 100       | 0      | 0          | 0       | 0          |
| <i>Crenicichla celidochilus</i>  | 30 | 91        | 9      | 0          | 0       | 0          |
| <i>Crenicichla missioneira</i>   | 44 | 71        | 12     | 17         | 0       | 0          |
| <i>Crenicichla lepidota</i>      | 26 | 33        | 63     | 4          | 0       | 0          |
| <i>Crenicichla scottii</i>       | 19 | 24        | 29.5   | 43         | 3.5     | 0          |
| <i>Crenicichla punctata</i>      | 18 | 23        | 36     | 38         | 3       | 0          |
| <i>Crenicichla tendybaguassu</i> | 26 | 0         | 90     | 0          | 7       | 3          |
| <i>Crenicichla minuano</i>       | 37 | 0         | 27     | 0          | 73      | 0          |

cal variables. Morphological variables were treated as response (dependent) variables, and dietary variables were treated as independent variables due to the well-documented plasticity of LPJ morphology in response to diet (Meyer 1987; Huysseune 1995; Muschick et al. 2011). However, dietary variables were treated as response (dependent) variables when analysed with pharyngeal gape, which was treated as the dependent variable. Means for each species were used in all analyses.

#### Results

The first relative warp described 74.45% of the variation in LPJ shape and reflects variation in the length of the lateral processes and relative size of the dentigerous area (Fig. 2). Positive scores of RW1 represent short lateral processes and large dentigerous area (e.g., *C. minuano*), and negative scores represent long lateral processes and small dentigerous area (e.g., *C. celidochilus*). The second relative warp describes 18.48% of the variation in LPJ shape and reflects variation in the orientation of the lateral processes (Fig. 2). Positive scores of RW2 were associated with widely spaced lateral processes (e.g., *C. celidochilus*), and negative scores were associated with narrowly spaced lateral processes (e.g., *C. vittata*).

Species varied in the relative proportions of prey items (Table 1) such that some species were piscivorous (e.g., *C. vittata*, *C. celidochilus* and *C. missioneira*), some consumed primarily large

macrocrustaceans (e.g., *C. scottii* and *C. punctata*), and one was molluskivorous (e.g., *C. minuano*). In all species, fish remains were largely intact, other than exhibiting various degrees of digestion, indicating that they were consumed whole. Macrocrustacean, snail and bivalve remains frequently showed signs of significant mastication such that they either occurred as fragments or were physically crushed. The first principal component described 66.3% of the variation in diet (Fig. 3). Positive PC1 scores were associated with high degrees of piscivory (Table 2; Fig. 3). Negative PC1 scores were associated with low degrees of piscivory and consumption of primarily insects (Table 2; Fig. 4). Principal component 2 (21.4%) and 3 (12.3%) described variation in consumption of molluscs and crustaceans respectively (Table 2; Fig. 3).

Diet (PC1) significantly predicted LPJ shape (RW1) ( $R^2 = 0.788$ ;  $F = 22.3$ ;  $P = 0.0033$ ; Fig. 4a). This relationship was primarily driven by a significant relationship between the proportion of fish consumed and RW1 ( $R^2 = 0.627$ ;  $F = 10.09$ ;  $P = 0.019$ ; Fig. 4b). Highly piscivorous species tended to have elongate lateral and medial processes (Figs 2 and 4). Additionally, there was a significant relationship between diet (PC1) and LPJ depth ( $R^2 = 0.619$ ;  $F = 9.77$ ;  $P = 0.024$ ; Fig. 4c), which was also driven by a significant relationship between the proportion of fish consumed and LPJ depth ( $R^2 = 0.574$ ;  $F = 8.08$ ;  $P = 0.029$ ; Fig. 4d). Species with deeper pharyngeal jaws tended to be less piscivorous (Fig. 4). There was also a significant relationship between LPJ depth and shape ( $R^2 = 0.539$ ;  $F = 7.03$ ;  $P = 0.038$ ; Fig. 5a). Pharyngeal gape had a significant negative relationship with rate of piscivory

Table 2. Factor loadings for the first three principal components explaining major variation in *Crenicichla* diet.

| Prey item   | Principal component |             |             |
|-------------|---------------------|-------------|-------------|
|             | PC1 (66.3%)         | PC2 (21.4%) | PC3 (12.3%) |
| Fish        | 0.818               | 0.109       | -0.265      |
| Insects     | -0.518              | 0.551       | -0.406      |
| Crustaceans | -                   | 0.139       | 0.859       |
| Molluscs    | -0.247              | -0.815      | -0.165      |
| Vegetation  | -                   | -           | -           |

( $R^2 = 0.551$ ;  $F = 7.36$ ;  $P = 0.035$ ; Fig. 5b). Lastly, pharyngeal gape was not predicted by LPJ shape ( $R^2 = 0.262$ ;  $F = 2.13$ ;  $P = 0.195$ ; Fig. 5c), but was predicted by LPJ depth ( $R^2 = 0.576$ ;  $F = 8.16$ ;  $P = 0.029$ ; Fig. 5d). The equations used to fit these relationships are listed in the legends of Figs 4 and 5. Relationships involving secondary axes of diet (PC2 and 3) and LPJ shape (RW2) variation were also explored, but were nonsignificant (results not shown).

## Discussion

Pharyngognathy is considered a key innovation associated with increased efficiency in processing prey items and improved capacity to consume diverse types of prey items. Thus, by providing access to different regions of the adaptive landscape, adaptation of the pharyngeal jaws may facilitate diversification. Among eight *Crenicichla* species (Kullander et al. 2010; Piálek et al. 2012), we found that rates of piscivory represented most of the variation in diet, whereas the length of the lateral and medial processes

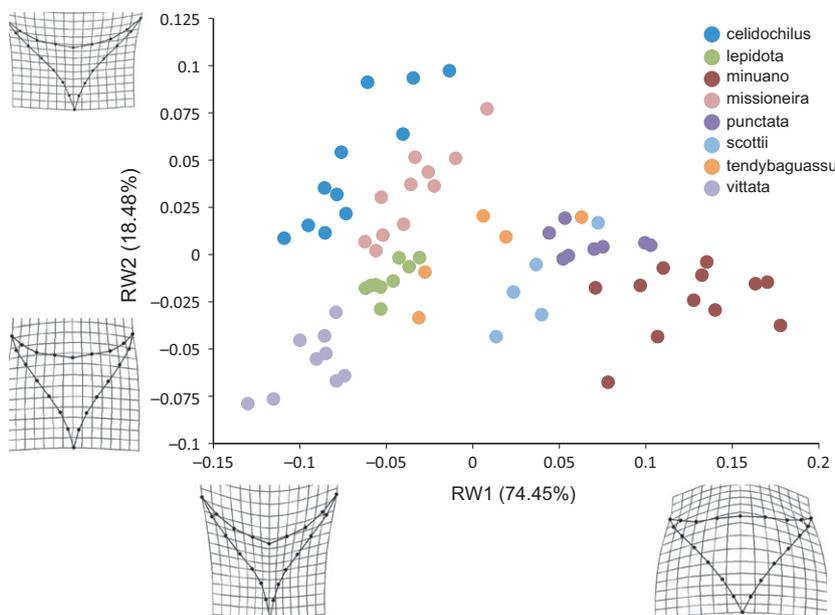


Fig. 2. Lower pharyngeal jaw shape among eight species of *Crenicichla* based on the RWs of 22 landmarks. Warp transformation grids depict the shape variation associated with the positive and negative extremes of each relative warp. Each point represents an individual.

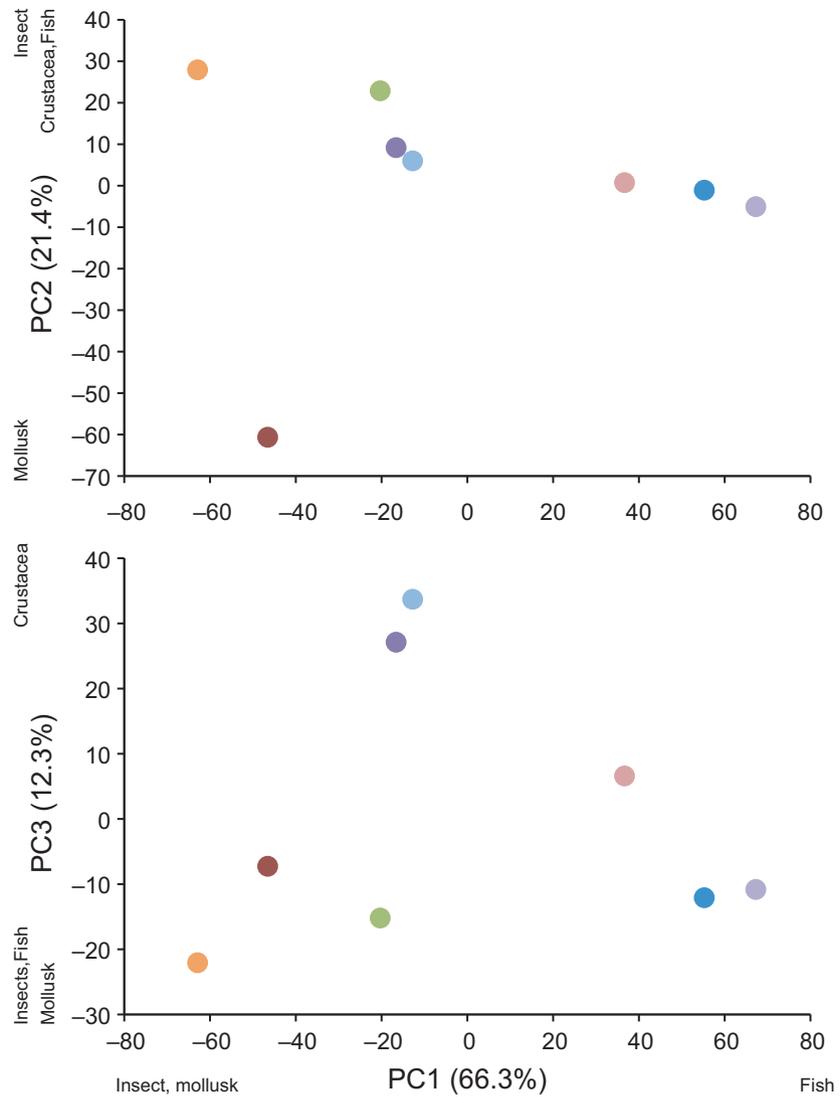


Fig. 3. *Crenicichla* diet based on principal component analysis of five general prey items: fish, insects, crustaceans, molluscs and vegetation. Factor loadings are associated with each axis (see Table 2 for loadings). Each point represents the consensus of each species. Colour codes follow Fig. 2.

represented most of the variation in the shape of the LPJ. Rates of piscivory significantly predicted the length of the lateral and medial processes (i.e., PC1), such that highly piscivorous species had LPJs with more elongate processes. Additionally, species varied in the depth of their LPJs, which is known to correlate with the ability to generate crushing force (Hulseley et al. 2008). Rates of piscivory also predicted LPJ depth such that highly piscivorous species had more shallow LPJs.

#### Morphology–diet relationships

Species differed significantly in their diets and LPJ shape. For example, *Crenicichla minuano* has hypertrophied LPJs with short lateral and medial processes and molariform teeth. This morphology is likely necessary to withstand the structural force incurred while crushing the shells of snails and bivalves, which are major food resources (Burruss et al.

2013a). *Crenicichla scottii* and *C. punctata* exhibit similar LPJ morphologies such that they have lateral processes that are intermediately spaced and of intermediate length. These species also have similar diets consisting largely of macrocrustaceans, fishes and benthic insects. These species LPJ is of intermediate depth, which is likely associated with their consumption of large fractions of macrocrustaceans and tertiary exploitation of snails eliciting some reinforcement of the LPJ. Highly piscivorous species exhibit two distinct LPJ morphologies. *Crenicichla celidochilus* and *C. missioneira* have elongate lateral processes that are widely spaced, whereas *C. vittata* has elongate lateral processes that are narrowly spaced. These species, particularly *C. celidochilus* and *C. vittata*, also have shallow LPJs. This reduced pharyngeal jaw morphology (i.e., long processes and shallow depth) is likely sufficient to grasp and manipulate fishes, which are generally consumed whole by Neotropical piscivores (Winemiller 1989;

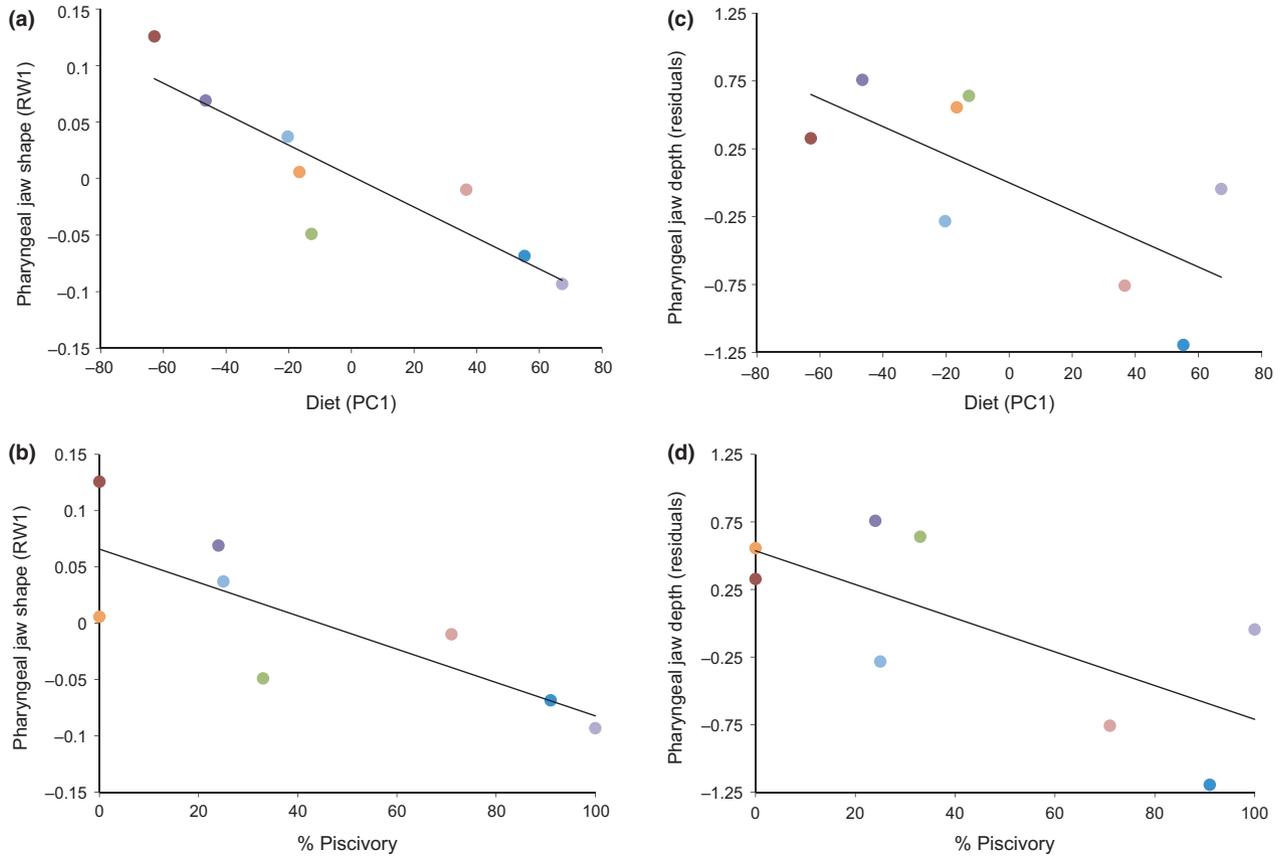


Fig. 4. Diet–shape relationships among *Crenicichla* lower pharyngeal jaws (LPJ). (a) Major variation in diet (PC1) significantly predicted major shape variation (RW1) in the LPJ ( $y = -0.00137x + 0.00218$ ), which was primarily due to (b) the relationship between rates of piscivory and LPJ shape ( $y = -0.00148x + 0.0658$ ). (c) *Crenicichla* diets ( $y = -0.0167x + 1.25^{-9}$ ) and (b) rates of piscivory ( $y = -0.0136x + 0.585$ ) also significantly predicted LPJ depth. Each point represents the mean for each species. Colour codes follow Fig. 2.

Burress 2015), but ill-equipped for handling the stress incurred by crushing prey items such as molluscs or large crustaceans.

It has been hypothesised that exploitation of soft-bodied invertebrates may not require any specific adaptations of the LPJ (Burress 2015). The four species that consume primarily invertebrates exhibit similar LPJ morphologies; however, *C. punctata* and *C. scotti* have more robust pharyngeal jaws than *C. lepidota* and *C. tendybaguassu*, which consume primarily large macrocrustaceans and benthic insect larvae respectively. Large crustaceans, such as crabs, likely require more processing by the pharyngeal jaws than soft-bodied insect larvae due to their relatively more robust size and exoskeleton (Burress 2015). *Crenicichla lepidota* has relatively more elongate processes than these species, likely due to their utilisation of piscivory as a secondary trophic mode.

#### Pharyngeal jaws as a functional constraint

The relationship between rates of piscivory and pharyngeal gape, which was predicted by the depth

of the LPJ, may infer that some species are precluded from consuming fishes, cannot do so efficiently, or are limited to smaller prey. Although changes in pharyngeal jaw morphology and dentition can be elicited by experimentally manipulating diet in cichlids (Meyer 1987; Huysseune 1995; Muschick et al. 2011); pharyngeal morphology still presents a short term constraint until such phenotypic changes occur. For example, gape constrains piscivory such that organisms must be capable of grasping and subsequently swallowing their prey (Wainwright 1991). Presumably, pharyngeal jaw morphologies that limit gape may indirectly constrain piscivory by reducing foraging capacity and efficiency. For example, juvenile *Cichla* have LPJ that are unsutured, which allows them to spread apart laterally (Stiassny & Jensen 1987) and thereby subvert gape limitations associated with having them. If the LPJs are sutured into a single structure, as they are in *Crenicichla*, then this is not possible. Having a robust pharyngeal jaw (e.g., *C. minuano*, *C. punctata* and *C. scottii*) or robust pharyngeal dentition (e.g., *molariform teeth*), may limit pharyngeal gape and thereby constraint

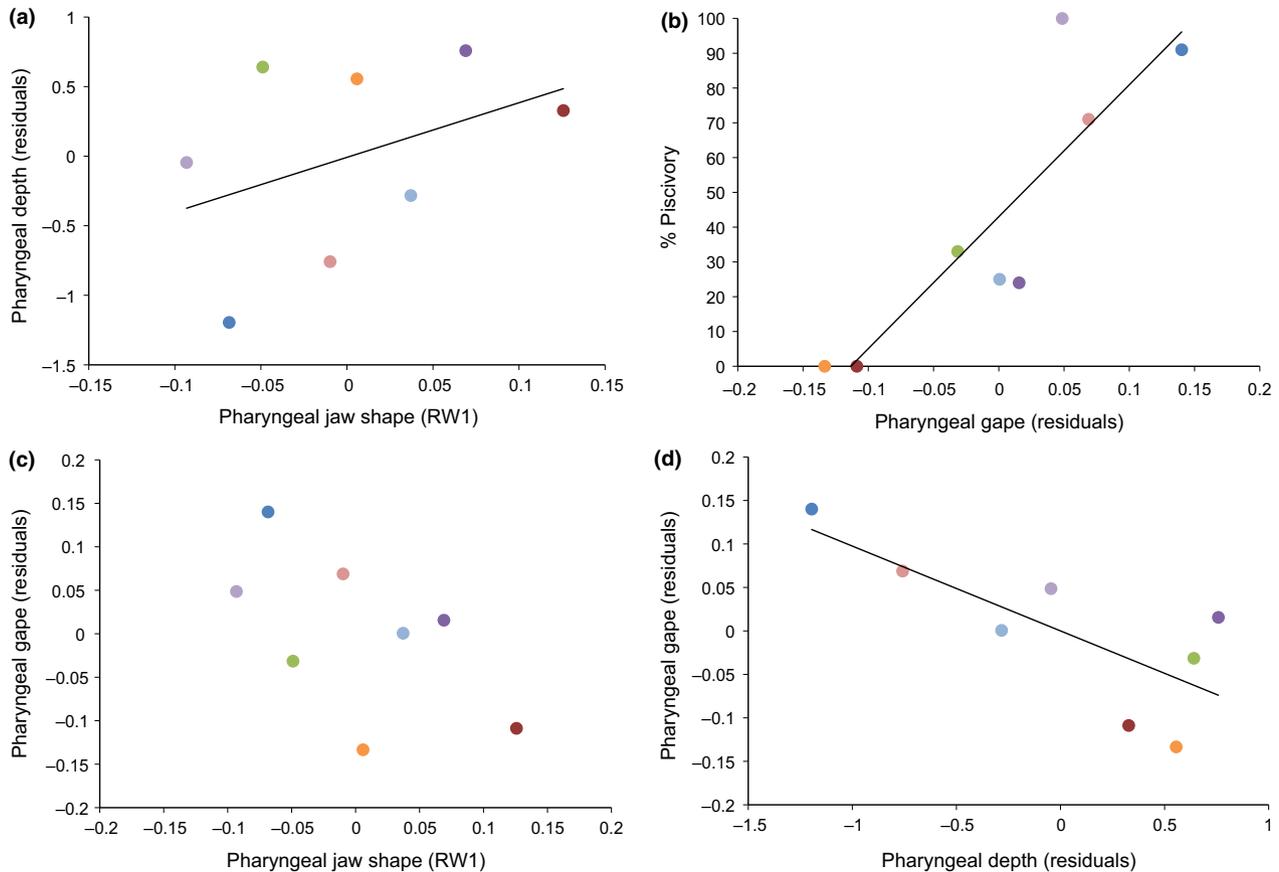


Fig. 5. Relationships between (a) lower pharyngeal jaw (LPJ) shape (RW1) and depth ( $y = 7.054x - 0.0154$ ), (b) pharyngeal gape and rate of piscivory ( $y = 321.67x + 43.0$ ), (c) LPJ shape (RW1) and pharyngeal gape ( $y = -0.631x + 0.00137$ ) and (d) LPJ depth and pharyngeal gape ( $y = -0.0976x + 2.469^{-10}$ ). Each point represents the mean for each species. Colour codes follow Fig. 2.

piscivory. Many species have robust LPJs (e.g., deep keel and short processes) necessary for processing foods that require considerable manipulation such as molluscs, fruits, seeds and crustaceans (Burruss 2015). In contrast, highly piscivorous species may also be constrained from exploiting alternative resources. LPJ morphologies associated with high rates of piscivory, such as shallow depth and long lateral and medial processes, with recurved conical teeth, are ill-equipped to tolerate the structural stress incurred from processing difficult to crush organisms (Hulsey et al. 2005, 2008; Hulsey 2006).

Specialisation of the LPJ in association with exploiting a specific resource may make it difficult to switch prey or utilise a broader array of resources. Disparity in pharyngeal gape may explain the role of prey size as an important source of ecological divergence among piscivores (van Oijen 1982). Piscivores are likely precluded from exploiting some resources due to structural limitations of their LPJ, whereas nonpiscivores may be constrained from consuming some fishes by spatial limitations associated with pharyngeal gape. This would be particularly important when temporarily (i.e., before such a switch

could elicit changes in pharyngeal morphology) utilising an alternative food resource in which the pharyngeal jaws are ill-equipped to exploit and/or when prey availability were temporally or spatially heterogeneous or unpredictable. Manifestations of such constraints may be frequent among Neotropical species with highly specialised LPJs (i.e., species along the extremes of an ecological continuum such as piscivory) as consumer-prey relationships are often temporally and spatially dynamic in response to environmental conditions (Winemiller 1990; Winemiller & Jepsen 1998).

#### Pharyngeal jaws as an adaptive tool

Regardless of the potential for pharyngeal jaws to constrain specific functions as outlined above, pharyngeal modification likely incurs an adaptive value with most functions (Liem 1973; Wainwright et al. 2012; Burruss 2015). Plasticity in response to mechanical stimulation during feeding allows the pharyngeal jaw and dentition to adapt to the utilisation of specific resources (Muschick et al. 2011), resulting in specialised phenotypes that increase

foraging capacity and efficiency in association with those resources (Liem 1973; Wainwright et al. 2012; Burress 2015). For example, reinforcement of the LPJ and dentition allows species to consume hard-shelled organisms such as snails and bivalves (Hulsey 2006). In addition to withstanding the structural stress incurred during mastication (Hulsey et al. 2008), hypertrophied pharyngeal jaws also improve handling time associated with manipulating and crushing these organisms (Hulsey et al. 2005). Alternatively, having reduced LPJ morphologies with recurved conical pharyngeal teeth improve grasping ability and manipulation of prey by piscivores (Casciotta & Arratia 1993). Additionally, shallow LPJs may relax constraints imposed by pharyngeal gape. Pharyngeal dentition may also improve the digestibility of nutrient poor resources by rupturing cells during mastication (Xie 2001). Thus, modification of the LPJ improves the capacity to exploit resources that would otherwise not be accessible to the consumer and improves efficiency during their exploitation (Hulsey et al. 2005), thereby improving ecological versatility.

## Conclusions

The pharyngeal jaw apparatus is a key innovation hypothesised to improve functional ability and efficiency among teleost fishes (Liem 1973; Wainwright et al. 2012; Burress 2015). Adaptation of the LPJ is associated with numerous trophic functions such as molluskivory and piscivory (Hulsey 2006; Burress et al. 2013a). Here, we show that important sources of variation in diet (i.e., rate of piscivory) predict major variation in LPJ shape (i.e., length of lateral and medial processes) across eight species in a predatory lineage of cichlid fishes. Specifically, rates of piscivory predict LPJ shape and relative depth based on geometric and linear morphometrics respectively. The relative depth of the LPJ likely infers a continuum of force generation and subsequently crushing force among species (Hulsey 2006; Hulsey et al. 2008). Lastly, rates of piscivory also predicted pharyngeal gape. These findings suggest a strong form-to-function linkage in cichlid fish pharyngeal jaws. Furthermore, we present potential means that pharyngeal jaw morphology may simultaneously facilitate the utilisation of some resources while precluding others by acting as an adaptive tool or a functional constraint depending on temporal scale and resource predictability.

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