

A peacock bass (*Cichla*) functional novelty relaxes a constraint imposed by the classic cichlid pharyngeal jaw innovation

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Innovations may provide access to new resources but often result in significant trade-offs. Pharyngognathy is a classic pharyngeal jaw innovation in which the left and right lower pharyngeal jaw (LPJ) bones are united into a single structure, producing a strong bite but reduced gape. Throughout cichlids, pharyngeal suturing occurs along the entire medial border between LPJ bones, except in peacock bass (*Cichla*), where these bones are connected by ligaments only in their anterior region. We show that this limited attachment permits the jaw bones to spread apart and we link this feature to an increase in pharyngeal gape that is comparable to non-pharyngognathous species. The capacity of the LPJ bones to spread apart is strongest in juveniles and is mostly lost during development. Juvenile *Cichla* exhibit size-specific pharyngeal gape similar to non-pharyngognathous percomorphs; however, adults exhibit pharyngeal gape on par with other predatory cichlids. Relaxation of pharyngeal suturing offsets a major deleterious consequence of pharyngognathy by reducing gape limitation and we propose this may accelerate the ontogenetic transition to piscivory. Partial reversal of the classic cichlid pharyngeal jaw innovation highlights the functional trade-offs that often accompany innovations and may be a major cause of variation in their macroevolutionary consequences.

ADDITIONAL KEYWORDS: adaptation – constraint – gape – morphology – piscivory – trade-off.

INTRODUCTION

Functional trade-offs impose a constraint on organismal evolution (Futuyma & Moreno, 1988; Koehl, 1996). A trade-off between force transmission and speed is central to many anatomical systems, ranging from feeding mechanics in fishes (Westneat, 1994; 1995) to powered flight in birds (Tobalske *et al.*, 2003), and can have a strong influence on diversification (Collar *et al.*, 2009; Wright *et al.*, 2016; Burress *et al.*, 2020). Functional innovations may permit organisms to achieve substantially enhanced performance that results in access to new resources (Simpson, 1953; Liem, 1973; Kingsolver & Koehl, 1994; Bond & Opell, 1998). However, an interesting feature of innovation is that functional break-throughs usually come with performance trade-offs, rather than universal benefits. While innovations may pave the way to exploitation of novel resources, trade-offs

can make use of other resources less viable (McGee *et al.*, 2015). Although there are widespread trade-offs in organismal evolution, these are rarely explicitly discussed in the context of major innovations despite that such trade-offs have the potential to influence the macroevolutionary impacts of the innovation.

All ray-finned fishes have a pharyngeal jaw apparatus formed from modified gill-arch elements that assists with prey processing (Lauder & Wainwright, 1992; Fig. 1). A derived condition of the pharyngeal jaw apparatus, pharyngognathy, is regarded as a major innovation that expanded the functional repertoire of several ecologically diverse lineages of fishes, including marine wrasse and freshwater cichlids (Liem, 1973; Liem & Sanderson, 1986). Pharyngognathy is characterized by three key modifications to the pharyngeal jaw apparatus (Liem, 1973; Stiassny, 1987; Stiassny & Jensen, 1987): (i) the left and right lower pharyngeal jaw bones, the fifth ceratobranchials, are united into a single structure, (ii) the upper pharyngeal jaws articulate directly against the neurocranium, and (iii) a muscular sling suspends the lower pharyngeal

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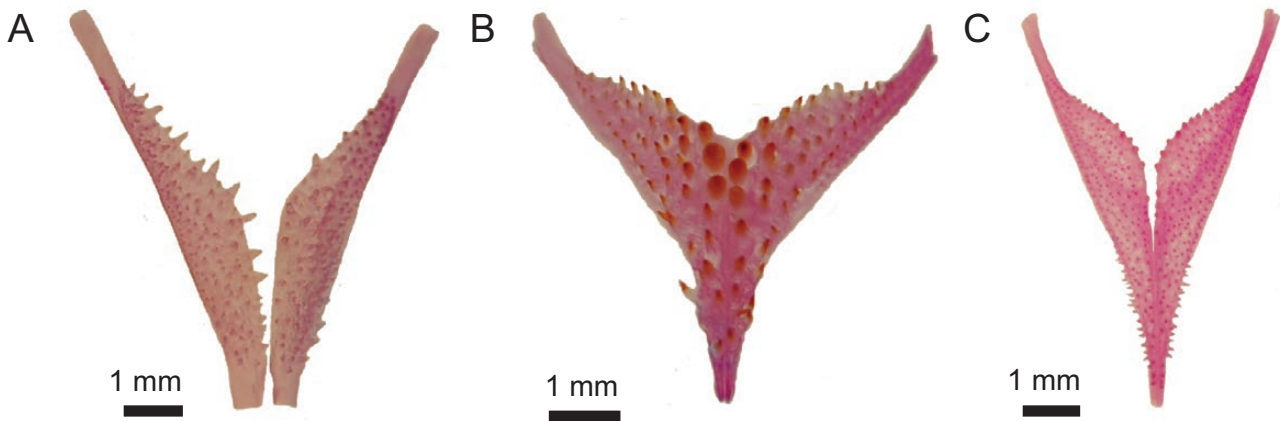


Figure 1. Pharyngeal jaws of percomorph fishes: (A) the widespread percomorph condition in which the left and right fifth ceratobranchials are separate elements (depicted by *Micropterus salmoides*), (B) the derived pharyngognathous state in which the ceratobranchials are sutured along their entire medial border into a single element (depicted by *Retroculus*), and (C) the modified *Cichla* pharyngeal jaw in which the ceratobranchials are united by a short suture at their anterior end (depicted by *Cichla ocellaris*).

jaw directly from the neurocranium. In combination, these features facilitate exploitation of hard and tough prey by providing a strong bite. In all cichlids, except *Cichla*, the left and right lower pharyngeal jaw bones are united by a suture along their entire medial border (Stiassny, 1981; Casciotta & Arratia, 1993; Fig. 1). In many species, especially those that consume hard and tough prey, this suture is complex and interdigitating, increasing the contact area between the bones (Hulsey, 2006) and presumably increasing the strength of the suture (Jaslow, 1990). In *Cichla*, only the anterior portion of the lower pharyngeal jaw bones are united by a short, straight suture (Stiassny, 1982, 1987; Stiassny & Jensen, 1987; Fig. 1). The functional consequences of this reduced suture is unknown; however, it has been hypothesized to permit the lower pharyngeal jaws to spread apart to accommodate larger prey such as fishes (Stiassny, 1982; Wainwright *et al.*, 2012).

The ontogenetic transition to piscivory is a critical period for many predatory fishes. Transitioning at a small body size can increase growth rate and reduce mortality (Werner & Gilliam, 1984). Body size plays a prominent role in mediating this niche shift because small predators have correspondingly small, more restrictive oral and pharyngeal jaw gapes, and subsequently have prolonged handling time consuming large prey or are prevented from consuming large prey altogether (Mittelbach & Persson, 1998). The horizontal gape of the oral jaws is a strong predictor of maximum prey size (Mihalitsis & Bellwood, 2017); however, pharyngognathous fishes are further limited by a reduced pharyngeal jaw gape due to the union of the lower pharyngeal jaws into a single structure that prevents the two bones from spreading apart to accommodate large prey. Thus, a reduced

pharyngeal gape is a consequence of pharyngognathy. Restricted pharyngeal gape and reduced swallowing performance are thought to have facilitated the extinction of piscivorous cichlids in Lake Victoria following the introduction of a non-pharyngognathous competitor (McGee *et al.*, 2015). Thus, the evolution of pharyngognathy imposes a functional trade-off—an expanded capacity to eat hard or tough prey such as molluscs or algae, but reduced capacity to feed on large prey items such as fishes.

In this study, we explore the functional consequences of reduced suturing of the lower pharyngeal jaw in *Cichla*. We test the hypothesis that the short, straight suture that connects the left and right lower pharyngeal jaws permits these bones to spread apart and increase the pharyngeal gape. We further explore whether this novelty offsets the pharyngeal gape trade-off of pharyngognathy associated with consuming large fish prey. We are particularly interested in the possible role of pharyngeal jaw spreading in juvenile individuals, around the ontogenetic shift to piscivory. We also ask whether this feature permits *Cichla* to achieve a pharyngeal gape similar to those of several non-pharyngognathous piscivores to determine whether there is a functional reversal to pharyngeal gape sizes associated with the non-pharyngognathous condition. To address these questions, we first measured mobility of the lower pharyngeal jaw and pharyngeal and oral gape across an ontogenetic series of *Cichla ocellaris* and two other cichlids that represent independent evolutionary origins of piscivory but have complete pharyngeal sutures (*Crenicichla lugubris* and *Parachromis dovii*), as well as a non-cichlid, non-pharyngognathous piscivore (*Micropterus salmoides*) that has been described as a North American

ecomorphological counterpart to *Cichla* (Norton & Brainerd, 1993). Finally, we compared pharyngeal gapes of juvenile *Cichla* to a broad spectrum of pharyngognathous and non-pharyngognathous piscivores sampled from across percomorph fishes.

MATERIALS AND METHODS

GAPE AND PHARYNGEAL JAW MEASUREMENTS

We measured oral and pharyngeal jaw gape across an ontogenetic series of *Cichla ocellaris* ($N = 28$; 2.7–27.0 cm standard length (SL)), two distantly-related Neotropical cichlid piscivores: South American *Crenicichla lugubris* ($N = 29$; 5.4–25.1 cm SL) and middle American *Parachromis dovii* ($N = 17$; 2.5–14.1 cm SL), and a non-pharyngognathous piscivore: North American *Micropterus salmoides* ($N = 37$; 6.2–32.5 cm SL). These are large-bodied species that principally eat fish as adults (Table 1). The horizontal gape of the oral jaws is a strong predictor of maximum prey size that fish are able to feed on (Mihalitsis & Bellwood, 2017); therefore, we used this measure to characterize oral gape. Measurements were taken on anesthetized individuals immediately after a lethal dose of MS-222 using digital calipers to the nearest 0.1 mm and defined as the maximum horizontal distance that could pass through the oral jaws and into the buccal cavity. Pharyngeal jaw gape was measured with a series of circular cross-section rods and defined as the maximum diameter that could easily pass through the upper and lower pharyngeal jaws and into the oesophagus (Burress *et al.*, 2015; McGee *et al.*, 2015). For *Cichla* specimens, the lower pharyngeal jaw was then removed by dissection. The distance between the posterior tips of the left and right lateral processes was measured at rest and then again after being gently spread to the maximum extent permitted by the suture. In small specimens, the lateral processes were somewhat flexible, a feature that may contribute to the mobility of the lower pharyngeal jaw; however, this was not considered in our measurements. We then calculated a response ratio by dividing the spread distance by the at-rest distance, which characterized the added separation permitted by the reduced suturing between the fifth ceratobranchial bones. All references to body size are standard length, measured from the anterior tip of the upper jaw to the posterior edge of the hypural plate.

Following the same protocol, we also measured oral and pharyngeal gape across a wider spectrum of piscivorous species, including other pharyngognathous cichlids as well as non-pharyngognathous percomorph fishes. We focused on juvenile size classes (6–15 cm) for comparison because the species reach very different

adult sizes and we were particularly interested in this body size range when many ontogenetic transitions to piscivory occur. We sampled six *Cichla* species (*Cichla ocellaris* ($N = 3$), *Cichla monoculus* ($N = 3$), *Cichla temensis* ($N = 2$), *Cichla piquiti* ($N = 3$), *Cichla kelberi* ($N = 3$) and *Cichla melaniae* ($N = 2$)). We also sampled other piscivorous cichlids that exhibit fully sutured lower pharyngeal jaws, including: five Neotropical species (*Crenicichla lugubris* ($N = 3$), *Parachromis dovii* ($N = 3$), *Petenia splendida* ($N = 3$), *Caquetaia myersi* ($N = 3$) and *Nandopsis haitiensis* ($N = 3$)); six species from Lake Malawi (*Rhamphochromis esox* ($N = 2$), *Nimbochromis livingstonii* ($N = 3$), *Dimidiochromis compressiceps* ($N = 3$), *Aristochromis christyi* ($N = 3$), *Champsochromis spilorhynchus* ($N = 3$) and *Champsochromis caeruleus* ($N = 3$)); three species from Lake Tanganyika (*Boulengerochromis microlepis* ($N = 1$), *Lepidolamprologus kendalli* ($N = 3$) and *Cyphotilapia frontosa* ($N = 3$)), and one species from Madagascar (*Paratilapia polleni* ($N = 3$)). We also sampled non-pharyngognathous species that are distributed across the percomorph phylogeny (Alfaro *et al.*, 2018), including the Centrarchidae (black basses and sunfishes: *Micropterus salmoides* ($N = 6$), *Pomoxis nigromaculatus* ($N = 3$), *Lepomis gulosus* ($N = 1$) and *Lepomis cyanellus* ($N = 3$)), Serranidae (groupers and sea basses; *Serranus tigrinus* ($N = 3$) and *Serranus baldwini* ($N = 3$)); the Sebastidae (rockfishes: *Sebastes ruberrimus* ($N = 1$)); the Scorpaenidae (scorpionfishes and lionfishes: *Pterois volitans* ($N = 1$)); the Antennariidae (frogfishes: *Antennarius commerson* ($N = 3$)); the Datnioididae (freshwater tripletails: *Datnioides microlepis* ($N = 3$)); the Anabantidae (African bush fish: *Ctenopoma aqutirostre* ($N = 3$)); the Nandidae (Asian leaf-fish: *Nandus nandus* ($N = 3$)); the Osphronemidae (Asian pikehead gourami: *Luciocephalus aura* ($N = 3$)), and the Polycentridae (South American leaf-fish: *Monocirrhus polyacanthus* ($N = 3$)). These species shift to varied degrees of piscivory as adults (Table 1). In order to correct for differences in body size, pharyngeal gape was expressed as a proportion of oral gape and SL, and oral gape as a proportion of SL. A key aspect of our measurements of pharyngeal gape is that we made measurements on anesthetized specimens, ensuring that soft tissues were supple and the degree of stretching could be realistically determined. The use of formalin fixed material, as in many previous studies, limits these inferences because fixation results in considerable stiffening of soft tissues. All of the data presented here are new and previously unpublished.

PHYLOGENETIC COMPARATIVE ANALYSES

We compared pharyngeal and oral jaw gape among pharyngognathous species, non-pharyngognathous

Table 1. Dietary and trait data for the species used in the study

Species	Region	Degree of piscivory (%)	Piscivory state	Trait state	References
<i>Antennarius commerson</i>	Pacific Ocean	100	High	NP§	Pietsch and Grobecker (1990)
<i>Aristochromis christyi</i>	Lake Malawi	–	High	P†	Konings (2016)
<i>Boulengerochromis microlepis</i>	Lake Tanganyika	–	High	P	Wagner <i>et al.</i> (2009); Konings (2015)
<i>Caquetata myersi</i>	South America	68*	High	P	Winemiller (1989)
<i>Champsochromis spilorhynchus</i>	Lake Malawi	–	High	P	Konings (2016)
<i>Champsochromis caeruleus</i>	Lake Malawi	–	High	P	Konings (2016)
<i>Cichla kelberi</i>	South America	100	High	INT‡	Gomiero <i>et al.</i> (2010)
<i>Cichla monoculus</i>	South America	100	High	INT	Novaes <i>et al.</i> (2004)
<i>Cichla ocellaris</i>	South America	100*	High	INT	Layman <i>et al.</i> (2005); Jepsen <i>et al.</i> (1997); López-Fernández <i>et al.</i> (2012); Montaña & Winemiller (2013)
<i>Cichla piquiti</i>	South America	100*	High	INT	Luiz <i>et al.</i> (2011)
<i>Cichla temensis</i>	South America	100	High	INT	Layman <i>et al.</i> (2005); Jepsen <i>et al.</i> (1997); López-Fernández <i>et al.</i> (2012); Montaña & Winemiller (2013); Aguiar-Santos <i>et al.</i> (2018)
<i>Cichla melaniae</i>	South America	100*	High	INT	Layman <i>et al.</i> (2005); Jepsen <i>et al.</i> (1997)
<i>Crenicichla lugubris</i>	South America	70–91	High	P	Layman <i>et al.</i> (2005); Montaña & Winemiller (2009, 2013); López-Fernández <i>et al.</i> (2012)
<i>Ctenopoma aquitrostre</i>	Africa	–	Moderate	NP	Dutta (1979)
<i>Cyphotilapia frontosa</i>	Lake Tanganyika	–	Moderate	P	Konings (2015);
<i>Danioides microlepis</i>	South-east Asia	–	Moderate	NP	Ou <i>et al.</i> (2017)
<i>Dimidiochromis compressiceps</i>	Lake Malawi	–	High	P	Konings (2016)
<i>Lepidolamprologus kendalli</i>	Lake Tanganyika	–	Moderate	P	Wagner <i>et al.</i> (2009); Konings (2015)
<i>Lepomis gulosus</i>	North America	26	Moderate	NP	Collar <i>et al.</i> (2009); Montaña & Winemiller (2013)
<i>Lepomis cyanellus</i>	North America	16	Moderate	NP	Collar <i>et al.</i> (2009)
<i>Luciocephalus aura</i>	Asia	–	High	NP	Lauder & Liem (1981)
<i>Micropterus salmoides</i>	North America	61–95	High	NP	Collar <i>et al.</i> (2009); Montaña & Winemiller (2013)
<i>Monocirrhus polyacanthus</i>	South America	90	High	NP	Catarino & Zuanon (2010)
<i>Nandopsis haitiensis</i>	Middle America	–	Moderate	P	Řičan <i>et al.</i> (2016)
<i>Nandus nandus</i>	Asia	80	High	NP	Parameswaran <i>et al.</i> (1971)
<i>Nimbochromis livingstonii</i>	Lake Malawi	–	Moderate	P	Konings (2016)
<i>Parachromis dovii</i>	Middle America	55	High	P	Winemiller <i>et al.</i> (1997)
<i>Paratilapia polleni</i>	Madagascar	–	Moderate	P	Stiassny & Gerstner (1992)
<i>Petenia splendida</i>	Middle America	87–100	High	P	Hinojosa-Garro <i>et al.</i> (2013); Cochran-Biederman & Winemiller (2010); Pease <i>et al.</i> (2018)
<i>Pomoxis nigromaculatus</i>	North America	22	Moderate	NP	Collar <i>et al.</i> (2009); Montaña & Winemiller (2013)
<i>Pterois volitans</i>	Indo-Pacific	78	High	NP	Morris & Akins (2009)

Table 1. Continued

Species	Region	Degree of piscivory (%)	Piscivory state	Trait state	References
<i>Rhamphochromis esox</i>	Lake Malawi	–	High	P	Hulsey <i>et al.</i> (2007); Konings (2016)
<i>Sebastes ruberrimus</i>	North Pacific	63–78	High	NP	York (2005); Bizzarro <i>et al.</i> (2017)
<i>Serranus baldwini</i>	Western Atlantic	11–77*	Moderate	NP	Labropoulou & Markakis (1998); Morato <i>et al.</i> (2000); Bilecenoglu (2009)
<i>Serranus tigrinus</i>	Western Atlantic	11–77*	Moderate	NP	Labropoulou & Markakis (1998); Morato <i>et al.</i> (2000); Bilecenoglu (2009)

*Data from representative congeners. †P = Pharyngognathous, §NP = Non-pharyngognathous, ‡INT = Intermediate.

species, and *Cichla* using phylogenetic ANOVA with a residual randomization permutation procedure (Collyer and Adams, 2018) implemented in the geomorph R package (Adams and Otárola-Castillo, 2013). Statistical significance of the model was determined using 1000 permutations. Statistical significance of pairwise comparisons was assessed using the pairwise function implemented in the RRPP package (Collyer and Adams, 2018). For these analyses, we used an existing phylogeny of fishes (Rabosky *et al.*, 2018), pruned to include only the species we sampled. In two cases, the species associated with the tip in the phylogenetic tree and morphological measurements were not exact matches. We associated morphological data for *Luciocephalus aura* with its congener *Luciocephalus pulcher* in the phylogenetic tree. We also associated morphological data from *Datnioides microlepis* with closely-related *Lobotes pacificus* in the phylogenetic tree (Near *et al.*, 2013).

RESULTS

PHARYNGEAL GAPE THROUGH ONTOGENY

In *Cichla*, pharyngeal gape increased with body size; however, the degree of mobility between the left and right LPJs was significantly negatively correlated with body size (Fig. 2). Juvenile specimens (2–3 cm SL) could separate their lateral processes to 1.7-times their resting distance, whereas this fell to 1.05-times in subadults and adults (>14 cm SL; Fig. 1). The suture between left and right lower pharyngeal jaw bones in *Cichla* was limited to 15% of the length of the ceratobranchial in small

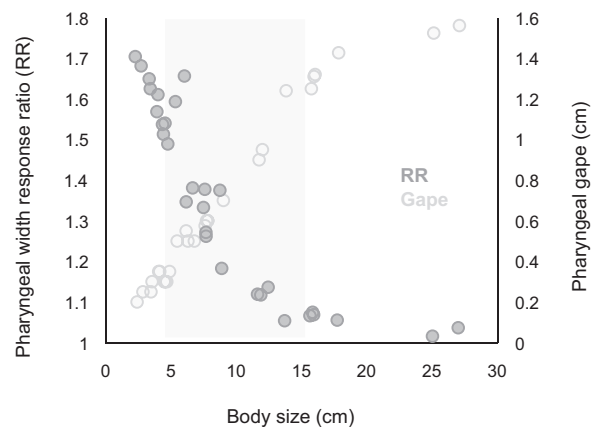


Figure 2. Ontogenetic series depicting the inverse relationship between pharyngeal gape and the expandability (response ratio (RR)) of the lower pharyngeal jaws of peacock bass (*Cichla ocellaris*). The shaded region depicts the general period in which *Cichla* switch to piscivory. Each point is an individual.

specimens (2–3 cm SL) but increased to 45% in 15 cm specimens. Except in the largest specimens, *Cichla* pharyngeal and oral gape were consistently higher than other cichlids, but less than *Micropterus* (Fig. 3A). In all four species, pharyngeal gape was smaller than oral gape throughout ontogeny (Fig. 3A); however, *Crenicichla* and *Parachromis* had shallower slopes indicating that they became more pharyngeal gape limited during ontogeny than *Micropterus* (Fig. 3A). In comparison, pharyngeal gape of juvenile *Cichla* was similar to *Micropterus*, but at larger body sizes was less than *Micropterus* and similar to other cichlids (Fig. 3A). This ontogenetic transition from a pharyngeal gape on par with a non-pharyngognathous piscivore to one that is similar to pharyngognathous species coincides with the period in ontogeny when *Cichla* exhibit a loss of mobility between the left and right lower pharyngeal jaws (Figs 2 and 3A).

PHARYNGEAL GAPE AMONG JUVENILE PERCOMORPHS

All 35 species of cichlids and non-pharyngognathous percomorphs had pharyngeal gapes that were smaller than their oral gape, indicating that they were pharyngeal gape limited (Fig. 3B). Cichlids, with the exception of *Cichla*, had smaller pharyngeal gapes than non-pharyngognathous species (Fig. 3B). After accounting for body size with a phylogenetic ANCOVA, pharyngeal gape differed between pharyngeal jaw

states ($f = 3.63$; $P = 0.032$). Pharyngognathous cichlids had significantly smaller pharyngeal gapes relative to their standard length than non-pharyngognathous percomorphs ($P = 0.0001$; Fig. 4). The pharyngeal gapes of *Cichla* species were significantly larger than pharyngognathous cichlids ($P = 0.003$) but were similar to the non-pharyngognathous percomorph fishes ($P = 0.799$; Fig. 4). Similarly, size of the pharyngeal gape relative to oral gape differed among pharyngeal jaw states ($f = 4.86$; $P = 0.012$). Pharyngognathous cichlids had significantly smaller pharyngeal gapes relative to oral gape than non-pharyngognathous percomorphs ($P = 0.0001$; Fig. 4). *Cichla* had significantly larger pharyngeal gapes relative to their oral gape than other cichlids ($P = 0.001$) and similar pharyngeal gapes as non-pharyngognathous percomorph fishes ($P = 0.784$; Fig. 4). Pharyngeal jaw states did not differ in their oral gapes ($f = 0.28$; $P = 0.744$).

DISCUSSION

Pharyngognathy has evolved independently at least five times, including in cichlids (Cichlidae), wrasses and parrotfishes (Labridae), damselfishes (Pomacentridae), surfperches (Embiotocidae), and within the Beloniformes—in halfbeaks (Hemiramphidae) and flying fishes (Exocoetidae) (Stiassny & Jensen, 1987;

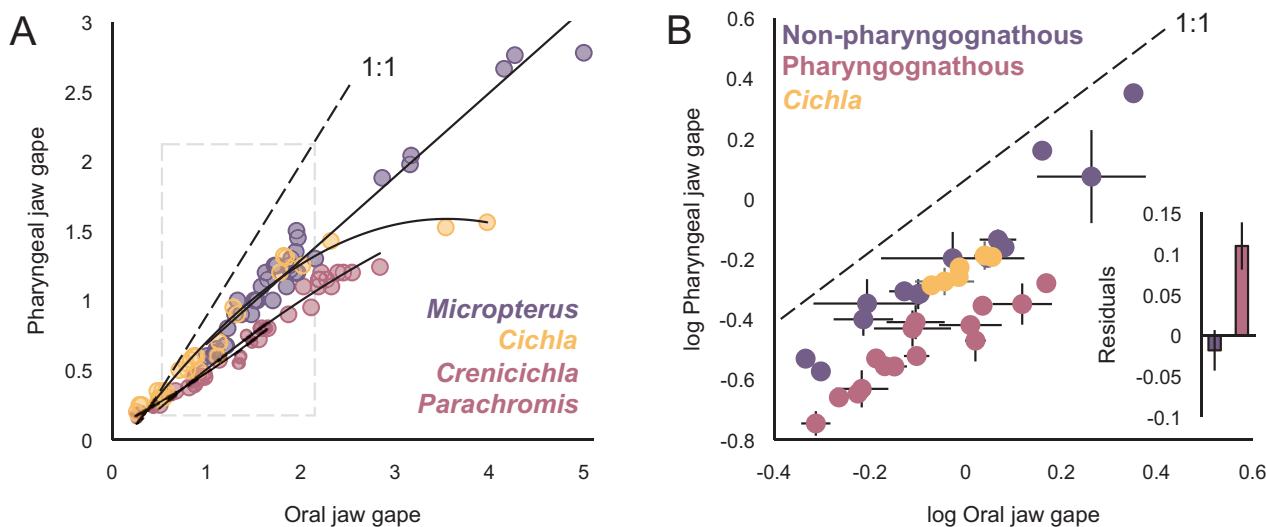


Figure 3. The relationship between oral and pharyngeal gapes among percomorph fishes. Ontogenetic series depicting the relationship between untransformed oral and pharyngeal gape (A). The relationship between log-transformed oral and pharyngeal gape among juveniles (B). The 1:1 line indicates where oral gape limitation (to the left) gives way to pharyngeal gape limitation (to the right). The inset graph depicts the residuals calculated for *Cichla* if considered an in-group of pharyngognathous and non-pharyngognathous datasets. The dashed box in panel A depicts the gape sizes depicted in panel B. Each point in panel A depicts an individual. Each point in panel B depicts 3 species means (\pm 95% confidence interval (CI)).

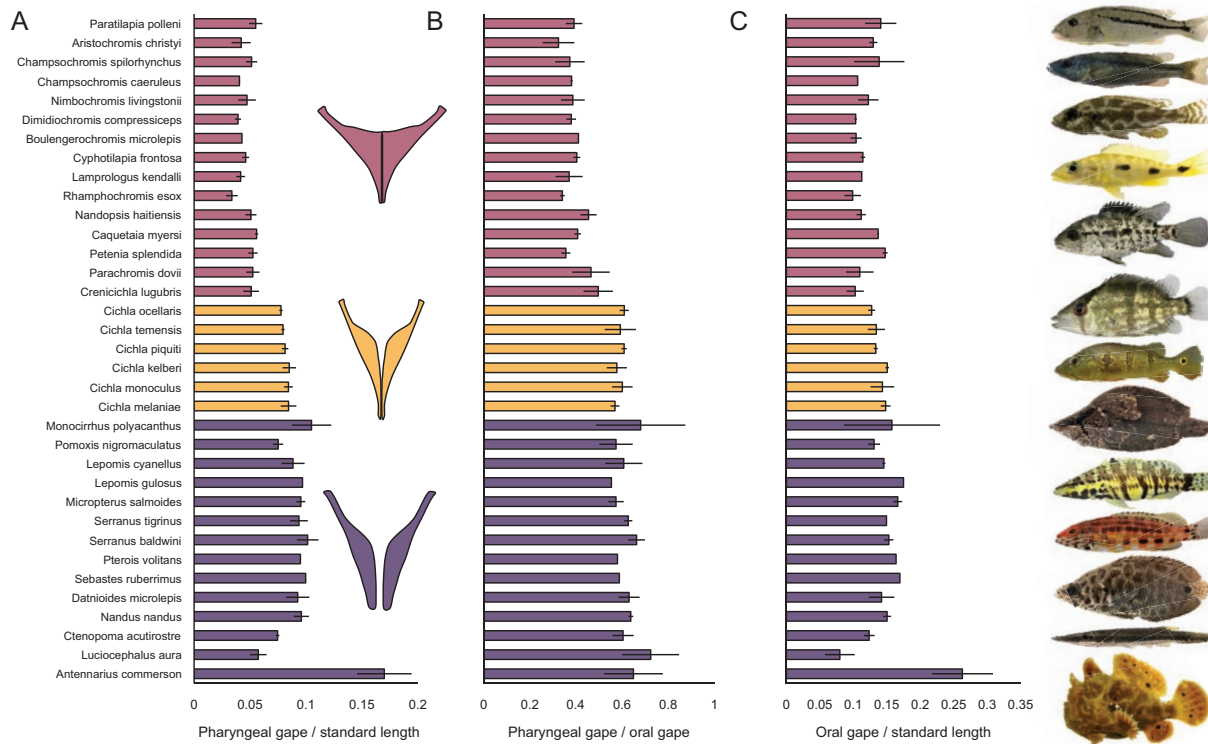


Figure 4. Gape among juvenile (5–10 cm) predatory percomorph fishes. Pharyngeal jaw gape relative to body size (A) and oral gape (B) as well as oral gape (C) relative to body size among pharyngognathous cichlids, *Cichla* and non-pharyngognathous percomorph fishes. Values are mean (\pm 95% CI). Illustrations depict the pharyngeal jaw morphology of each group. Images depict an adjacent species (top-to-bottom): *A. christyi*, *C. caeruleus*, *N. livingstonii*, *B. microlepis*, *C. myersi*, *C. melaniae*, *M. polyacanthus*, *S. tigrinus*, *S. baldwini*, *C. acutirostre*, *L. aura*, and *A. commerson*.

Wainwright *et al.*, 2012). Diets that require intense pharyngeal processing have evolved at an elevated rate in pharyngognathous lineages (McGee *et al.*, 2015). In particular, durophagy has evolved frequently in labrids (Wainwright, 1988; Bellwood *et al.*, 2005) and cichlids (Hulse, 2006; Burress, 2016). Conversely, piscivory is relatively uncommon in pharyngognathous groups. Labrids eat primarily shelled invertebrates, with only a handful of piscivorous species (Bellwood *et al.*, 2005; Burress & Wainwright, 2019). Damselfish and surperches feed on algae, crustaceans and other small invertebrates (Schmitt & Coyer, 1983; Holbrook & Schmitt, 1992; Letourneur *et al.*, 1997; Frédéric *et al.*, 2009). Halfbeaks are omnivorous, feeding upon drifting algae, seagrasses and plankton (Tibbets & Carseldine, 2005; Tibbets *et al.*, 2008), whereas flying fishes feed principally upon plankton (Van Noord *et al.*, 2013). The only pharyngognathous group in which piscivory is widespread is the cichlids, where it has evolved independently at least a dozen times, including

in Lakes Tanganyika, Malawi and Victoria, as well as the Americas (Muschick *et al.*, 2012; Seehausen, 2015; Burress, 2016).

It is unclear how cichlids have frequently transitioned to piscivory despite pharyngognathy. These lineages are usually either single species (e.g. *Boulengerochromis microlepis* and *Petenia splendida*) or are relatively species-poor (e.g. *Bathybates* and *Cichla*), perhaps indicating that piscivory is functionally demanding or that piscivory represents a high adaptive peak that limits subsequent diversification (Collar *et al.*, 2009). Piscivorous cichlids tend to have a dorsal-ventrally shallow lower pharyngeal jaw with long, slender lateral processes and, in some cases, numerous, simple, low-profile teeth (Burress *et al.*, 2015; Burress, 2016). This gracile morphology may ease gape limitation by increasing pharyngeal gape; however, our results show that these species exhibit significantly smaller pharyngeal gapes than our sample of non-pharyngognathous

fishes (Fig. 4; see also McGee *et al.* (2015)). Large body size is associated with piscivory in some cichlids, such as *Boulengerochromis*, *Parachromis* and some *Crenicichla*, a pattern that at least in part reflects that gape scales with body size (Mittelbach & Persson, 1998). In combination with a transition to piscivory, large body size would ease the effect of gape limitation. Although fish are the dominant prey item in adult diets of most piscivorous cichlid species, there is a large amount of variation in how fully and quickly cichlids shift to piscivory during ontogeny (Burress *et al.*, 2013a). Species often progress through a gradual transition in which they also eat crustaceans and insects rather than shift exclusively to fishes or only do so at a large body size (Winemiller, 1989; Layman *et al.*, 2005; Montaña & Winemiller, 2009). *Cichla* appear to shift almost exclusively to piscivory at a relatively small body size. Juveniles (up to 5–7 cm) feed on zooplankton and midges and then shift towards piscivory, consuming principally fish by 10–15 cm (Arcifa, 1993; Jepsen *et al.*, 1997; Meschiatti & Arcifa, 2002; Novaes *et al.*, 2004). In comparison, 5–7 cm *Crenicichla* generally consume less than 25% fish prey, even species that go on to consume > 75% as adults (Burress *et al.*, 2013a; Montaña & Winemiller, 2009), 6–7 cm *Parachromis* consume about 34% fish prey (Figueiredo *et al.*, 2015), and 5–7 cm *Caquetaia* consume about 10% fish prey, but shift to about 60% at around 8–10 cm (Winemiller, 1989).

The transition to piscivory that occurs during ontogeny is a crucial event for piscivorous fishes (Buijse & Houthuijzen, 1992; Olson *et al.*, 1995; Mittelbach & Persson, 1998; Post, 2003). The switch is typically associated with an acceleration in growth rate fuelled by the higher quality diet and can translate into larger body size and higher long-term survival (Olson, 1996; Post *et al.*, 1998). We suggest the possibility that the small-bodied shift to piscivory in *Cichla* may be supported by their reduced pharyngeal suturing, which permits dynamic expansion of the pharyngeal gape of juveniles (Fig. 2). It is interesting that the shift to piscivory occurs at a similar body size in *Cichla* and the largemouth bass (*Micropterus salmoides*), a species that has been held up as an ecomorphological counterpart (Norton and Brainerd, 1993). *Micropterus salmoides* shift to piscivory between 5–10 cm and ultimately feed mostly upon fishes (up to 95% of diet; Mittelbach & Persson (1998)). The rapid ontogenetic shift to piscivory affects survival and growth rate in *Micropterus* (Post, 2003), and in *Cichla* the shift to piscivory has also been linked to growth rate and mortality rates (Winemiller *et al.*, 1997).

A noteworthy strategy that may have allowed some cichlids to feed on fishes is specialization on small fishes. Diets in several highly piscivorous Neotropical cichlids are dominated by small-bodied characids (Winemiller,

1989; Montaña & Winemiller, 2009; Burress *et al.*, 2013b) that are well below any limitations set by maximum gape. Small-bodied characids are often dominant components of fish assemblages throughout the Americas and Africa (Arrington & Winemiller, 2006; Montaña *et al.*, 2015), and their high availability may have been a factor in the widespread evolution of piscivory in cichlids. *Cichla* have been found to rely on small characids during the dry season, but otherwise are known to consume comparatively large prey (Winemiller *et al.*, 1997), including anecdotal evidence that juveniles are capable of consuming prey one-third their body size (Stiassny, 1991).

CICHLA PHARYNGEAL JAW INNOVATION

In all cichlids other than *Cichla*, the left and right lower pharyngeal jaw bones are sutured together along their entire medial border (Stiassny, 1981; Casciotta & Arratia, 1993). The suturing of these bones produces a single lower jaw structure, a robust jaw element that can resist occlusal forces (Hulsey, 2006). Further reinforcement of the lower pharyngeal jaw element, suture and musculature are associated with consumption of hard-shelled prey and the diversity of these features occurs largely along the soft-body to hard-shell prey axis (Hulsey, 2006; Burress, 2016). On one extreme of this axis, prey processing by the pharyngeal jaws does not require forceful biting or shearing of prey items. Piscivores use their pharyngeal jaws to grasp and transport prey to the oesophagus. Pharyngognathy makes this process less efficient due to reduced pharyngeal gape (McGee *et al.*, 2015; Fig. 4).

In *Cichla*, the left and right lower pharyngeal jaw bones are united by a short, straight suture at their anterior tip (Stiassny, 1981; Casciotta & Arratia, 1993; Fig. 1). This configuration allows the lateral processes of the lower pharyngeal jaw bones to spread apart, producing an increased pharyngeal gape (Fig. 2). The capacity for spreading in the lower pharyngeal jaws declines sharply during ontogeny and is negligible by 14 cm. In juveniles, mobility in the midline joint is made possible by a relatively loose ligamentous connection between the bones. During ontogeny, the suture expands and becomes tighter, spanning about 15% of the length of the lateral process in juveniles (~ 1.5 cm SL) and up to about 45% in adults, reducing the capacity of the pharyngeal jaw bones to spread. The initial suturing of the lower pharyngeal jaw occurs sometime between 1 and 3 months of age in Nile tilapia, *Oreochromis niloticus* (Pabie *et al.*, 2009). It is unknown if this process proceeds from the anterior end and expands posteriorly; however, a heterochronic mechanism through retardation of suture growth rate or delay in the onset of its development may be involved in the evolution of the reduced suturing found in *Cichla*.

The potential for evolution to lead to a reduction of the connection between the pharyngeal jaw bones in *Cichla* may depend on an important feature of cichlid pharyngognathy. The left and right lower pharyngeal jaw bones are sutured together in cichlids (as they are in the false scorpion fish *Centrogenys*); however, they are fused together in the other pharyngognathous groups, including labrids, pomacentrids, embiotocids and beloniforms (Wainwright *et al.*, 2012). This sutured condition may have presented less of a barrier to its reduction in *Cichla*, as there are no other known instances of such a feature in taxa with fused lower pharyngeal jaws.

The reduced connection between lower pharyngeal jaw bones in *Cichla* allows them to overcome one functional trade-off incurred with pharyngognathy when they are young. An expandable pharyngeal gape facilitates consumption of large prey and may be an important factor in permitting the switch to piscivory to occur at a small body size. A relatively early ontogenetic shift to piscivory may have positive consequences for growth, fitness, and survivorship in *Cichla*, as it does in some other piscivores (Post, 2003). Therefore, gape limitation is especially influential for juveniles because gape scales strongly with body size (Mittelbach & Persson, 1998). The *Cichla* pharyngeal jaw novelty permits juveniles to have a pharyngeal gape size that is similar to non-pharyngognathous percomorphs (Figs 3 and 4). As adults, *Cichla* pharyngeal jaw mobility wanes and their pharyngeal gape becomes similar to other pharyngognathous cichlids; however, at this point in ontogeny, large body size may ease gape limitation (Mittelbach & Persson, 1998).

The reduced suturing in the lower pharyngeal jaw of *Cichla* is one of several anatomical features that have previously been proposed to relate to piscivory (Stiassny, 1982, 1991; Norton and Brainerd, 1993). Other noteworthy pharyngeal features include an extreme lower pharyngeal jaw shape (Burruss, 2016), simplified dentition of the lower jaw and enlarged third pharyngobranchial bones of the upper jaw (Casciotta & Arratia, 1993), several specific positional and shape changes in bones of the upper pharyngeal jaws and the presence of a dorsal articulating facet on pharyngobranchial 3 (Stiassny, 1982), reduced cross sectional diameter of the muscular sling (Burruss *et al.*, 2020), and the loss of the semi-circular ligament system (Stiassny, 1991). This latter trait is plesiomorphic or widespread among percomorphs, was lost in other cichlids, and appears again in *Cichla* (Stiassny, 1982, 1991). Reduction of pharyngeal suturing could also be thought of as a return to a more ancestral condition, although reduced suturing is not known in outgroup

taxa. Other traits, such as the dorsal articulating facet on pharyngobranchial 3, show no parallel in outgroup taxa. Reappearance of the semi-circular ligaments in *Cichla* has been termed atavistic (Stiassny, 1991) and the appearance of a more ancestral condition in this trait and the suturing of the lower pharyngeal jaws of *Cichla* raises the possibility that they may be united by a common developmental genetic process that has been slowed or started later in development in *Cichla*, resulting in derived traits that represent more plesiomorphic conditions found outside cichlids (Stiassny, 1991). Although we have identified important functional consequences of one of these novelties, the reduced suturing of the lower pharyngeal jaw bones, we consider it likely that some of the other derived traits contribute to functional aspects of piscivory in *Cichla* and we look forward to future research that explores the functional morphology of this taxon more fully.

Our observations on the functional consequences of reduced pharyngeal suturing in *Cichla* highlight the importance of trade-offs that often accompany functional innovations. Trade-offs may be expected to affect the evolutionary consequences of innovations by biasing subsequent diversification away from niches that are blocked by the trade-off (McGee *et al.*, 2015). We suggest that significant trade-offs are a general feature of functional innovations and should be considered when exploring their impacts on ecological diversification. Indeed, it may be that the more substantial the innovation, the more substantial the trade-off. As an example, the evolution of powered flight clearly affected bird diversification in positive ways (Padian & Chiappe, 1998), but it also introduced a constraint on body mass due to metabolic and performance demands (McNab, 1994; Tobalske & Dial, 2000; Elliot *et al.*, 2013). There is a tendency to focus on the enabling consequences of functional innovations; however, the potency of trade-offs may be a major factor in shaping the diversity of macroevolutionary outcomes from life's innovations.

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SHARED DATA

Data deposited in the Dryad digital repository ([Burress & Wainwright, 2020](#)).