Function of a key morphological innovation: fusion of the cichlid pharyngeal jaw

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The pharyngeal jaw of cichlids may represent a key innovation that facilitated their unparalleled trophic divergence. In cichlids, ‘fusion’ of the lower pharyngeal jaw (LPJ) results from suturing between the two lower ceratobranchials. To examine, what novel abilities a more extensively fused pharyngeal jaw may confer, the function of LPJ suturing was examined in Heroine cichlids. Greater LPJ suturing, pharyngeal jaw splitting under compression and the forces used to crush molluscs in the wild suggest increased LPJ fusion in the trophically polymorphic Herichthys minckleyi operates to strengthen the pharyngeal jaw. Among Heroine cichlid species, the presence of an external LPJ suture and feeding specialization on molluscs was evolutionarily quite variable, but greater LPJ fusion estimated from the amount of external suturing was highly correlated with molluscivory. Throughout cichlid diversification, increased pharyngeal jaw fusion via suturing has likely helped to reinforce the LPJ during pharyngeal processing thereby facilitating the ability of cichlids to exploit durable prey.

Keywords: Cichlidae; comparative methods; feeding; macroevolution; molluscivory

1. INTRODUCTION

The innovations in the cichlid pharyngeal jaw may have facilitated the utilization of novel prey and ultimately led to the unparalleled trophic diversification of these fishes (Liem 1973). Although most bony fishes have pharyngeal gill arches modified to process prey (Liem 1986; Wainwright 1989), the cichlid pharyngeal jaw uniquely exhibits novel upper pharyngeal jaw joints, a ‘muscular sling’ and suturing between the two-fifth ceratobranchial elements (figure 1). This suturing results in a functionally fused lower pharyngeal jaw (LPJ) (Liem 1973), but the degree of fusion via suturing is highly variable (Kullander 1998). As the cichlid LPJ both resists and exerts forces during prey processing, this variability in LPJ fusion should relate to forces exerted on prey (Stiasnys & Jensen 1987; Kullander 1998). To examine the trophic consequences of cichlid pharyngeal jaw fusion, I investigated whether greater LPJ suturing enhances the ability to exploit durable prey in the trophically polymorphic Herichthys minckleyi and tested the evolutionary association in Heroine cichlids between LPJ suturing and crushing hard-shelled molluscs.

Suturing integrates the two halves of the LPJ into a single unit. Because the pharyngeal jaw is the primary location of prey processing in most bony fishes (Liem 1973), pharyngeal jaw modifications frequently determine, what prey fishes can exploit (Wainwright 1989; Galis & Drucker 1996; Grubich 2003). The importance of pharyngeal jaw modifications to cichlid trophic diversity is clearly evident in species that are polymorphic in their pharyngeal morphology. For example, in H. minckleyi (Kornfield & Taylor 1983), one pharyngeal morphotype specializes in crushing molluscs (molariform), while the other pharyngeal jaw type (papilliform) utilizes prey that require less force to process (Hulsey et al. 2005). These alternative pharyngeal morphotypes (figure 2a,b) occur sympatrically (Kornfield & Koehn 1975), interbreed (Kornfield & Taylor 1983) and differ in little other than what prey they utilize (Sage & Selander 1975). Of all the fresh water prey, molluscs that molariform H. minckleyi and other cichlids crush should require the most forceful pharyngeal bite to process (Vermeij & Covich 1978; Vermeij 1987). Therefore, if greater pharyngeal jaw fusion is important in adapting the jaw to exploit more durable prey, molariform H. minckleyi should have more heavily sutured LPJs and better resist compressive forces encountered when crushing molluscs.

Adaptations for exploiting particular prey likely arise within populations (Meyer 1990; Schluter & Nagel 1995), but macroevolutionary divergence is often the best evidence available that a particular innovation was key to a clade’s diversification (Simpson 1953). Linking modifications within a species like H. minckleyi to changes among species would increase the mechanistic understanding of how LPJ fusion may have generally influenced cichlid trophic divergence. As molluscivory has likely evolved multiple times in the Heroine cichlid clade that includes H. minckleyi (Winemiller et al. 1995; Hulsey et al. 2005), this cichlid lineage is ideal for examining the macroevolutionary association between greater cichlid LPJ fusion and crushing durable mollusc shells.

I examined cichlid LPJ fusion using morphometrics, empirical tests of the strength of the LPJ, diet analyses and phylogenetic comparative methods. I first quantified external suturing in H. minckleyi molariforms and papilliforms. Then I tested if, the forces that split the LPJ along the suture differed between molariforms and papilliforms and if suturing may reduce damage to the pharyngeal jaw.
The labroid pharyngeal anatomy, implicated as a key innovation (Liem 1973) has three basic components: (a) the muscular sling formed from the pharyngeal muscles, (b) two synovial joints in the upper pharyngeal jaw and (c) a single ‘fused’ LPJ. In cichlids, the fusion of the LPJ is formed from the two-fifth ceratobranchials being sutured together.

Figure 1. The labroid pharyngeal anatomy, implicated as a key innovation (Liem 1973) has three basic components: (a) the muscular sling formed from the pharyngeal muscles, (b) two synovial joints in the upper pharyngeal jaw and (c) a single ‘fused’ LPJ. In cichlids, the fusion of the LPJ is formed from the two-fifth ceratobranchials being sutured together.

Figure 2. The dorsal view of LPJs of H. minckleyi. (a) The papilliforms are specialized to shred plants. (b) The molariforms are specialized to crush snails and are diagnosable by their large molariform teeth.

2. MATERIAL AND METHODS
(a) Suture quantification
To measure the amount of LPJ suturing, the LPJ was removed from fishes that were collected from their native range (sites available from the author). After measuring standard length (SL), fishes were cleared using trypsin and dyed with Alcian blue cartilage stain and Alizarin red bone stain (Dinkerhus & Uhler 1977). The LPJ of the specimens examined could not be destroyed to examine internal interdigitation. Therefore, I quantified the external suturing of the LPJ (figure 3). Although external suturing is not a direct measure of the internal interdigitation of the pharyngeal jaw, three-dimensional computed tomography scans of the LPJ suggest greater external suturing reflects greater internal integration between the paired ceratobranchial bones that form the LPJ of H. minckleyi (Hulsey, personal observation).

To estimate the percentage of the LPJ that was sutured, the total length of the jaw, LT, from anterior tip of the keel to the posterior centre of the jaw was measured to the nearest 0.1 mm using calipers (figure 3b). Then, the linear distance from the anterior-most initiation of suturing to the posterior-most end, LS, along the centre of the jaw was measured (figure 3c). If, there was no suture, LS was zero. Subsequently, the suturing of the dried LPJ was photographed using a digital microscope. The image was then imported into NIH Image (http://rsb.info.nih.gov/nih-image/about.html) and two measurements were taken. First, the winding length, LW, of the suture was traced digitally (figure 3c) and its length calculated. Then, the linear length, Lp, between the anterior-most point, where suturing of the jaw began and the posterior-most end of jaw suturing was calculated using a straight line. The winding length was then divided by the linear length. This value was multiplied by the percentage of the length of the LPJ that was sutured in order to calculate the percentage the suture increased in the perimeter of contact, Pp (equation (2.1)), between the two halves of the pharyngeal jaw as compared to an unsutured jaw

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P_L = \frac{L_S}{L_T}(L_W/L_S). 
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(b) Quantifying suture and its function in H. minckleyi
I compared Pp between individuals exhibiting the alternative pharyngeal dentition in H. minckleyi (figure 2). Nine molariform (Range: 69.9–146.0 mm SL) and nine papilliform H. minckleyi (Range: 66.4–133.2 mm SL) were cleared and stained, pharyngeal jaws extracted and suture Pp quantified. Then, with an ANCOVA, I tested whether Pp was significantly different between morphotypes using SL as a covariate.

I also determined if the LPJ in the H. minckleyi pharyngeal morphotypes resisted different amounts of compressive force. For 12 molariforms (Range: 80–147.2 mm SL) and 12 papilliforms (Range: 77.1–145.4 mm SL), wild-caught fishes were sacrificed with an overdose of MS222, their SL measured and their LPJ removed by dissection. Subsequently, the LPJ was laid on the lower force plate of an Accuforce Cadet force gauge (0–1000 Newton, Ametek, Inc. Pennsylvania, USA) with the dorsal side of the jaw facing the upper force plate. I then placed a Mexithauma quadriplanatum snail, approximately 5 mm in shell length, aperture down, on the dorsal crushing surface of the LPJ to mimic the position of a snail during a pharyngeal crushing event. This snail is frequently crushed by molariform H. minckleyi (Hulsey et al. 2005). The snail and LPJ were then squeezed between the opposing force plates of the force gauge until the LPJ split in half along the suture. Using SL as a covariate, an ANCOVA with SL as a covariate. This maximum molariform crushing force was estimated from snail opercula taken from gut contents of wild-caught fishes (Hulsey et al. 2005).

(c) Molluscivory
To determine if LPJ suturing was evolutionarily correlated with molluscivory, I obtained the percent volumetric contribution of molluscs to the gut contents of 32 Heroine species (see electronic supplementary material, appendix 1). For 22 species, the proportional contribution of molluscs to their diet was extracted from published sources. However,
only the frequency of occurrence of prey was reported for five of these species (Chavez-Lomeli et al. 1989). In two of these five species, molluscs were never recovered. But, for Para-theraps fenestratus, Astatheros robertsoni and Thorichthys meeki molluscs were recorded and for these the contribution of molluscs was estimated. The volumetric contribution of all prey types to the diet of each species was estimated from the frequencies reported. These frequencies were transformed using the average of a prey type’s volumetric contribution when included in the diet of a single H. minckleyi (Hulsey et al. in press). The estimated contribution for all major prey types was added together and molluscivory for the three species was estimated. For 10 additional species, I quantified molluscivory from gut contents (figure 4). The gut contents were examined in fishes collected from localities reported in Hulsey et al. (2004) in approximately 10 individuals per species (Astatheros macracanthus, n = 5; Herichthys bartoni, n = 10; Herichthys labrident C; n = 10; H. labrident ML, n = 6; Herichthys tamasopoensis, n = 10; Parameenroplus bulleri, n = 10; Paratheraps guttulatus, n = 10; Thorichthys callolepis, n = 9; Thorichthys ellioti, n = 10; Thorichthys helleri, n = 10). The volumetric contributions of all diet items were identified as molluscs or other (Thorpe & Covich 1991) and measured using water displacement. For the phylogenetic correlations, arcsin transformations of molluscivory were used because the proportions were non-normally distributed.

(d) Comparative analyses of LPJ suturing and molluscivory

After $P_L$ was quantified as detailed above for approximately three specimens per species in 31 Heroine species (excluding H. minckleyi), the correlation between molluscivory and $P_L$ was examined (figure 4). The range of $L_S/L_T$ and $L_Q/L_S$ are reported, but the species mean $P_L$ was used in the comparative analyses. Because species are not evolutionarily independent (Felsenstein 1985), the correlation was examined using an independent contrast analysis. For the phylogenetic backbone of this analysis, I used the phylogeny in Hulsey et al. (2004) based on sequences of the cytochrome b gene (1137 bp). The phylogenetic topology (figure 4) with branch lengths was first imported into Tree EDIT 1.0 (Rambaut & Charleston 2002). The branch lengths in the topology were smoothed using non-parametric rate smoothing (Sanderson 1997) with mid-point rooting because there was substantial heterogeneity in branch lengths due to non-clocklike molecular evolution (Hulsey et al. 2004). Species for which the LPJs were not examined and all but one sequence for each species examined were then pruned from the topology. The branch lengths and topology for the remaining species were exported into comparative analysis by independent contrasts (CAIC) (Purvis & Rambaut 1995).

The phylogenetic independent contrast analyses were performed in several ways. First, the correlation of $P_L$ and arcsin transformed values of molluscivory were examined using the ‘crunch’ algorithm that assumes all variables are continuous. Then, because many species had zero or low contribution of molluscs to the diet, I also examined the correlation when mollusc feeding was treated as a categorical variable. Species that included less then 2% molluscs in their diet were categorized as (0) non-molluscivores and species with greater than 2% molluscs in their diet as (1) molluscivores. Then, with the ‘branch’ algorithm, which allows dichotomous variables to be tested in an independent contrast framework in CAIC, it was determined if $P_L$ was consistently greater in those clades coded as molluscivores. Finally, because the $P_L$ of the jaws in H. minckleyi appeared to be slightly correlated with SL, I reanalysed the above correlations using the residuals of a reduced major axis regression between average SL of specimens and $P_L$. Also, the presence of greater than 2% molluscs in the diet was mapped onto the phylogeny using parsimony (Maddison & Maddison 2000) to provide an initial estimate of the number of times molluscivory may have evolved in Heroine cichlids.

3. RESULTS

(a) Quantifying suture and its function in H. minckleyi

In H. minckleyi, both $L_S/L_Q$ and $L_Q/L_S$ were greater in molariforms (see electronic supplementary material, appendix 1). The molariforms had significantly greater $P_L$, than papilliforms (ANCOVA, $n = 9$ molariforms and 9 papilliforms, $F = 11.2, p = 0.004$), although, there was also an effect of SL on the amount of suturing ($F = 15.4, p = 0.001$). When the jaws of H. minckleyi were crushed, the LPJ always split along the suture. The teeth of the papilliforms sometimes broke prior to jaw splitting, but the molariforms’ large molars were never visibly damaged. The force (figure 5) needed to split molariforms’ jaws increased substantially with SL ($\log N = 3.33 \ (\log SL) - 4.75, R^2 = 0.72$). The increase in force needed to split the

Figure 3. There is substantial variation in suturing of the ventral LPJ in cichlids. In (a) A. robertsoni, the two halves of the LPJ meet but there is no external suture, while other species (b and c) exhibits extensive suturing. (b) To estimate the suture length, the length of the jaw from the tip of the LPJ keel to the posterior centre end of the LPJ, $L_S$, was first measured using calipers and then (c) the length of the suture, $L_W$, was measured. Subsequently, the dried bone was photographed using a digital microscope and the suture quantified. The $L_D$, $L_S$ and $L_W$ were used to calculate (equation (2.1)) the percent the suture increased the perimeter of contact between the two halves of the LPJ, or $P_L$, as compared to an unsutured jaw.

papilliform jaw ($\log N = 0.67$ (log SL) + 0.39, $R^2 = 0.72$) was much less than the force needed to split the molariform LPJ (ANCOVA, $n=12$ molariform LPJ and $n=12$ papilliform LPJ, $F=11.3$, $p=0.002$). The LPJ of the molariforms required greater force to split than the maximum force this morphotype used in the wild to crush snails (ANCOVA, $n=12$ molariform LPJ and $n=33$ estimates of maximum force from molariform gut contents, $F=27.3$, $p<0.001$). However, this was not true in the papilliforms (ANCOVA, $n=12$ papilliform LPJ, $F=29.2$, $p<0.001$). The jaw of the papilliforms split along the suture at forces that were generally less than

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**Figure 4.** The phylogenetic relationships, evolution of molluscivory and photos of LPJ suturing in representative Heroine species. The percent contribution of molluscs to the diet of each species and the mean $P_L$ are depicted next to the species name. The subscript above the percent indicates the source of the diet information: 1, Hulsey et al. 2005; 2, this study; 3, Darnell 1962; 4, Chavez-Lomeli et al. 1989; 5, Winemiller et al. 1995; 6, Bussing 1993; 7, Winemiller 1989; 8, Gestring & Shafland 1997; 9, Yanez-Arancibia 1978; 10, Martinez-Palacios & Ross 1988. The evolution of molluscivory (greater than 2.0% molluscs in the diet) is mapped onto the phylogeny using parsimony. The parsimony reconstructions suggest molluscivory may have evolved six times independently in Heroine cichlids. The six examples of closely related non-molluscivorous and molluscivorous cichlid LPJs display the variability in Heroine LPJ fusion.
Media Luna (figure 4). feeding habit evolved at least six times independently in molluscivory (greater than 2% in the diet) suggest this all included greater than 5% molluscs in H. minckleyi ‘Media Luna’, amount of molluscs (less than 2%), or no molluscs in and Petenia splendida (suturing were T. ellioti Proc. R. Soc. B in the wild. Cichlasoma salvini crush snails in the wild (broken lines; Hulsey estimated maximum force molariform H. minckleyi H. minckleyi suggest obtained from the few individuals examined within species increased suturing. However, the limited range of values that was sutured as well as the amount the winding length species, there was variability in the proportion of the LPJ material, appendix 1). For the Heroine species, 26% was the greatest proportion of its jaw sutured (55%) of any Heroine cichlid studied (see electronic supplementary g). The amount of molluscs obtained (continuous values of molluscivory: d.f. = 30, slope = 0.36, r = 0.84, p < 0.001; and categorical values of molluscivory: d.f. = 7, slope = 0.10, r = 0.75, p = 0.033).

what an equivalent sized molariform used to crush snails in the wild. 

(b) Molluscivory Astatheros alfarji, A. macracanthus, A. robertsoni, ‘Cichlasona’ trimaculatum, Paratheraps maculicauda, T. callolepis, T. elliott, T. meeki, H. labridens ‘Cascadas’, H. labridens ‘Media Luna’, Herichthys pantosticus and molariform H. minckleyi all included greater than 5% molluscs in their diet (figure 4). Many species included a small amount of molluscs (less than 2%), or no molluscs in their diet. Unordered parsimony reconstructions of molluscivory (greater than 2% in the diet) suggest this feeding habit evolved at least six times independently in Heroine cichlids (figure 4).

(c) Suture quantification Cichlasoma salvini, Herotilapia mulitispina, A. robertsoni and Petenia splendida completely lacked suturing (P2 = 0.00). Caquetaia kraussi (P2 = 0.19), Nandopsis dovii (P2 = 0.20) and Archocentrus centranuchus (P2 = 0.02) displayed very limited suturing. Although A. robertsoni had an unsutured LPJ, its close relative A. alfarji had the greatest proportion of its jaw sutured (55%) of any Heroine cichlid studied (see electronic supplementary material, appendix 1). For the Heroine species, 26% was the average proportion of the LPJ that was sutured within species, there was variability in the proportion of the LPJ that was sutured as well as the amount the winding length increased suturing. However, the limited range of values obtained from the few individuals examined within species suggest P2 differs consistently and substantially among species. The cichlid species having the greatest amount of suturing were A. macracanthus (P2 = 1.18), H. labridens Media Luna (P2 = 1.39) H. labridens Cascadas (P2 = 1.36) and molariform H. minckleyi (P2 = 1.77).

(d) Comparative analyses of LPJ suturing and molluscivory A significant correlation between P2 and molluscivory was robust to all coding of the variables. The correlation of independent contrasts was highly significant whether quantitative measures (d.f. = 30, slope = 0.37, r = 0.83, p < 0.001) or categorical designations (d.f. = 7, slope = 0.10, r = 0.75, p = 0.031) of molluscivory were used. When the residuals of the reduced major axis regression of P2 versus specimen SL were used, similar results were obtained (continuous values of molluscivory: d.f. = 30, slope = 0.36, r = 0.84, p < 0.001; and categorical values of molluscivory: d.f. = 7, slope = 0.10, r = 0.75, p = 0.033).

4. DISCUSSION
In the polymorphic H. minckleyi, the amount of suturing adds to the list of putatively adaptive characteristics that differ between molariform snail crushers and papilliform plant processors (Kornfield & Taylor 1983; Liem & Kaufman 1984; Hulsey et al. 2005). Molariform H. minckleyi possess the greatest average amount of external suturing of any Heroine cichlid examined (figures 3c and 4) and much greater suturing throughout ontogeny than papilliforms. However, it is unclear, if the amount of suturing is genetically controlled in this species or in any other Heroine. Although, the different pharyngeal morphologies in H. minckleyi appear to have some genetic basis (Trapani 2003), much of the pharyngeal jaw variation may be a phenotypically plastic response to crushing the unusually robust snail prey found in their native habitat (Vermeij & Covich 1978; Liem & Kaufman 1984; Hulsey et al. 2005).

In H. minckleyi, the LPJ consistently split along the suture prior to extensive damage occurring to the remainder of the jaw. It took substantially more force to split the molariform LPJ along the suture than the force used by molariforms to crush snails in the wild. Whereas a molariform that is 150 mm in SL can produce 115 N of crushing force (Hulsey et al. 2005), its LPJ can resist approximately 600 N of crushing force before splitting along the suture. A similarly sized papilliform LPJ resists only about 60 N before splitting at the suture. Because greater suturing should act to reduce damage to the jaw and damage to the feeding apparatus should be selected against (Vermeij 1987; Van Valkenburgh 1988), greater LPJ fusion through increased suturing may be a critical modification of the molariform jaw. The minimal fusion of the papilliform LPJ and its inability to resist substantial crushing forces may explain why papilliforms rarely utilize snails as prey (Hulsey et al. 2005). Strikingly, if papilliforms generated the forces that molariforms frequently use to crush molluscs, papilliform H. minckleyi would likely split their LPJ into separate halves at the suture.

Specialization in molluscs probably evolved several times within Heroine cichlids (Winemiller et al. 1995, figure 4). Twelve of the 32 species included herein had gut contents composed of more than 5% molluscs by volume and molluscivory may have evolved at least six times, independently. Notably, molluscivory has also evolved numerous times in other cichlid clades such as Aequidens (Winemiller et al. 1995), Astatoreochromis, Lamprologus (Liem 1973) and Serranochromis (Winemiller et al. 1995). Suturing of Heroine cichlid jaws is also exceptionally

Figure 5. The LPJ of an onontogenetic series of molariform and papilliform H. minckleyi were crushed using a force gauge. When the jaws split at the suture, the force was recorded. The compressive resistance of the jaws was then compared to the estimated maximum force molariform H. minckleyi used to crush snails in the wild (broken lines; Hulsey et al. 2005). The failure of molariform jaws (filled circle) was much greater than the maximum force they use to crush snails in the wild (p < 0.001). However, the onontogenetic trajectory of failure of papilliform jaws (open square) was significantly lower than both the resistance of the molariform jaws (p = 0.002) and the forces molariforms used in the wild to crush snails (p < 0.001).
variable (figure 4) and suturing has probably evolved and been lost multiple times in Heroinae, as it has in other cichlids (Kullander 1998). Pharyngeal musculature and other skeletal elements are undoubtedly important in adapting the cichlid pharyngeal jaw to mollusc crushing (Liem 1973; Hulsey et al. 2005; Wainwright 2005). However, there is a clear relationship between greater suturing and mulluscivory both among evolutionarily independent lineages of Heroine cichlids and within H. minckleyi. Micro- and macroevolutionary lability in LPJ fusion likely makes it easy for cichlids to evolve to exploit durable prey.

Cichlids share several morphological innovations in their pharyngeal jaw with wrasses (Labridae), damselfish (Pomacentridae), parrotfish (Scaridae) and the surfperches (Embiotocidae). These major groups of fishes were once included in a putatively closely related group named the Labroidei (Kaufman & Liem 1982) that is now recognized as being paraphyletic (Streelman & Karl 1997). Monophyly of the Labroidei was originally named the Labroidei (Kaufman & Liem 1982) that is now recognized as being paraphyletic (Streelman & Karl 1997). Monophyly of the Labroidei was originally hypothesized because of their structurally similar pharyngeal jaws, although, the LPJ in non-cichlid labroids hypothesized because of their structurally similar pharyngeal jaws, although, the LPJ in non-cichlid labroids are frequently consumed by cichlids (Stiassny & Jensen 1987). Like cichlids with extensive LPJ suturing, many wrasses and surfperch feed upon hard-shelled crustaceans or molluscs (Liem 1986; Randall et al. 1997) and parrotfish pharyngeal jaws are likely modified to break down extremely tough prey such as coral (Bellwood 1995). As in cichlids with extensive LPJ suturing, labroid LPJ fusion may have facilitated the exploitation of durable prey (Wainwright et al. 2004; Wainwright 2005). Most bony fishes and, therefore, the ancestors to all groups with a labroid pharyngeal jaw likely had a divided LPJ with no suturing (Liem 1986; Wainwright 1989). However, LPJ fusion through suturing is not limited to cichlids. Suturing of the two ceratobranchials composing the cichlid LPJ resemble the condition found in a several non-Labroidei fish clades such as Gerres, Lepomis and Pogonias that lack a muscular sling but frequently consume molluscs (Stiassny & Jensen 1987; Galis & Drucker 1996; Grubich 2003). The repeated coupling of greater LPJ fusion and durophagy during teleost evolution makes the apparent pharyngeal jaw convergence between cichlids and other labroids functionally less surprising.

Both the splitting of LPJs in H. minckleyi and the phylogenetic comparative analyses indicate a more extensively fused jaw is advantageous for the exploitation of durable prey. However, the variation in cichlid suturing suggests there are probably disadvantages to completely fused jaws. When manipulating prey, less fusion might facilitate independent movement or greater bending of the two halves of the LPJ (Wainwright 2005). Fused jaws may also decrease the pharyngeal gape and hinder swallowing larger prey like fishes (Wainwright 1987). Piscivory is rare in the other labroid groups (Randall et al. 1997; Wainwright et al. 2004) and cichlid groups that are primarily piscivorous like Cichla, Crenicichla and Petenia (Chavez-Lomeli et al. 1988; Winemiller et al. 1995; Hulsey & Garcia de Leon in press) all have limited LPJ fusion (Kullander 1998). Having a flexibly sutured LPJ as opposed to a single bony element may have permitted cichlids to exploit both large prey types such as fishes as well as hard-shelled prey like no other group of aquatic vertebrates.

Evaluating if a complex key innovation (sensu Simpson 1953) like the cichlid pharyngeal jaw is responsible for trophic diversification is difficult. Evolutionary novelties in organismal design are not always replicated (Levinton 1988; Padian 2001) and novel structures cause changes that could themselves be interpreted as innovations (Cracraft 1990). However, when variability in transitional phenotypes exists, what favoured the evolution of a putative innovation can be tested (Greene 1983). Furthermore, verifying that a phenotype is favoured under realistic ecological circumstances can provide support for the hypothesis that particular character states, like greater LPJ fusion, are crucial to specialization on particular prey (Wainwright 1987). In order to evaluate the evolutionary and ecological consequences of their unique trophic apparatus, it may be key to more critically assess the structural and functional consequences of diversity in the cichlid pharyngeal jaw.

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