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## SYMPOSIUM

# Do Coral Reefs Promote Morphological Diversification? Exploration of Habitat Effects on Labrid Pharyngeal Jaw Evolution in the Era of Big Data

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**Synopsis** Coral reefs are complex marine habitats that have been hypothesized to facilitate functional specialization and increased rates of functional and morphological evolution. Wrasses (Labridae: Percomorpha) in particular, have diversified extensively in these coral reef environments and have evolved adaptations to further exploit reef-specific resources. Prior studies have found that reef-dwelling wrasses exhibit higher rates of functional evolution, leading to higher functional variation than in non-reef dwelling wrasses. Here, we examine this hypothesis in the lower pharyngeal tooth plate of 134 species of reef and non-reef-associated labrid fishes using high-resolution morphological data in the form of micro-computed tomography scans and employing three-dimensional geometric morphometrics to quantify shape differences. We find that reef-dwelling wrasses do not differ from non-reef-associated wrasses in morphological disparity or rates of shape evolution. However, we find that some reef-associated species (e.g., parrotfishes and tubelips) exhibit elevated rates of pharyngeal jaw shape evolution and have colonized unique regions of morphospace. These results suggest that while coral reef association may provide the opportunity for specialization and morphological diversification, species must still be able to capitalize on the ecological opportunities to invade novel niche space, and that these novel invasions may prompt rapid rates of morphological evolution in the associated traits that allow them to capitalize on new resources.

### Introduction

Coral reefs are one of the premier biodiversity hotspots for marine organisms. They are highly productive and physically complex (Wood 1999). Reef habitats frequently host complex coral-faunal interactions, which are thought to facilitate niche partisubsequent morphological tioning and and functional specialization. Among fish species in particular, coral reef habitats host over 4000 species and have been shown to promote both lineage and morphological diversification (Alfaro et al. 2007; Kiessling et al. 2010; Cowman and Bellwood 2011; Price et al. 2011, 2013).

Among marine fishes, the wrasses (Labridae: Percomorpha) constitute the second largest family with over 600 species (Parenti and Randall 2000). Species in this clade are represented in both reef and non-reef habitats where they exhibit a broad range of trophic diversity ranging from planktivores, molluscivores, piscivores, ectoparasite cleaners to detritivores (Cowman et al. 2009; Burress and Wainwright 2018). Studies have found that wrasses underwent two different periods of trophic diversification, one in the Oligocene, where two distinct forms of herbivory appeared in excavating scarines and algae scraping odacines, and one in the Miocene with foraminifera feeding, fish cleaning, coral feeding, piscivory and planktivory all appearing over a roughly 13 million year period (Cowman et al. 2009; Cowman and Bellwood 2011).

Along with their trophic diversity, wrasses exhibit a high degree of morphological diversity in their oral

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jaws (Westneat 1994; Wainwright et al. 2004; Westneat et al. 2005), and in their pharyngeal jaw apparatus (Wainwright et al. 2012). Wrasses possess a specialized condition called pharyngognathy, which consists of three major evolutionary modifications: (1) fusion of the fifth ceratobranchials into a robust plate-like structure; (2) a muscular sling that connects the fused plate to the neurocranium and (3)a diarthrosis between the dorsal surface of the upper pharyngeal tooth plate and the base of the neurocranium that permits a wide range of movements (Kaufman and Liem 1982; Wainwright et al. 2012). Within wrasses, parrotfishes (Scarinae: Labridae) have further adapted their pharyngeal jaw apparatus to become a "pharyngeal mill" through a series of modifications that include: a laterally expanded fourth epibranchial, laterally compressed pharyngobranchials with a sliding joint between the neuroepibranchial, anterior-posterior cranium and progression of tooth rows, and a novel anterior muscular sling (Gobalet 1989). These innovations are thought to facilitate the processing of hard prey items (e.g., mollusk shells and coral skeletons). Pharyngognathy has also been proposed as a key innovation that spurred the diversification of wrasses along ecological lines by allowing species to access a broader range of prey items (Liem and Sanderson 1986; Liem 1993). However, recent analyses have shown that the evolution of pharyngognathy in wrasses is not correlated with increased diversification rates (Alfaro et al. 2009).

Among wrasses, coral reefs have been shown to promote increased rates of morphological and functional diversification, particularly in traits associated with trophic ecology (Price et al. 2011). However, despite the importance of the pharyngeal jaw apparatus to the ecological diversification of wrasses, most studies have focused primarily on the morphology of the muscular sling with few studies directly examining the structure of the lower tooth plate (Wainwright 1988; Price et al. 2010; Fruciano et al. 2011). The complex shape of the pharyngeal apparatus and the tooth plate's highly three-dimensional (3D) structure limits the descriptive power of traditional linear and 2D approaches (Buser et al. 2018). Here we integrate a species-dense, time-calibrated phylogeny, and a novel 3D geometric morphometric approach to study the effect of coral reef association on the rates of shape evolution and the morphological disparity of the lower pharyngeal tooth plate in wrasses. We hypothesize that reef-associated species will exhibit more morphological disparity and exhibit faster rates of shape evolution due to the ecological opportunity afforded by coral reefs.

### Materials and methods

#### Specimens, traits, and phylogeny

Pharyngeal jaw shape was characterized across 134 species of labrid fishes (21% taxon sampling) with most species represented by a single adult specimen. Specimens were micro- computed tomography (CT) scanned at the University of Washington using a Bruker SkyScan 1172, in conjunction with the #oVert project. Specimens were also scanned at the University of Chicago using a GE Phoenix v/tomex/ xs 240 microCT scanner. Specimens were segmented in Amira and exported as surface mesh files. Surface models were then imported into Stratovan Checkpoint for digitizing. Lower pharyngeal tooth plates for each specimen were digitized on the left side with six landmarks in three-dimensions (Table 1; Fig. 1). While our approach allowed us to collect high-resolution morphological data for the lower pharyngeal tooth plate, it is important to note that our limited intraspecific sampling does not account for a range of potential intraspecific variation (e.g., phenotypic plasticity and sexual dimorphism).

To determine coral reef and non-coral reef affiliation, we followed the designations from Price et al. (2011). We used Fishbase to determine habitat affiliation for species that were not present in the Price et al. (2011) analysis (Fig. 2). Habitat traits and pharyngeal shape were visualized at the tips of the most recent time-calibrated phylogenetic tree of the Labridae (Aiello et al. 2017), a topology containing 340 labrid species. This topology includes the subfamily Scarinae nested within Labridae and includes "Reef-clade" the (consisting of Cetoscarus, Hipposcarus, Chlorurus, and Scarus) and "Seagrassclade" consisting of (Leptoscarus, Calatomus, Cryptotomus, and Sparisoma). This tree was pruned

Table 1Landmark descriptions for the six landmarks used in the3D geometric morphometric analysis of pharyngeal tooth plateshape

Landmark #	Description		
1	Most anterior tooth on tooth plate		
2	Distal most point on anterior keel		
3	Proximal-most point of lateral wing contacting the central tooth plate		
4	Proximal-most point on anterior keel reaching medial- most point on ventral surface of tooth plate		
5	Distal-most point on lateral wing		
6	Posterior medial-most point on tooth plate beneath posterio-most tooth		



**Fig. 1** Landmark diagram of the lower pharyngeal tooth plate of *Hologymnosus doliatus* (FMNH 121072) showing six 3D landmarks in lateral (**A**), dorsal (**B**), and posterior (**C**) views.

to create a topology for the 134 species present in the current morphological dataset (Fig. 2).

#### **Geometric morphometrics**

To account for differences in the size and scaling of individual specimens, we performed a generalized Procrustes superimposition in *Stratovan Checkpoint*. Species that were represented by more than one specimen were pooled together and the species mean was used. Procrustes coordinates were then imported into the r-package *Geomorph* (Adams and Otárola-Castillo 2013) for subsequent analyses.

We quantified the significance of allometric effects for the shape of the lower pharyngeal tooth plate using a Procrustes ANOVA (Collyer et al. 2015). This analysis calculates the degree of covariation between shape and size (log-centroid size) in a linear model.

Morphological disparity (a statistical measure of the amount of dispersion of pharyngeal jaws in morphospace) was calculated and compared for the two habitat types using the *morphol.disparity* function in *Geomorph*. This function estimates the Procrustes variance for reef and non-reef groups using the residuals of a linear model. Absolute differences in Procrustes variance were used to test for differences in morphological disparity through permutation where vector residuals are randomized between habitat types (Zelditch et al. 2012).

To illustrate the evolutionary trajectory of pharyngeal jaw shape in labrids, a phylomorphospace (Sidlauskas 2008) was constructed using the first two principal components (PCs) from a principal components analysis and the Aiello et al. (2017) phylogeny.

#### Quantifying rates of shape evolution

We compared rates of pharyngeal jaw shape evolution between reef and non-reef species using the compare.evol.rates function in geomorph (Adams 2014). This function compares the net rates of shape evolution between two groups of species under a Brownian motion model of evolution. The analysis was performed on the Procrustes shape coordinates of reef and non-reef species and run for 10,000 iterations. The species Labrus merula was removed from the analysis due to its very recent divergence from its sister species L. viridis resulting in short branch lengths that have the potential to bias the rate analysis. Significance was evaluated using phylogenetic simulation where the common evolutionary rate under a Brownian motion model was obtained for all species in the phylogeny (see Denton and Adams [2015] for more details).

In order to study shifts in the rate of pharyngeal jaw shape evolution across the phylogeny, we used the program BayesTraitsV3 (www.evolution.rdg.ac. uk/) which allowed us to quantify branch-specific rates of shape evolution. This method uses a reversible jump Markov Chain Monte Carlo algorithm to detect shifts in the rate of continuous trait evolution across a single phylogenetic tree. Due to issues related to fitting and comparing models of trait evolution to high-dimensional landmark data, we performed our analysis using the first seven PC axes (94% of total shape variance) as input data following the approach of Felice and Goswami (2017). Mathematically, PC axes are uncorrelated with one another. However, they are evolutionarily correlated (Adams and Collyer 2018). To account for this correlation, we used the "TestCorrel" function in BayesTraits to fit correlated multivariate evolutionary models. Three models were tested for the shape dataset: an equal rates model that assumes a single rate of trait evolution across the phylogeny, a variable rates model that allows for rate heterogeneity and identifies regions of the tree where evolutionary rates differ significantly (Venditti et al. 2011), and a



Fig. 2 Phylogenetic tree based on the Aiello et al. (2017) topology of the 134 wrasse species included in the analysis of pharyngeal jaw shape evolution with habitat designation.

variable rates model with a lambda transformation to account for phylogenetic non-independence in trait values between species. We used default uniform priors and each run was set for 100,000,000 iterations with the first 50,000,000 iterations discarded as burn-in with sampling every 1,000,000 iterations after convergence. We assessed mixing and convergence of the MCMC chains, before the first 50 million generations were removed as a burn-in. Alternative Model comparisons were performed by calculating Bayes Factors from the marginal likelihoods of the equal rates and variable rates models. The resulting output of this analysis produces a phylogeny where each branch is scaled by its Brownian motion rate of evolution.

In addition to using the variable-rates model to test for differential rates of shape evolution, we also used a variable-rates regression model to test for the effect of habitat on the rate magnitudes and shift locations of pharyngeal jaw shape evolution. We used the same settings as the variable-rates analysis (i.e., burn-in and sampling, etc.) and the same priors. Similar to the variable-rates analysis, the variable-rates regression produces a phylogeny where the branch lengths are scaled by the rate of trait evolution. However, in the regression model, rate



Fig. 3 Pharyngeal jaw shape evolution in wrasses. (A) Phylomorphospace analysis of pharyngeal jaw shape for 134 wrasse species. Insets depict shape extremes for each PC axis. (B) Principal components analysis for pharyngeal jaw shape showing the distribution of shapes and substantial overlap in shape space between reef and non-reef species.

shifts and magnitudes that are explained by the dependent variable (habitat, in this case) are represented with branch lengths scaled to 0, while unexplained variation in rates are displayed as stretched branches (see Baker and Venditti [2019] for more information).

### Results

#### Pharyngeal jaw shape diversity in Labridae

Labrid fishes exhibit a wide diversity of pharyngeal jaw shapes (Fig. 3A). The first two PC axes explain 66.7% of the total shape variance. The first PC axis corresponds to differences in the relative width of the tooth plate with *Labroides dimidiatus* exhibiting the most narrow tooth plate and *Scarus forsteni* 

exhibiting the widest tooth plate. The second PC axis corresponds to differences in the relative length of the tooth plate (anterior to posterior) with *Calotomus carolinus* exhibiting the most truncated tooth plate, while *S. forsteni* exhibits the most elongate tooth plate. We also recover a significant (P=0.001) effect of size on pharyngeal jaw shape. However, we refrain from correcting for allometric scaling in the shape to avoid removing relevant biological information.

Labrid pharyngeal jaw shape diversity is significantly (P = 0.001) phylogenetically structured with species distributed across three major clusters in shape space. Parrotfishes exhibit a broad diversity of pharyngeal tooth plate shapes and have colonized a unique region of shape space exhibiting the highest PC scores on both axes. Species from the "sea grass clade" (e.g., Calotomus) typically possess short and wide plates while the corallivorous species in the "reef clade" (e.g., Scarus) exhibit elongated tooth plates. Interestingly, our analysis detected one independent case of colonization of this shape space in the species Pseudodax mollucanus. Cleaner and wrasses tubelip (Labrichthys, Labroides, and Labropsis) have colonized the other extreme of shape space exhibiting the lowest scores along PC1. These species have all dramatically reduced their pharyngeal tooth plates into a "wishbone"like structure. The planktivore, Clepticus parrae has also independently reduced its tooth plate and has thus converged on a similar region in the morphospace. Interestingly, aside from the extreme shapes exhibited by cleaners, tubelips, and parrotfishes, most other wrasse species form a tight cluster along the intermediate PC values. These species typically exhibit a highly triangular (in dorsal view) tooth plate and vary slightly in the relative length and width of the plate.

We find that coral reef and non-reef wrasses overlap substantially in shape space (Fig. 3B). Both habitats feature many of the same pharyngeal jaw shapes with the exception of the highly reduced tooth plates (low PC1 scores), which are only seen amongst the reef fishes. An analysis of morphological disparity recovered no significant differences (P=0.46) in disparity between the two habitat types.

#### Rates of pharyngeal jaw shape evolution in Labridae

For rates of pharyngeal tooth plate shape evolution in labrids, we find that a "variable rates" model of shape evolution with a lambda transformation has the highest support (Table 2; Fig. 4A). We recover strong rate shifts at the base of the parrotfishes (Scarinae) and an additional shift within the scarines in the "reef clade." These findings suggest that the evolution of the pharyngeal mill resulted in accelerated rates of shape evolution and that the further modifications that were made in the corallivorous "reef clade" resulted in a second smaller shift. Similarly, another rate shift was found in P. mollucanus with the independent evolution of a similarly shaped pharyngeal mill. A strong shift was found in the cleaner and tubelip wrasses (most notably, Labroides), which have dramatically reduced their pharyngeal tooth plates. Other notable include Inistius and shifts umbrilatus Macropharyngodon both of which have evolved slender anterior regions of their pharyngeal tooth plates.

Table 2 Marginal likelihoods and Bayes factors for the three models of trait evolution that were fit to the pharyngeal jaw shape dataset using BayesTraits V3

Model	Log (Marginal likelihood)	Log (Bayes factor)
Equal rates	1253.27	417.94
Variable rates	1458.58	7.32
Variable rates + lambda	1462.24	0

#### Reef versus non-reef rates of evolution

The results of our variable-rates regression analysis recover a median  $r^2$  of -0.092, suggesting a poor fit of our data to the habitat model. Several stretched branches can also be seen in the re-scaled phylogeny with unexplained rate shifts in the "sea grass clade" of parrotfishes and *Hipposcrarus longiceps* independently (Fig. 4B). Other shifts include several branches within the hypsigenynes (including: *Choerodon, Achoerodus*, and *Xiphocheilus*), most novaculine species and four julidine species.

We find that net rates of shape evolution do not differ significantly (P=0.654) between reef and non-reef fishes (Fig. 4C). After examining mean tip rates from the variable-rates model output we find that many of the fastest rates of shape evolution belong to a few groups of reef fishes (e.g., parrotfishes and cleaner wrasses), while most other reef fishes exhibit rates that are indistinguishable from non-reef fishes. Furthermore, several non-reef fishes exhibit exceptionally high rates of pharyngeal jaw shape evolution including *I. umbrilatus* and several of the *Stethojulis* species.

### Discussion

# Are coral reefs a cauldron for morphological diversification?

Coral reef habitats have been hypothesized to facilitate functional and ecological diversification. Previous studies involving coral reef fishes have demonstrated the relationship between coral reef association and rates of functional trait evolution (Price et al. 2011). In our study, we find that coral reef fishes and non-reef fishes exhibit indistinguishable rates of pharyngeal tooth plate shape evolution and that both groups are largely overlapping in shape space. These results suggest that coral reef association alone is insufficient to spur rapid rates of morphological evolution among species.

Although we do not recover significant differences in rates or shape disparity between reef and non-reef labrid fishes, we find that some reef-associated clades with specialized trophic ecologies (e.g., parrotfishes and cleaner wrasses) exhibit elevated rates of shape



Fig. 4 Pharyngeal jaw shape diversification in wrasses. (A) Results from the variable-rates analysis showing the Aiello et al. (2017) phylogeny with branch lengths scaled by the rate of pharyngeal jaw shape evolution, red colors correspond to faster rates while bluer colors correspond to slower rates. (B) Results from the variable-rates regression analysis showing the Aiello et al. (2017) phylogeny with branch lengths scaled by rates of shape evolution unexplained by the habitat model. (C) Comparison of net rates of shape evolution between reef and non-reef species. The red arrow indicates the observed rate ratio.

evolution relative to other wrasse clades. Furthermore, we find that the primary axis of shape variation (PC1) for pharyngeal jaw shape appears to range from species that feed on soft prey (e.g., *Labroides* and *Clepticus*) to species with more durophagous diets (e.g., *Scarus*). In the case of species that feed on soft prey, these fishes typically exhibit a highly reduced pharyngeal tooth plate, perhaps associated with a reduced force regime during pharyngeal jaw chewing. In both trophic extremes, increased rates of shape evolution are seen across taxa that exhibit these diets; this can even be seen in the case of Macropharyngodon, which independently evolved a highly robust pharyngeal jaw associated with a durophagous diet of foramaniferans. These findings suggest that prey toughness and not habitat may play a more important role in structuring the tempo and mode of evolution in the lower pharyngeal tooth plate. The weak relationship between habitat and rates of shape evolution may therefore be explained by the fact that hard and soft prey items can be found in both habitats. Similar findings have been reported in bats where species at trophic extremes exhibited the fastest rates of morphological evolution (Dumont et al. 2012).

Our results differ from previous studies that have examined rates of morphological evolution and compared rates of morphological evolution between reef and non-reef wrasse species. A study comparing rates of morphological evolution between reef and nonreef wrasses found that functional traits associated with trophic ecology evolve faster in reef species (Price et al. 2011). The underlying incongruence between these studies may stem from methodological differences. Previous studies utilized functional traits with known effects on organismal performance; for example, the dimensionless ratio of maxillary Kinematic Transmission in the feeding system, as well as jaw muscle mass, instead of geometric morphometric traits. It is interesting to note that data on the pharyngeal jaw apparatus was included in these studies, either as pharyngeal muscle mass measurements, or coded as a discrete character at the base of major clades (Alfaro et al. 2009; Price et al. 2010, 2011). Here, we conclude that the 3D shape analysis of an important structure-function complex can contribute alternative ways of viewing the evolutionary patterns in musculoskeletal systems. The interactions between pharyngeal musculature, 3D tooth plate morphology, and biomechanical function will be necessary to elucidate the subtler patterns of morphological diversification that may play major roles in the colonization of novel regions of niche space and morphospace across major radiations.

# Is morphological specialization an evolutionary dead-end?

The "dead-end" hypothesis states that the evolution of a specialized ecology or morphology should constrain rates of speciation and morphological diversification and result in increased extinction risk as it becomes more difficult for specialized species to adapt to dramatic environmental changes (Cope 1886; Huxley 1942; Rensch 1959). The pharyngeal mill in parrotfishes (and Pseudodax), is a highly specialized structure that allows for the processing of tough prey items including epiphytic algae and coral skeletons (Gobalet 1989; Streelman et al. 2002). Our analysis indicates that the evolution of the pharyngeal mill resulted in increased rates of shape evolution and the colonization of a novel region of the morphospace. This initial finding is not particularly surprising, as the evolution of specialized divergent morphologies frequently result in the colonization of new morphospace (Futuyma and Moreno 1988). Interestingly, however, we find that a second burst in shape diversification occurred within the scarines in the "reef" clade as these species further adapted their already specialized pharyngeal jaw apparatus to feed on coral skeletons. The modifications to this apparatus were so substantial that the "reef" clade colonized yet another novel region of morphospace. These results suggest that for parrotfishes, the evolution of the pharyngeal mill was not an evolutionary dead-end and that they were able to further modify a seemingly highly specialized aspect of their trophic morphology. Within parrotfishes, similar patterns of increased rates of lineage diversification and functional evolution (e.g., the evolution of the intramandibular joint) have also been reported in other studies (Smith et al. 2008; Alfaro et al. 2009; Kazancıoğlu et al. 2009; Price et al. 2010). A study by Smith et al. (2008) found evidence for a recent burst of diversification within parrotfishes over the last 3 million years, along with bursts in the rate of regulatory gene evolution, including dlx2, which has a known role in pharyngeal patterning. These results further suggest that the specialized trophic ecologies exhibited by parrotfishes did not constrain their evolutionary trajectories.

#### Conclusion

As high-resolution morphological datasets and species-dense, time-calibrated phylogenies become more readily available, we predict that in-depth reappraisals of evolutionary theories and relationships will become more feasible (Evans et al. 2019a, b). In this current study, we use 3D geometric morphometrics derived from micro-CT scans and a species-dense time calibrated phylogeny to study the shape evolution of the lower pharyngeal tooth plate in labrid fishes. In testing the relationship between habitat and rates of morphological evolution with shape disparity, we find that coral-reef and non-reef fishes do not differ in either shape disparity or rates of shape evolution. Instead, most reef-associated species exhibit generalized pharyngeal jaw shapes and unremarkable rates of shape evolution commensurate with non-reef species. Additionally, we hypothesize that pharyngeal tooth plate shape variation is structured along a gradient ranging from soft to hard prey with a few clades colonizing either extreme in diet or morphospace. We find that a few exceptional reef species have evolved novel reef-specific trophic ecologies and have adapted their pharyngeal jaw apparatus to closely track those ecologies while undergoing rapid rates of shape evolution as they colonized novel regions of morphospace. We also find evidence for subsequent specialization of the pharyngeal mill within the "reef" clade of parrotfishes. This subsequent specialization suggests that parrotfishes represent an exception to the "dead-end" hypothesis. Our findings suggest that other factors including aspects of diet instead of coral reef association may drive the tempo and mode of shape evolution in the lower pharyngeal tooth plate. Future studies should aim to quantify different aspects of diet to further test the effect of diet on the shape diversification of this highly specialized structure.

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