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Original Article

Beaks promote rapid morphological diversification along distinct evolutionary trajectories in labrid fishes (Eupercaria: Labridae)

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Abstract

The upper and lower jaws of some wrasses (Eupercaria: Labridae) possess teeth that have been coalesced into a strong durable beak that they use to graze on hard coral skeletons, hard-shelled prey, and algae, allowing many of these species to function as important ecosystem engineers in their respective marine habitats. While the ecological impact of the beak is well understood, questions remain about its evolutionary history and the effects of this innovation on the downstream patterns of morphological evolution. Here we analyze 3D cranial shape data in a phylogenetic comparative framework and use paleoclimate modeling to reconstruct the evolution of the labrid beak across 205 species. We find that wrasses evolved beaks three times independently, once within odacines and twice within parrotfishes in the Pacific and Atlantic Oceans. We find an increase in the rate of shape evolution in the *Scarus*+*Chlorurus*+*Hipposcarus* (SCH) clade of parrotfishes likely driven by the evolution of the intramandibular joint. Paleoclimate modeling shows that the SCH clade of parrotfishes rapidly morphologically diversified during the middle Miocene. We hypothesize that possession of a beak in the SCH clade coupled with favorable environmental conditions allowed these species to rapidly morphologically diversify.

Keywords: evolutionary innovation, geometric morphometrics, coral reef

Introduction

Evolutionary innovations are adaptations that allow organisms to expand into novel environments and access previously unavailable ecological resources (Alfaro et al., 2009; Dumont et al., 2011; Evans et al., 2021; Goffredi et al., 2005; Hunter, 1998; Simpson, 1944). These innovations allow organisms to dramatically change the economy of their respective environments and alter the ecologies of the other organisms around them.

In addition to evolutionary innovation, ecological opportunity has the potential to promote rapid morphological diversification and even adaptive radiation by relaxing sources of natural selection that act on ecological traits (Yoder et al., 2010). Ecological opportunity can present itself in the form of a key innovation, dispersal into a novel habitat, or extinction of an antagonist species (Simpson, 1944). This opportunity can then promote ecological release that can manifest in the form of increased trait variation, increased variation in habitat or resource use, and increased population size. Ecological opportunity, coupled with ecological release, has been hypothesized to promote rapid speciation and morphological diversification (Yoder et al., 2010).

Coral reef ecosystems are hotspots for marine biodiversity across disparate clades of organisms and have been shown to promote rapid rates of speciation and morphological diversification among their inhabitants, with marine fishes being particularly impacted (Cowman & Bellwood, 2011; Fisher et al., 2015; McCord et al., 2021; Nash et al., 2022; Price et al., 2011). The speciation and proliferation of marine fishes closely track patterns of coral diversification and proliferation (Alfaro et al., 2007; Bellwood et al., 2017; Cowman & Bellwood, 2011; Evans, Williams, et al., 2019; Kiessling et al., 2010; Price et al., 2011, 2013; Siqueira et al., 2019a, 2020). Historically, global coral abundance has experienced several expansions and contractions due to changes in climate and tectonic activity (Bellwood et al., 2017; Budd et al., 1995; Cahuzac & Chaix, 1996; Edinger & Risk, 1994; Johnson et al., 2009; Klaus & Budd, 2003; Pomar & Hallock, 2007). One of the major events that structured modern-day patterns of coral reef distribution and diversity occurred during the Oligocene–Miocene transition 23 million years ago (mya). This was a period of dramatic cooling in global seas as well as a period of tectonic activity in what is today the Indo-Pacific as current-day India collided with the Asian continent, resulting in a dramatic expansion of warm, shallow water habitats

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(Bellwood et al., 2017; Siqueira et al., 2019b). During this time, there was an expansion of fast-growing hermatypic corals and an increase in the abundance of coral outcrops. This expansion of reef-building corals in the Indo-Pacific eventually shifted the biodiversity hotspot for corals and other reef-associated species from the Western Tethys to the Indo-Australian Archipelago, where it remains today. Interestingly, while the Oligocene–Miocene transition was a period of expansion and diversification for corals in the Indo-Pacific, the opposite is true for corals in the Atlantic. In the Atlantic Ocean, the thermal isolation of Antarctica resulted in stronger patterns of thermohaline circulation, which resulted in stronger nutrient upwelling and increases in turbidity in shallow marine habitats in the Atlantic (Budd et al., 1995; Edinger & Risk, 1994; Johnson et al., 2009). During this time, we also see cooling in the Mediterranean that is associated with a reduction in coral size and diversity (Cahuzac & Chaix, 1996). These factors worked together throughout the Atlantic to drive the extinction of several coral species and a large reduction in the abundance of reef-building corals during the early Miocene. Atlantic corals would experience a second extinction event 15 mya after the Miocene Climatic Optimum and throughout the Miocene Climatic Transition, which cooled global ocean temperatures continuously until today. These reefs would not rebound until later during the Pleistocene (Klaus & Budd, 2003). The complex biogeographic histories of the coral reef fauna in these two oceans may have also constrained or promoted morphological diversification in the various clades of fishes that have inhabited and associated with them throughout deep time.

In addition to coral reefs, seagrass beds also function as productive biodiverse ecosystems in shallow water coastlines worldwide. Seagrasses represent a paraphyletic assemblage of angiosperm plants that have adapted to marine life and form vast aggregations. These valuable ecosystems function as important structures and habitats for a wide range of organisms that use these habitats as shelter, food, or nursery grounds. Seagrass beds are also important carbon sinks because they are immensely productive and store large amounts of biomass in below-ground ungrazed detritus (Duffy, 2006). Unlike corals, seagrasses are not calcified and thus have a much sparser fossil record typically inferred by the carbonate sediments that they trap or the organisms that associate with them. As a result, it can be more challenging to reconstruct the historical biogeography of seagrass distributions (Brasier, 1975; Duffy, 2006; Haig et al., 2020; Vélez-Juarbe, 2014). However, fossil evidence, namely fossil beds of foraminifera that have been known to associate with seagrasses, suggests that seagrass beds originated in the Cretaceous and had reached a nearly complete Tethyan distribution by the Eocene. While it has been difficult to confirm with direct fossil observation, there is indirect evidence that suggests that seagrass distributions may have expanded during the late Oligocene and early Miocene and established themselves in the temperate Western Pacific Ocean (Conran et al., 2015; Haig et al., 2020). There has also been additional evidence that the expansion of seagrass beds in the Indo-Pacific during the Oligocene promoted the morphological diversification of seahorses, which are known to frequently associate with seagrasses (Teske & Beheregaray, 2009).

Among the fishes that inhabit coral reef and seagrass ecosystems, some wrasses (Eupercaria: Labridae) have emerged as critically important ecosystem engineers and bioeroders that play important roles as herbivorous grazers in their respective habitats (Alwany et al., 2009; Bellwood, 1995, 1996; Bonaldo et al., 2014; Bruggemann et al., 1996; Grupstra et al., 2022). In particular, the parrotfishes (labrid tribe: Scarini) are microphages that feed on endolithic and epilithic autotrophic microbes living on and within coral skeletons, as well as on the surface of macroalgae and other sessile marine organisms (Clements & Choat, 2018; Clements et al., 2017). These fishes are able to feed directly on hard corals and other hard surfaces using their specialized "beaks," which consist of dentition that has been coalesced into a strong, durable cutting edge in the upper and lower jaws (Bellwood, 1994; Price et al., 2010; Streelman et al., 2002). This beak is composed of some of the strongest biological material on the planet and allows many parrotfishes to scrape and excavate the calcium carbonate skeletons of corals (Marcus et al., 2017). Studies have shown that this constant grazing by some labrid species exerts tremendous pressure on the growth rate of coral colonies and that the resulting calcium carbonate sediment that is excreted during the grazing process forms the foundation of shallow water tropical coastlines worldwide (Bellwood, 1995, 1996; Perry et al., 2015).

While the ecological implications of the beak are well recognized, the evolutionary history of this important innovation remains poorly understood, as well as the effect of this innovation on the tempo and mode of morphological evolution within the family Labridae. Phylogenetic hypotheses for the family Labridae (Aiello et al., 2017; Westneat & Alfaro, 2005) and for the parrotfish tribe Scarini (Smith et al., 2008) have suggested that the parrotfishes have radiated into their present diverse assemblage quite recently, within the last 10 million years, although the latest time-calibrated trees and phylogenomic analyses (Hughes et al., 2023; Larouche et al., 2023) have pushed both the root Labridae age and the origin of parrotfishes earlier in time.

Here, we examine the evolution of the labrid skull and beak using three-dimensional geometric morphometric data collected from high-resolution micro-computed tomography (micro-CT) scans, a species-dense, time-calibrated phylogeny, and a phylogenetic comparative toolkit to reconstruct the evolution of the labrid beak across both space and time. We reconstruct the ancestral state of beaks in labrids to test whether beaks have evolved multiple times within this clade. We additionally use the latest time-calibrated phylogenetic topologies to date the evolution of beaks within labrids to examine whether the beak evolved as a response to changes in global coral reef and seagrass cover during the Oligocene and Miocene. Moreover, the beak in labrids (specifically parrotfishes) is often viewed as an evolutionary innovation (Price et al., 2010); as such, we test for shifts in the rate of skull shape evolution associated with the evolution of beaks across the different taxa. If we recover increases in the rate of skull shape evolution associated with the evolution of beaked dentition, this will suggest that this adaptation promoted rapid rates of morphological diversification as these species moved toward a specialized foraging ecology. Inversely, decreases in the rate of skull shape evolution associated with the evolution of beaks would suggest that the specialized foraging ecology among beaked labrids may constrain rates of morphological diversification. Lastly, the presence or absence of ecological opportunity can shape the downstream effects of adaptations on patterns of morphological diversification. The Miocene was a period of rapid climatic and tectonic changes that strongly influenced global patterns of coral and seagrass diversification, abundance, and proliferation. We therefore also employ paleoclimate modeling to reconstruct the sea surface temperatures of the tropical Atlantic and Pacific Oceans during the middle and late Miocene to quantify changes in paleoclimate temperatures. If shifts in paleoclimate created ecological opportunities for labrids, we expect to see increases in rates of morphological evolution that coincide with changes in sea surface temperature across geological time scales.

Materials and methods

Phylogenetic hypothesis

To reconstruct the evolution of the labrid beak, we used a recently published phylogenetic analysis of 410 species of labrid fishes (Larouche et al., 2023; Supplementary Figure 1). This phylogeny was built as a subset of a larger in-progress study of 550 species using a set of 12 genes accumulated by a series of recent studies (Aiello et al., 2017; Smith et al., 2008; Westneat & Alfaro, 2005) and analyzed using the same fossil calibration framework as the recent phylogenomic analysis of the Labridae (Hughes et al., 2023). The resulting time-calibrated tree was then pruned down to the 205 taxa for which we collected morphometric data using the *drop.tip* function in the R-package *ape* (Paradis et al., 2004). We retained 100 randomly sampled tree topologies from the posterior distribution of the *BEAST* (Bouckaert et al., 2019) run for downstream analyses.

Defining a beak

Across the vertebrate tree of life, the term "beak" has come to refer to a broad range of dental and oral morphologies ranging from the lack of dentition, coupled with the presence of a keratinous rhamphothecae in birds and turtles (Ingle et al., 2023), to the coalescence of multiple generations of teeth within an osteodentine mass in pufferfishes and their relatives (Thiery et al., 2017). Within labrid fishes, several distinct patterns of dental coalescence have been documented among the genera ranging from completely uncoalesced in *Cryptotomus*, various intermediate levels of coalescence in *Nicholsina*, *Calotomus*, and *Leptoscarus*, to more completely coalesced dentition in *Sparisoma*, *Bolbometopon*, *Cetoscarus*, *Hipposcarus*, *Scarus*, *Chlorurus*, and the distantly related odacine wrasses (Odacini: Labridae; Bellwood, 1994). Previous studies have reconstructed the evolutionary history of coalesced or "cutting-edge" dentition and have found varying levels of support for multiple origins of coalesced dentition among labrid fishes (Bellwood, 1994; Burress & Wainwright, 2018; Wainwright et al., 2018). In this study, we focus on one particular form of coalescence in which the teeth of the premaxilla and dentary are coalesced into a cutting edge forming a unified dental wall with overlapping tooth rows, as opposed to being completely isolated (as is the case for most non-parrotfish wrasses) or arranged into isolated oblique rows (as is the case with *Leptoscarus* and to a lesser degree *S. radians*; Bellwood, 1994; Viviani et al., 2022; Supplementary Figures 2 and 3). This pattern of coalescence (herein referred to as a beak) is seen in several of the reef-associated parrotfish species that exhibit durophagy and have been documented either feeding directly on calcium carbonate coral skeletons (alive or otherwise) or scraping algae from hard surfaces. In odacines, this beak is used to feed on algae, seagrass, and shelled invertebrates (Baker, 2011; Choat & Clements, 1992; Clements & Choat, 1993; Mountfort et al., 2002; Sogard et al., 1989). The overlapping pattern of the replacement tooth rows has been hypothesized to allow the beak to self-sharpen as individual teeth are lost and replaced (Marcus et al., 2017). This specific pattern of coalescence has also been documented in the very distantly related oplegnathid fishes (referred to as "jaw-tooth"), which also feed on hard-shelled invertebrate prey (Kakizawa et al., 1980), further suggesting that beaks can emerge convergently in fishes as adaptations to durophagy. In this present study, we apply our specific definition of a beak to 205 wrasse species to code for the presence or absence of this character.

Shape analyses

For the analysis of skull shapes, we used three-dimensional geometric morphometrics to quantify shape variation and diversity among our labrid data set. We digitized the left side of each specimen with 79 landmarks and 118 semilandmarks (Supplementary Table 1; Supplementary Figure 4) following the approach described in Larouche et al. (2023). Landmarks encompassed the skull, jaws, hyoid region, and pharyngeal jaws. The teleost fish skull exhibits immense biomechanical complexity, with highly kinetic, articulating elements (Hulsey et al. 2005; Westneat, 2004). This kinesis poses a challenge to studies of shape change across the skull because preservational artifacts related to the relative positions of these individual elements can strongly bias any downstream analyses (Evans, Vidal-García, et al., 2019; Vidal-García et al., 2018). To account for this rotation and translation of mobile elements, we performed a local superimposition to standardize the position of the different skull elements (Rhoda et al., 2021a, 2021b). Specimen positions were standardized to the specimen that was closest to the mean shape (*Ophthalmolepis lineolata*) using the *findMeanSpec* function in *geomorph*. To study the shape evolution of the individual beak elements, we subset our larger skull shape data set into smaller premaxilla and dentary data sets, the raw coordinates of which were individually superimposed. After the local superimposition, a principal component analysis (PCA) was performed to assess the primary axes of shape variation across all three of our wrasse data sets. All geometric morphometric analyses were performed in the R-package *geomorph* version 4.0.3 (Adams et al., 2016).

Morphological sampling

Skull shape was sampled across 234 wrasse specimens representing 204 different species of wrasse (25% taxon sampling). For most species, sampling was limited to a single adult individual per species due to limitations associated with the overall size of many of the large parrotfish species and the time associated with the data collection process (Supplementary Table 2). For our shape analysis, we excluded a subadult *Bolbometopon muricatum* specimen. The lack of intraspecific sampling in our data set prohibits the ability to estimate morphological variation within species and can inflate the estimation of rates of morphological evolution between species. However, studies using geometric morphometric data have shown that across datasets where sample variance is high (as is the case with our dataset) shape relationships between species tend to be accurately estimated with even a low number of individuals per species (Cardini & Elton, 2007). To further demonstrate this, we performed an intraspecific analysis using five individuals of *Chlorurus spilurus* that were all collected from the same place (Moorea, French Polynesia) around the same time (within 3 weeks of each other, June 2021) and show that the specimens of this species have significantly (p = .006) less Procrustes variance (0.00015), than the other species in our data set (0.00078; Supplementary Figure 5). We used micro-CT scanning to collect three-dimensional osteological data for each specimen. Scans were conducted at Rice University, the University of Minnesota, the University of Chicago and the University of Washington Friday Harbor Labs in conjunction with the oVert initiative. Scans were segmented in Amira to isolate the skull, and exported as three-dimensional mesh files. Mesh files were then imported into Stratovan Checkpoint where they were digitized.

Phylogenetic comparative methods

We analyzed patterns of skull and jaw shape variation and shape diversification using a phylomorphospace analysis (Sidlauskas, 2008), which displays the principal component scores of each species with an underlying phylogeny and estimates the skull shapes at ancestral nodes.

Beaks are typically considered to be discrete characters and defined by the fusion or coalescence of teeth in the upper and lower jaws. However, for our analyses, we were also interested in the overall shape of the beak among labrid fishes. To determine whether shape could predict the presence or absence of beak morphology, we tested for the relationship between beak presence and skull shape using a Procrustes analysis of variance (ANOVA) and a Procrustes phylogenetic generalized least squares (PGLS; *procD. pgls* function in *geomorph*) analysis to account for phylogenetic non-independence of our shape data (Adams & Collyer, 2018). We performed these analyses on the entire skull shape configuration, as well as the individual dentary and premaxillary dataset. We recover significant relationships across all Procrustes ANOVAs but not for PGLS analyses suggesting that shape is strong predictor of beak presence, but that this relationship is phylogenetically restricted, which implies that some beaked species may have evolved beaks that differ substantially in shape from other beaked species in different clades (Supplementary Tables 3–8).

To reconstruct the evolution of beaks across space and time in labrids and specifically parrotfishes, we estimated the ancestral parrotfish skull shape by warping a mesh of the specimen closest to the shape mean (*Ophthalmolepis lineolata*) to the ancestral parrotfish node using *geomorph*.

Ancestral state reconstruction

The ancestral state of beaks for 205 wrasse species was estimated using the R-package *phytools* version 1.0-1 (Revell, 2012). Species were designated as beaked or nonbeaked following visual inspections via micro-CT scans. We used stochastic character mapping (Bollback, 2005; Huelsenbeck et al., 2003) to reconstruct the evolutionary history of the presence or absence of a beak. Stochastic character mapping was performed using the *make.simmap* function in the R-package *phytools* (Revell, 2012). The maximum likelihood Q-matrix was estimated from the data, and the prior for the root state was determined using its stationary distribution, conditional on the Q-matrix. We used the *fitDiscrete* function from *geiger* to determine the best-fitting model of character evolution between equal rate (ER), symmetrical (SYM), and all-rates-different (ARD) models. To account for phylogenetic uncertainty, we fit different models of discrete trait evolution across 100 randomly sampled trees from the posterior distribution of the *BEAST* run used to build the consensus phylogeny. We also used these randomly sampled trees for our stochastic character mapping analysis and estimated the ancestral state at each node using posterior probabilities summarized across 1,000 simulations for each of the 100 phylogenies. For the evolutionary history of the presence or absence of a beak, the lowest AIC values were obtained for the ER and SYM models (as transition rate matrices are identical for binary characters); however, these models were not found to be substantially better fitting compared with an ARD model with a ΔAIC of only 0.93. We conservatively chose to perform the stochastic character mapping for beak presence/absence using an ER model of trait evolution.

Assessing convergent evolution hypotheses

After recovering support for multiple independent origins of beaked dentition among labrids, we tested whether these beaked species evolved similarly shaped skulls and beaks via convergence or whether the shapes of the skull and beak are entirely distinct among the different taxa. We used the distance-based metrics of Stayton (2015; C1–C4) to test for convergence between beaked wrasses. We also used these metrics to quantify the degree of convergence between these species. We ran our convergence analysis on the entire skull configuration as well as on the premaxilla and dentary bones separately.

Quantifying rates of shape evolution

To test the effect of beaks on rates of morphological diversification, we used the *compare.evol.rates* function in *geomorph*, which calculates the rate of shape evolution between groups of specimens under a Brsownian motion model (Denton & Adams, 2015). To account for phylogenetic uncertainty in our rate estimates, we ran this analysis over 100 randomly sampled phylogenies from the posterior distribution of the *BEAST* run and used a paired t-test to test for differences in the mean evolutionary rate between beaked and nonbeaked labrids following the approach of Evans, Vidal-García, et al. (2019). We also estimated the branch-specific rates of skull shape evolution for 204 labrid species. Rates were estimated using a variable-rates model implementation in the *BayesTraitsV4* program (Venditti et al., 2011). This Bayesian method uses a reversible-jump MCMC chain approach to estimate the probability of rate shifts in trait data across a phylogeny revealing clade and species-specific rate shifts in trait data. To reduce the dimensionality of our data, we used the first 23 principal components (PCs) because they accounted for 85% of our total shape variance. While PC axes are mathematically orthogonal, and thus uncorrelated, trait variation can still be evolutionarily correlated. To account for this, we ran our analyses using the "*TestCorrel*" function which constrains the correlation between trait axes to zero. We used uniform, uninformative priors and ran four independent chains each for 200,000,000 generations discarding the first 60,000,000 as burn-in. The chain was sampled every 1,400,000 generations after convergence using a stepping stone. Model convergence was evaluated for each model by running the analysis a second time and visually assessing the trace of the marginal likelihoods using *Tracer* (Rambaut et al., 2018). We evaluated a "variable rates" model that allows for rate heterogeneity and identifies regions of the tree where evolutionary rates differ across different branches and internal nodes (Venditti et al., 2011). The resulting output of the variable-rates analysis is a set of phylogenies where each branch is scaled by its Brownian motion rate of evolution. The *BayesTraits* analyses were run for the entire skull shape configuration. Additionally, due to the fact that many of the species in our analysis are represented by a single specimen, we ran the *BayesTraits* analysis using a lambda transformation of 0.754 estimated from the trait data, which lengthens the branches at the tips of a phylogeny, accounting for measurement error and within-species variation (Baken et al., 2021; Goswami et al., 2022). We also performed a variable-rates regression in BayeTraits following the approach of Kubo et al. (2019) and Baker and Venditti (2019) using the same parameters mentioned above. Briefly, this method simultaneously estimates shifts in the rate of trait evolution using the variable-rates model while also estimating the parameters of a phylogenetic regression. This method has the advantage of accounting for background rates of trait evolution, which has been shown to be important for accurately estimating the effect of discreet characters on rates of trait evolution (May & Moore, 2020).

Model simulations of the Miocene

To evaluate our evolutionary rate results alongside available paleoclimate simulations of the Miocene, we obtained four time-slice simulations from the Hadley Centre Coupled Model version 3 (HadCM3). While paleoclimate model simulations are sparse during time periods relevant to this study, Bradshaw et al. (2012, 2021) produced coupled ocean–atmosphere simulations from the Miocene, including the Miocene Climatic Optimum (MCO, ~15.5 Ma, CO_2 ~850 ppm), the Miocene Climatic Transition (MCT, ~13.9 Ma, CO_2 ~400 ppm), and the Late Miocene Tortonian stage (LMT, ~7.5 Ma, CO_2 ~400 ppm). A control simulation for the preindustrial period provides a baseline for comparison with CO_2 ~280 ppm. We extracted annual mean sea surface temperatures (SSTs) from the four simulations to examine key differences in ocean habitats in the tropical Atlantic and Pacific Sectors. Two key regions were defined in the model simulations: Atlantic SST (0N:30N, 260E:330E) and Pacific SST (30S:30N, 50E:240E). Differences in Atlantic versus Pacific SSTs were determined using a two-tailed *t*-test of the distributions in all three Miocene periods. Due to the limitations of the model simulations before the MCO, we were unable to reconstruct the paleoclimates for the odacine wrasses, which have an Oligocene root age of ~32 million years (Hughes et al., 2023).

Results

Wrasses and parrotfishes evolved beaks multiple times independently

The ancestral state estimation analysis recovers three independent evolutionary transitions to beaks across the wrasse phylogeny (Figure 1; Supplementary Figure 6). The first beak evolved within the odacine wrasses (*Siphonognathus*, *Neodax*, *Haletta*, *Olisthops*, *Heteroscarus*, and *Odax*) between 40 and 32 mya. In this clade, species evolved a fully coalesced beak comprised of small teeth in both the upper and lower jaws. Within parrotfishes, beaks have evolved twice independently: once in the "reef" clade (*Bolbometopon*, *Cetoscarus*, *Hipposcarus*, *Chlorurus*, and *Scarus*) between 37 and 28 mya and again within the "seagrass" clade in the endemic Atlantic Ocean genus *Sparisoma* between 25 and 16 mya. Our analysis shows that parrotfishes evolved beaks from a nonbeaked ancestor and that this ancestral condition was retained in some "seagrass" clade genera (*Calotomus*, *Leptoscarus*, *Nicholsina*, and *Cryptotomus*).

Beaked wrasses exhibit divergent skull shapes

Geometric morphometric analyses indicate that the three groups of beaked labrids explored independent evolutionary shape trajectories, resulting in a novel restructuring of the feeding apparatus. We recover nonsignificant results for the analysis of convergence in skull shape between the three independent transitions to beaks (Table 1; Figure 2). Across all four distance-based convergence metrics (and premaxillary and dentary bones; Supplementary Tables 9 and 10), the beaked labrids do not resemble each other more than expected by chance, and their respective evolutionary trajectories have not led them to become more similar in shape than expected. These divergent morphologies can be seen in the results of our PCAs. For overall skull shape, our first principal component axis (PC1) corresponds primarily to variation in orbit position, dentary width, skull width, urohyal depth, and the length of the supraoccipital crest (Figure 2A). Along this axis, parrotfishes possess the highest scores and exhibit wide skulls with posteriorly displaced orbits and deep dentaries, while non-parrotfish labrid species such as *Symphodus rostratus* possess a narrow skull with an anteriorly displaced orbit and exhibit the lowest scores along PC1. A clear division between "seagrass" and "reef" clade parrotfishes is also apparent with the "reef" clade species exhibiting wider skulls than their "seagrass" clade counterparts, which more closely resemble other labrids in skull shape. The odacines, however, possess some of the narrowest skulls and exhibit the lowest values along the PC1 axis. Along the second PC axis, variation corresponds to skull depth, with the tube-snouted *Siphonognathus argyrophanes* and other odacines exhibiting the shallowest skulls and *Xyrichtys martinicensis* exhibiting the deepest skull. Along this axis, parrotfishes exhibit intermediate scores. The third and fourth PC axes reveal additional partial separation in skull shape between the three beaked clades, corresponding to variation in the position of the orbit, origin of the supraoccipital crest, length of the neurocranium, and the depth of the lower pharyngeal tooth plate (Figure 2B). Along the third PC axis, the beaked labrids overlap entirely as they all possess elongated neurocrania. Additional separation is found along the PC4 axis, which corresponds to skull width, parasphenoid depth, and the angle of the ascending process of the premaxilla. We find that most of the "seagrass" parrotfishes and the odacines exhibit narrower, shallower skulls, while most "reef" parrotfishes (except *Hipposcarus*) possess wider, deeper skulls.

When we examine patterns of shape variation in the dentary and premaxillary bones separately, clear patterns of separation between the beaked labrids are apparent. For dentary shape, "reef" clade parrotfishes are tightly clustered at the higher extreme of PC1 and exhibit the shallowest dentaries with expanded posterior margins, while the "seagrass" species (including the beaked *Sparisoma*) exhibit more intermediate values with deeper dentaries and partially overlap with non-parrotfish labrids. The odacines exhibit more disparate values along the PC1 and PC2 axes with some species such as *Heteroscarus* overlapping in shape with the "seagrass" parrotfishes, while *S. argyrophanes* occupies a more distant position along the PC1 axis relative to the other odacines. Along the second PC axis (which corresponds to the length

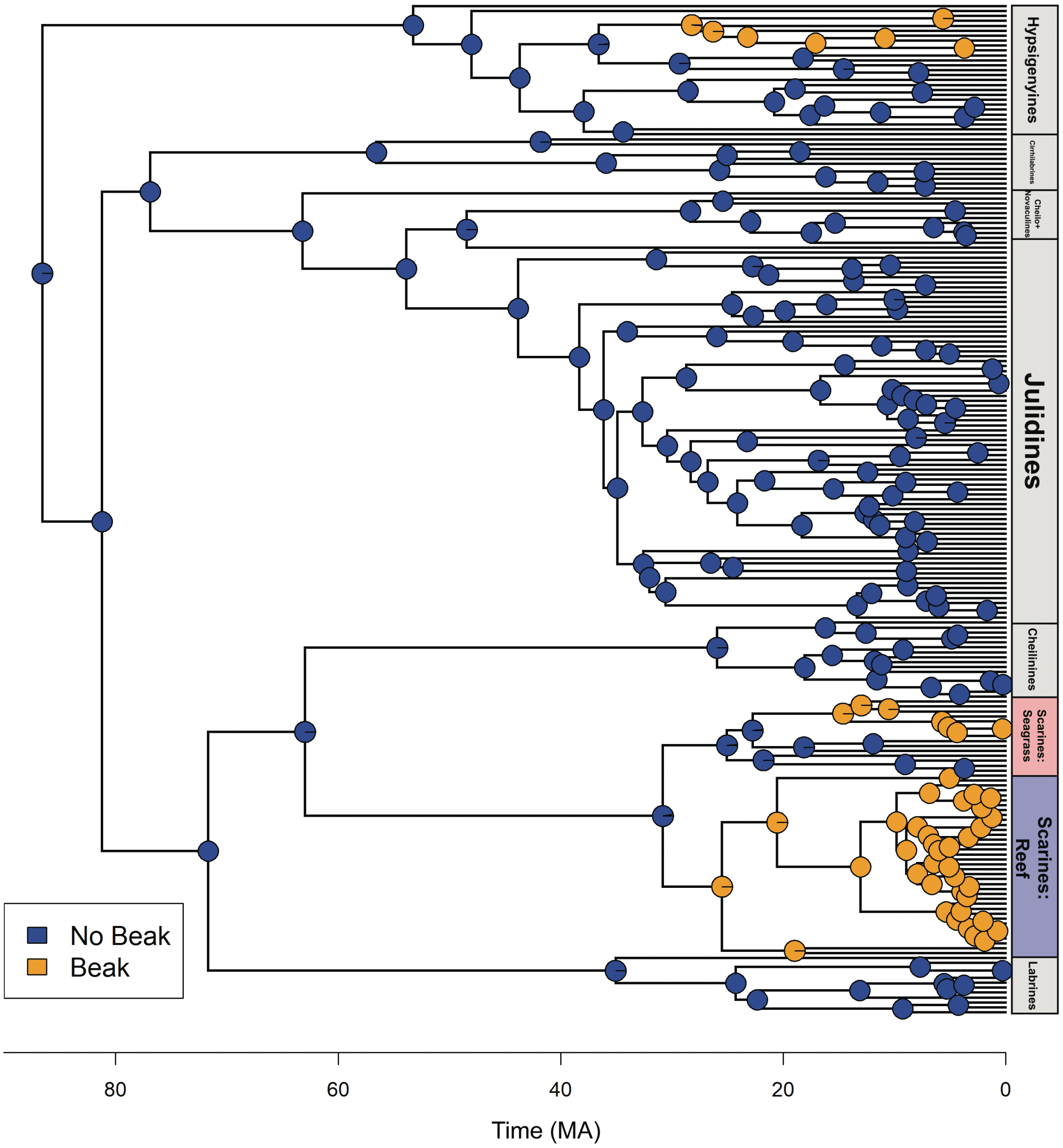

Figure 1. Wrasses evolved beaks three times independently. Ancestral state estimation of beak evolution across 205 wrasses showing posterior probabilities of 1,000 character histories across 100 randomly sampled phylogenies from a posterior distribution of a *BEAST* run mapped onto the time-tree.

Table 1. Similarity-based convergence metrics for skull shape among beaked parrotfishes. Bold values indicate statistical significance.

Metric	Value	*p*
C1	0.055	.478
C2	0.017	.066
C3	0.023	.619
C4	0.000	.638

of the dentary) most beaked labrids (except *S. argyrophanes*) exhibit intermediate scores and broadly overlap in shape space (Figure 2C). In premaxillary shape, we recover a similar pattern of partial separation among parrotfish clades with odacines exhibiting broader distribution in shape space relative to the other beaked labrids. Here, all beaked species broadly overlap along the first PC axis, which corresponds to the angle of the ascending process and the length of the caudal tooth-bearing process, but exhibit more separation along PC2, which corresponds to the length of the ascending process and the curvature of the anterior region of the premaxilla, coupled with the angle of the caudal process. Along this axis, "reef" clade parrotfishes exhibit deeply anteriorly curved premaxillae and truncate caudal processes, while "seagrass" clade species exhibit less curved premaxillae and more elongate caudal processes (Figure 2D). The odacines span most of the PC2 axis indicating a broad diversity in premaxilla shape among species.

Beaks alone do not promote rapid rates of morphological evolution across wrasses

Evolutionary rate analyses indicate that beaked labrids evolved at significantly ($p < .001$) faster rates than nonbeaked

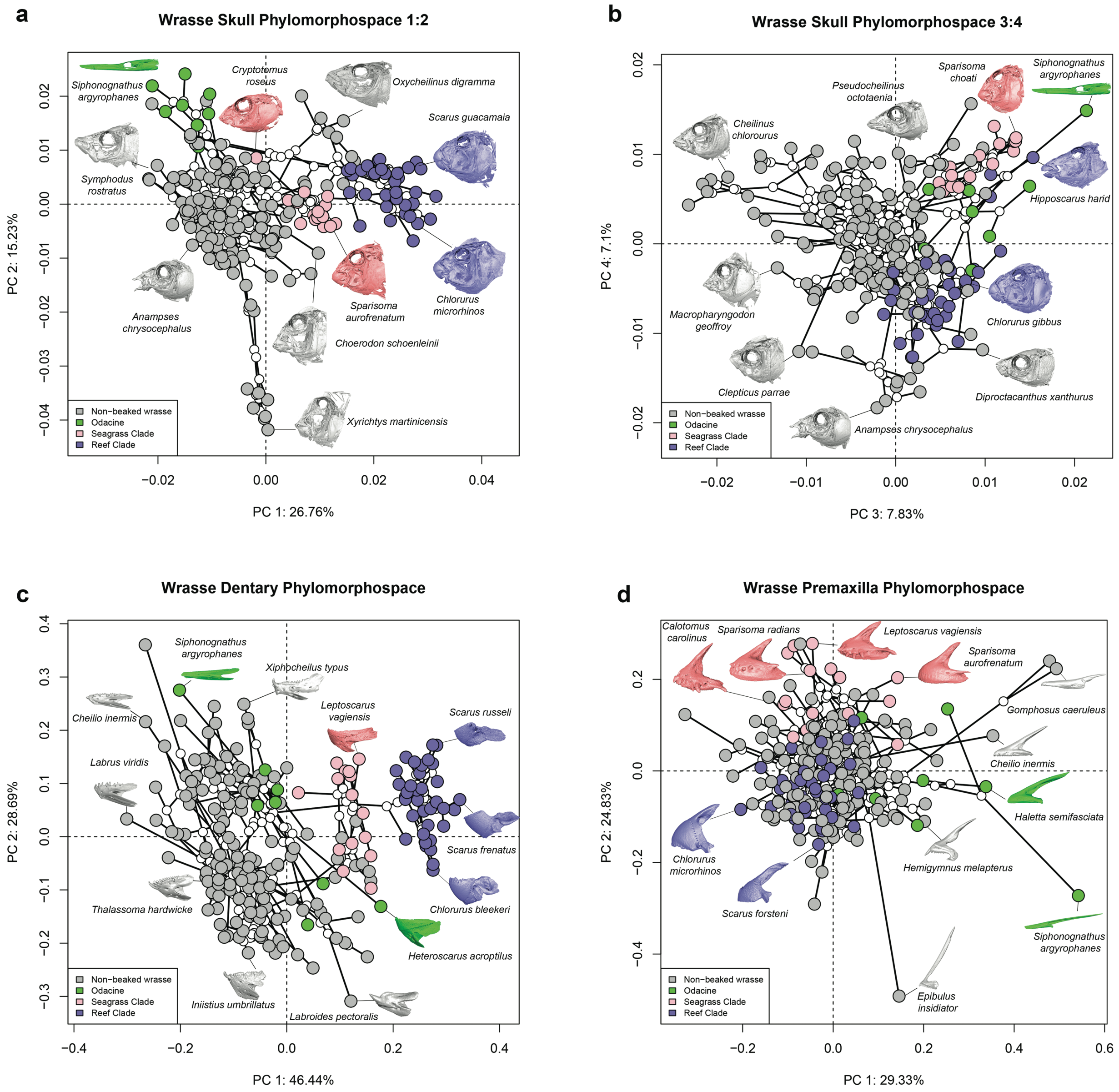

Figure 2. Beaked parrotfishes exhibit nonconvergent skull shapes. Phylomorphospace analysis of skull shape for PCs 1 and 2 (A) and PCs 3 and 4 (B), dentary shape (C), and premaxillary shape (D) across 204 wrasse species showing the primary axes of shape variation across this clade. "Reef" clade parrotfishes are colored in purple, and "seagrass" clade parrotfishes are colored in pink. Insets depict representative shapes for respective regions of shape space.

labrids (Supplementary Figure 7). However, after taking into account background rate variation using a variable-rates regression, we recover a nonsignificant result ($p = .15$). The conflict in these findings suggests that some beaked lineages exhibit fast rates of morphological evolution, while many others do not. When we examine branch-specific rates of evolution we find a more nuanced story (Figure 3A; Supplementary Figure 8). Among the odacines, we observe a rapid increase in the rate of skull shape evolution that coincides with the origin of the beak in this clade ~32 mya and a subsequent rate increase in the tube-snouted species *S. argyrophanes*. Interestingly, among parrotfishes, we do not recover any rate shifts associated with the evolution of a beak in either the "reef" clade or the "seagrass" clade (Figure 3B). Instead, we recover a rate shift in the branch leading to the SCH clade during the Oligocene–Miocene transition ~24 mya and again at the base of the *Scarus*+*Cholrurus* clade during the middle Miocene ~15 mya. We also recover additional rate increases in *Scarus hypselopterus* and in the *S. spinus* + *S. viridifucatus* clade. Within the "seagrass" clade, we recovered a rate shift during the early Oligocene ~32 mya, with no other rate shifts present within this clade. These results suggest that the morphological diversification dynamics differ substantially among the beaked lineages and especially among the two parrotfish subclades.

When we combine our rate analyses with biogeographic studies from the literature (Bellwood & Schultz, 1988; Siqueira et al., 2019b; Streelman et al., 2002; Westneat & Alfaro, 2005), we are able to reconstruct the evolution of beaks across both space and time (Figure 4). We estimate that the first beak appeared in the temperate West Pacific ~32 mya within the odacines. Within parrotfishes, we estimate that

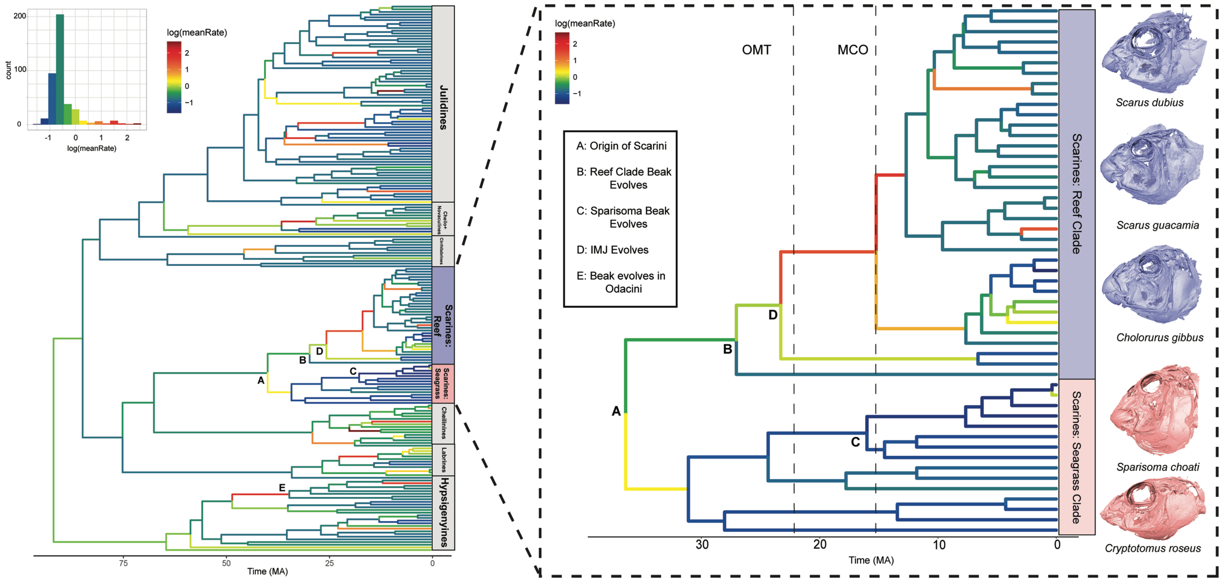

Figure 3. Labrid rates of skull shape evolution. Results from the *BayesTraits* analysis of skull shape for 204 labrid species showing variable-rates of trait evolution. Insets depict representative skull morphologies for major clades.

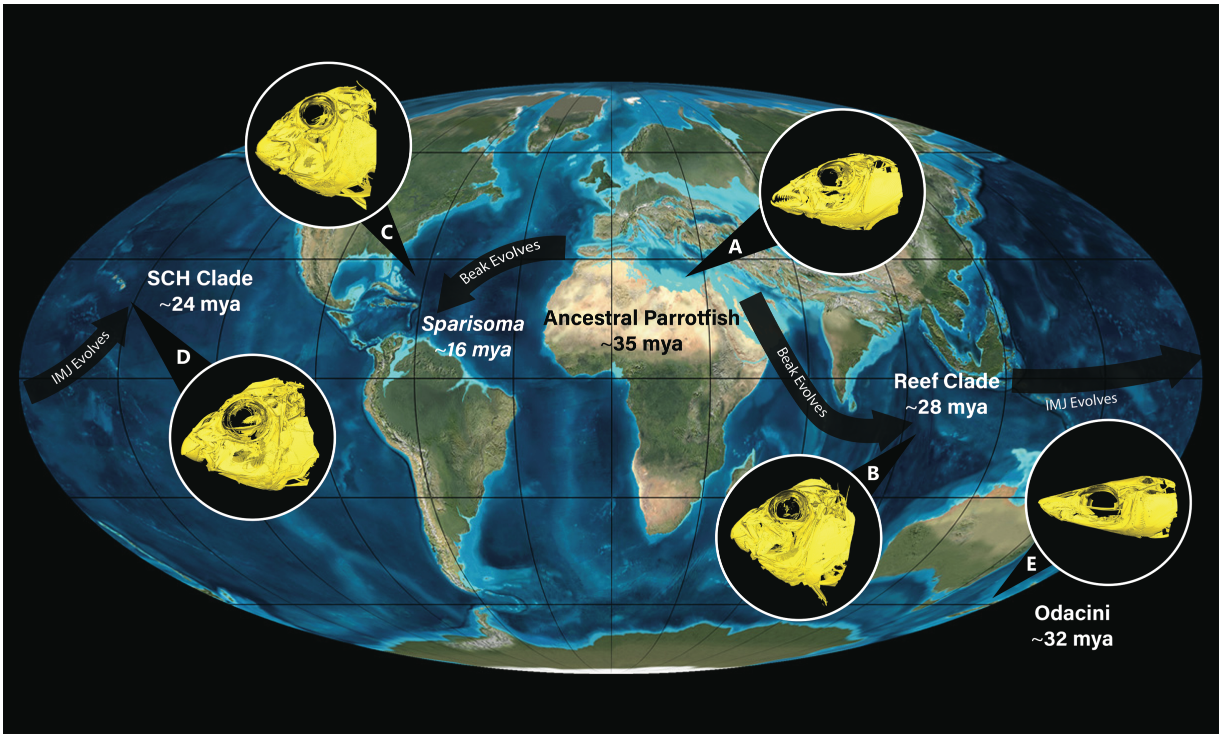

Figure 4. The evolution of the labrid beak across space showing a map of the Tethys Sea 35 mya (copyright Ron Blakey, Colorado Plateau Geosystems, Inc). (A) with the origin of parrotfishes in the Tethys Sea showing the estimated ancestral skull shape for Scarini, (B) the evolution of the beak in "reef" clade parrotfishes in the Central Indo-Pacific, and (C) the independent evolution of the beak in *Sparisoma* in the Atlantic Ocean, (D) the origin of the intramandibular joint in *Scarus*, *Chlorurus*, and *Hipposcarus* in the Central/Western Indo-Pacific, and (E) origin of the beak in odacine wrasses in the temperate Western Pacific Ocean. Biogeographic designations follow reconstructions from Siqueira et al. (2019b) and Westneat and Alfaro (2005). Insets depict representative skull shapes for each major clade.

the ancestral parrotfish originated in the Tethys Sea roughly 30–40 mya without a beak and colonized the Indo-Pacific region westwards 10 million years later where they later evolved beaks. Shortly thereafter, the "seagrass" clade species colonized the Atlantic Ocean from the East Tethys. Our ancestral state estimation indicates that the colonization of the Atlantic by a nonbeaked "seagrass" clade lineage ~25 mya was followed by a second independent evolution of a beak ~10 million years later in *Sparisoma*. There was also a subsequent remodeling of the beak in the SCH clade when they evolved an intramandibular joint ~24 mya in the Central/Western Indo-Pacific.

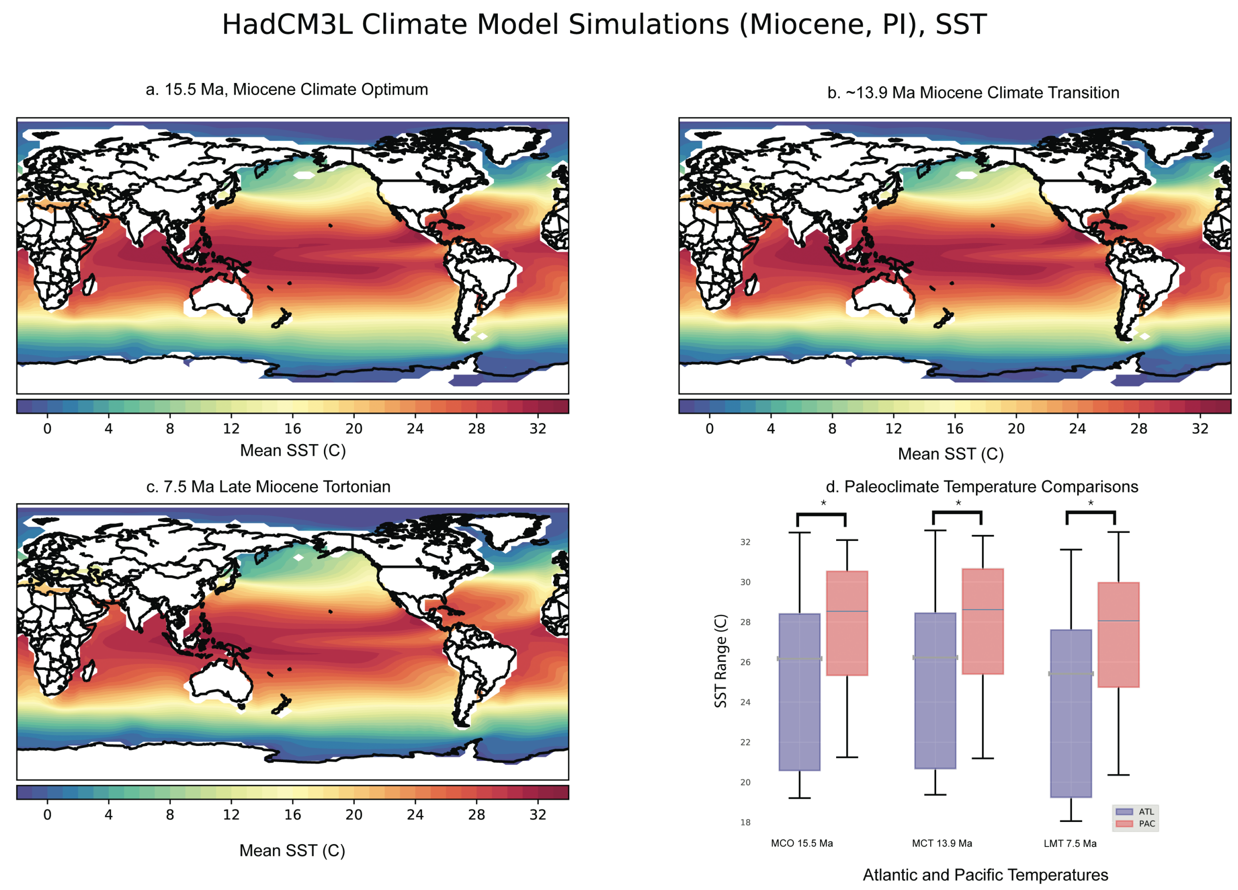

Figure 5. Paleoclimate model simulations of the Miocene from the HadCM3 coupled climate model (Bradshaw et al., 2012, 2021). Simulated annual mean sea surface temperatures (SST) for the (A) Miocene Climatic Optimum (MCO), (B) Miocene Climate Transition (MCT), and (C) Late Miocene Tortonian (LMT). (D) Boxplots of the simulated SST range (°C) for the tropical Atlantic (0N:30N, 260E:330E; blue) and tropical Pacific (30S:30N, 50E:240E; red). A two-tailed *t*-test was used to establish significant differences between the distributions of Atlantic versus Pacific SSTs in all three Miocene periods.

Miocene paleoclimates differed significantly between the Atlantic and Pacific Oceans

Analysis of Miocene paleoclimate simulations for the Atlantic and Pacific Ocean basins suggests that *Sparisoma* and the Indo-Pacific "reef" clade evolved under significantly different SST ranges (Figure 5); tropical Atlantic SSTs show a larger range of temperature variability compared to Pacific SSTs, and differences between annual mean SST ranges are significant at the 95% level ($p < .05$, two-tailed t-test).

Discussion

Multiple origins of beaks within wrasses

The beak is a striking evolutionary innovation that enables many labrid species to engage in durophagy. Our results indicate three independent origins of beaked dentition within labrid fishes: once in the odacines ~32 mya, another in the "reef" clade of parrotfishes ~28 mya, which evolved beaks in the Central and Indo-Pacific, and then again within the endemic Atlantic "seagrass" lineage *Sparisoma* ~16 mya. Previous studies that have reconstructed the evolution of various forms of coalesced dentition in parrotfishes (but not "beaks" specifically) have also recovered multiple independent origins within labrids (Bellwood, 1994; Burress & Wainwright, 2018). However, the ancestral state of coalesced dentition in the upper and lower jaws for parrotfishes has proven more difficult to estimate. An earlier study by Wainwright et al. (2018) found ambiguous results at the root of parrotfishes suggesting that coalesced dentition in the upper and lower jaws either evolved once at the base of all parrotfishes and was lost multiple times within some of the "seagrass" clade lineages (*Calotomus*, *Nicholsina*, *Cryptotomus*) or evolved three times independently in the "reef" clade, "seagrass" clade, and *Leptoscarus*. This ambiguous result was likely recovered due to coding *Leptoscarus vaigiensis* as having coalesced dentition. *Leptoscarus* is a monotypic species and has an important and informative position in the labrid phylogeny as previous studies have shown that *Leptoscarus* is among the earliest branching lineages of parrotfishes with a Tethyan origin (Aiello et al., 2017; Cowman et al., 2009; Kazancıoğlu et al., 2009; Siqueira et al., 2019b; Smith et al., 2008; Streelman et al., 2002). In addition to its phylogenetic position, the coding of *Leptoscarus* presents an interesting challenge because this species exhibits a pattern of coalescence that is unique among parrotfishes in which the teeth in the upper and lower jaws are arranged in oblique, nonoverlapping rows (Bellwood, 1994; Viviani et al., 2022). This condition is further complicated among sexually mature adults where the males exhibit large canines that protrude anteriorly and laterally from the premaxilla and contact the occlusal surface of the dentary, giving the appearance of coalesced dentition in the lower jaws and incompletely coalesced dentition in the upper jaws (Robertson et al., 1982; Viviani et al., 2022; Supplementary Figure 9). This condition is apparently absent in females. In our analysis, we coded *Leptoscarus* as not having a beak due to the fact that the dentition in the upper and lower jaws are nonoverlapping and arranged into oblique rows as has been noted in Bellwood (1994) and Viviani et al. (2022). This condition is also present to a lesser degree in *S. radians* but in this case, we coded this species as having a beak because the tooth rows overlapped more than in *Leptoscarus*. However, out of caution, we reran the ancestral state estimation analysis with *S. radians* coded as not having a beak, and we still recovered three independent origins of beaks within wrasses, although with an additional reversal within *S. radians*. The incomplete coalescence of teeth into a beak that we observe in *Leptoscarus* coupled with the potential reversal to this condition in *S. radians* suggests that *Leptoscarus* represents a potential ancestral intermediate phenotype among "seagrass" parrotfishes.

Labrid beaks are nonconvergent and morphologically distinct

Trophic ecology is known to be a strong driver of patterns of convergent evolution (Kelley & Motani, 2015; Pigot et al., 2020; Rüber & Adams, 2001). Beaked labrids have been documented engaging in various forms of herbivory and durophagy (Baker, 2011; Burkepile et al., 2019; Choat & Clements, 1992; Clements & Bellwood, 1988; Clements & Choat, 1993; 2018; Ezzat et al., 2020; Nicholson & Clements, 2021). However, our results show that the skull and beak shapes of these clades are nonconvergent and, in some cases, differ dramatically. We hypothesize that these shape differences may reflect differences in the usage of their beaks among the different species. Within odacines, the beak is used to graze on seagrasses and feed on hard-shelled prey in different species, and the shape of the skull and individual beak elements appears to differ substantially between even closely related taxa. In "reef" clade parrotfishes, there is a striking diversity in the shapes and functions of the beaks ranging from robust beaks that are used in excavating feeding behaviors (e.g., *Cetoscarus*) to more gracile beaks with an intramandibular joint that allow for faster bites and surface-scraping behaviors during feeding (Bellwood, 1994; Bellwood & Choat, 1990; Bruggemann et al., 1994; Hoey & Bellwood, 2008; Price et al., 2010). However, in *Sparisoma*, we generally recover less shape diversity in beak morphology and instead find that the overall shapes of the beak elements more closely resemble some non-parrotfish wrasse species. From a functional perspective, the beaks of *Sparisoma* appear to be used in a more generalized fashion where species have been reported to scrape and excavate hard coral substrates as well as macroalgae and sponges (Bruggemann et al., 1994; Dromard et al., 2015, 2017; Lobel & Ogden, 1981). The lack of morphological diversity within *Sparisoma* relative to "reef" clade parrotfishes has also been documented in "functional" traits (Pombo-Ayora & Tavera, 2021; Wainwright et al., 2018). These results suggest that beaks are a common tool that labrid lineages employ to exploit grazing substrates wherever and whenever they encounter them in search of hard-shelled prey, algae, detritus, cyanobacteria, and other microbes.

While the specific shapes of the skull and beak elements are divergent among the labrid lineages, the evolutionary trait of coalescing teeth into a beak appears to be convergent. Studies of trophic morphology among parrotfishes specifically have also noted similarities in gill raker, pharyngeal mill, and soft tissue morphology between *Sparisoma* and "reef" clade parrotfishes, suggesting that the convergence extends beyond the beak in these species (Bellwood, 1994; Board, 1956; Clements & Bellwood, 1988; Clements & Choat, 2018; Evans, Williams, et al., 2019; Gobalet, 1989).

Complex climatic and biogeographic histories drive distinct evolutionary trajectories across two oceans

Studies of reef fish evolution have recovered increases in the rate of trait diversification and speciation during the late Oligocene–Miocene period and have found close links between patterns of reef fish diversification and patterns of coral diversification and reef expansion (Bellwood et al., 2017; McCord et al., 2021; Siqueira et al., 2019a, 2020). In corals specifically, studies have shown that coral reef cover expanded in the Indo-Pacific during the late Oligocene to early Miocene in-part due to a decrease in global temperatures and the expansion of shallow water habitat as a result of tectonic activity that together created favorable conditions for carbonate formation (Bellwood et al., 2017; Fulthorpe & Schlanger, 1989; Perrin & Bosellini, 2012; Perrin & Kiessling, 2011). Meanwhile, in the Atlantic during the same time, corals were experiencing one of many extinction events associated with changes in ocean temperature and water quality. This historical pattern has recently been shown to be associated with diversification rates and dietary ecotype patterns in the damselfishes (McCord et al., 2021). Our evolutionary rate analysis recovers mixed results for the effect of beaks on the tempo and mode of skull shape evolution during this period of time (Budd et al., 1995; Cahuzac & Chaix, 1996; Edinger & Risk, 1994). Within the SCH clade of parrotfishes, we recover increases in the rate of evolution during the Oligocene–Miocene transition and later in the middle Miocene. The rate increases are likely associated with the evolution and modification of the intramandibular joint in this clade as previous studies have found similar increases in rates of morphological evolution within parrotfishes associated with this trait (Price et al., 2010). However, the evolution of the beak in the "reef" clade predates the Oligocene–Miocene boundary, which suggests that some parrotfishes already had beaks before the expansion of coral reef cover that would occur several million years later. We see the inverse pattern in *Sparisoma* where this clade evolved a beak during the Middle Miocene but is instead not associated with any change in the rate of shape evolution. Indeed, skull shapes in *Sparisoma* were generally found to overlap with other "seagrass" clade species and even some non-parrotfish wrasses suggesting minimal divergence in overall skull shape. Our reconstructions of paleoclimate temperatures show that during the middle to late Miocene, the Atlantic Ocean experienced cooler temperatures and more climatic variability than the Pacific Ocean. The cooler temperatures of the Atlantic during the Miocene may have selected more cold-tolerant coral species while driving the extirpation and extinction of other less-tolerant species (Cahuzac & Chaix, 1996; Edinger & Risk, 1994).

We hypothesize that the differences in biogeographic histories between the coral faunas of the Atlantic and Pacific Oceans have played an important role in promoting or constraining patterns of morphological diversification among the beaked parrotfishes. In the Indo-Pacific, the expansion of coral reef habitat during the Oligocene–Miocene boundary likely presented ecological opportunity to the "reef" clade of parrotfishes that were already in possession of beaks and thus in prime position to take advantage of this expansion of their trophic resource and grazing substrate. This ecological opportunity may have provided ecological release and spurred subsequent rapid morphological diversification and specialization leading to the emergence of the intramandibular joint within the SCH clade. In the Atlantic Ocean however, *Sparisoma* evolved beaks in a more variable climates and during a prolonged period of decline in the abundance and diversity of reef-building corals. Interestingly, while reef-building corals declined during this time, solitary corals proliferated in seagrass beds which were the likely habitats of ancestral *Sparisoma* (Budd et al., 1995; Pomar & Hallock, 2007). This may also explain the more generalized diets in the *Sparisoma* species that include seagrass and other macroalgae in addition to coral skeletons (Burkepile et al., 2019; Clements & Choat, 2018; Wainwright et al., 2018). Hermatypic corals would not see a distinct rebound in the Atlantic until the Pleistocene (2.5 mya). But by the time these corals began to rebound, *Sparisoma* would have been faced with new competition by the "reef" clade parrotfishes that invaded the Atlantic Ocean through the Isthmus of Panama from the Pacific Ocean ~6.5 mya (Siqueira et al., 2019b) and have been shown to compete for similar resources (Adam et al., 2015; Burkepile et al., 2019; McAfee & Morgan, 1996). In short, we hypothesize that the Atlantic *Sparisoma* never had the ecological opportunity that the "reef" clade of parrotfishes experienced in the early Miocene because of when and where they evolved their beaks and as a result we see a reduction in the rate of skull shape evolution after evolving beaks and more generalized skull shapes and diets among these species relative to "reef" clade species.

In the odacines, beaks evolved in the temperate West Pacific during the Oligocene ~32 mya. Today, many of these species are found in seagrass habitats where they either feed directly on the seagrass or feed on the invertebrate prey that inhabit the seagrass beds. Ancestral state estimations of diet in previous studies have found that the ancestral odacine likely fed on hard-shelled invertebrate prey and some species later shifted to more herbivorous diets (Burress & Wainwright, 2018; Cowman et al., 2009). Unlike hermatypic corals, seagrasses have a sparse fossil record which limits the reconstruction of their paleobiogeography to the use of proxy species that have been known to associate with seagrasses (Brasier, 1975; Vélez-Juarbe, 2014). As a result, it is difficult to accurately estimate the distribution of specific seagrass communities during the Oligocene beyond the general expansion of shallow water habitat that occurred as a result of tectonic events in the Indo-West Pacific around that time that may have provided suitable habitat (Brasier, 1975). However, recent studies that examined the Trealla Limestone in Western Australia, which contains the oldest evidence for seagrass communities in Western Australia, have found evidence for widespread seagrass meadows during the early Miocene 19–16 mya (Haig et al., 2020). It is therefore possible that seagrass communities were present in the region earlier and did not manage to fossilize until later. Interestingly, studies of other seagrass-associated fishes (Syngnathidae) have also found dramatic morphological changes during the Oligocene and hypothesized that these adaptations arose in response to the expansion of seagrass distributions during this time (Teske & Beheregaray, 2009). It is therefore possible that the expansion of seagrass habitats in the Oligocene spurred the evolution of the beak in odacines and the rate shift that we observed in our shape data.

Our findings show that evolutionary innovation alone may not be enough to spur subsequent morphological diversification and that the timing and ecological context of the innovation may be equally important for determining the subsequent evolutionary trajectories of the clades that possess them.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Data and code for all analyses is available at Dryad: doi:10.5061/dryad.prr4xgxrz.

Author contributions

K.M.E. designed project, collected data, ran analyses, and wrote manuscript. O.L. collected data, ran analyses, and wrote manuscript. S.M.G. collected data, ran analyses, and wrote manuscript. R.E.F. collected data. S.G.D. collected data and ran analyses. M.W.W. collected data, ran analyses, and wrote manuscript.

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