The rise of biting during the Cenozoic fueled reef fish body shape diversification

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Diversity of feeding mechanisms is a hallmark of reef fishes, but the history of this variation is not fully understood. Here, we explore the emergence and proliferation of a biting mode of feeding, which enables fishes to feed on attached benthic prey. We find that feeding modes other than suction, including biting, ram biting, and an intermediate group that uses both biting and suction, were nearly absent among the lineages of teleost fishes inhabiting reefs prior to the end-Cretaceous mass extinction, but benthic biting has rapidly increased in frequency since then, accounting for about 40% of reef species today. Further, we measured the impact of feeding mode on body shape diversification in reef fishes. We fit a model of multivariate character evolution to a dataset comprising three-dimensional body shape of 1,530 species of teleost reef fishes across 111 families. Dedicated biters have accumulated over half of the body shape variation that suction feeders have in just 18% of the evolutionary time by evolving body shape ~1.7 times faster than suction feeders. As a possible response to the ecological and functional diversity of attached prey, biters have dynamically evolved both into shapes that resemble suction feeders as well as novel body forms characterized by lateral compression and small jaws. The ascendance of species that use biting mechanisms to feed on attached prey reshaped modern reef fish assemblages and has been a major contributor to their ecological and phenotypic diversification.

macroevolution | suction feeding | benthic grazing | evolutionary rates | RevBayes

Reef habitats are renowned for high biodiversity (1–5). Often, this pattern is attributed to the structural complexity of reefs, as complex habitats provide increased opportunity for microhabitat-related adaptations and niche partitioning (6–8). Among reef fishes, many major drivers of phenotypic and ecological diversity have been recognized at a range of phylogenetic scales (9–13), but we still lack a clear understanding of the processes and mechanisms that have made reef fish faunas the most diverse in modern oceans.

One striking axis of diversity that distinguishes reef fish communities from those in other marine habitats is the variety of feeding modes used to capture prey. Fishes can employ a direct biting mechanism to remove attached prey from hard substrates or can use suction feeding, which relies on the density and viscosity of an aquatic medium to pull in water and prey via rapid expansion of the head. Suction feeding, which is most effectively used to capture mobile prey (14–19), is both ancestral for teleost fishes (20) and well represented on modern reefs (21). However, direct biting feeding mechanisms characterize many iconic reef fish groups, including parrotfishes, butterflyfishes, surgeonfishes, and triggerfishes. The evolution of biting has allowed fishes to exploit a variety of benthic prey that are firmly attached to reef surfaces and thus, resist suction, including molluscs, echinoderms, cnidarians, sponges, algae, and other primary producers (22–27). The ecosystem importance of this functional breakthrough in trophic habits is perhaps best represented by the many benthic biting herbivores and detritivores (27–32) that play a central role in energy transfer through reefs and regulating the composition of benthic communities (33–37).

Benthic biting has been a major facet of the trophic diversity of reef fishes since at least the Eocene. Herbivores were well established in the Monte Bolca lagerstätte (~50 Ma), marking the first evidence that teleosts could graze upon the reef surface and signaling a major shift in reef community functions (38–40). These herbivores appear to have risen to dominance within reef ecosystems globally through expansion and colonization following the split of the Tethys Sea and the increased availability of reef flat habitats in the Late Cenozoic (40–44), although the implications of biting for phenotypic diversification of reef fishes remain unknown (40). Use of a biting feeding mode prior to the Eocene appears to be primarily the domain of nonteleost fishes. As long ago as the Devonian, lungfishes and some arthrodire placoderms captured and crushed hard prey with their jaws (45–48). Several lineages of early-branching ray-finned fishes used

Significance

We demonstrate that the stunning trophic diversity of modern reef fishes is a relatively recent state driven by a dramatic transformation in representation of major feeding modes. Since the Early Cenozoic, when over 95% of teleost lineages were suction feeders, there has been a steady increase in direct biting feeding modes. A variety of novelties and jaw modifications permitted reef fishes to feed on substrate-bound prey using direct biting and grazing behaviors and opened this rich adaptive zone, which we show elevated rates of body shape evolution. Taken together, our results indicate that recent diversification of the feeding mechanism played a major role in ecologically and phenotypically shaping the modern fauna of reef fishes.

biting for prey capture throughout the Mesozoic, including pycnodonts, macrosemiids, and semionotids (38, 49–51); of these, pycnodonts persisted until the Eocene (51). The striking lack of biting teleosts prior to the Eocene (38) may be due to a 20-My gap in major deposits of spiny-rayed (Acanthomorph) fishes from the Late Campanian (~75 Ma) to the Late Paleocene (~55 Ma) (52), during which biting by teleost fishes most likely proliferated to its Eocene prominence. The ambiguity regarding the origins of the expansion of biting among teleosts and its role in morphological diversification presents an opportunity for comparative phylogenetics to provide insight into the history of modern reef fishes.

In this study, we explored the evolutionary history of benthic biting feeding mechanisms in reef fishes and the impact this novelty had on their phenotypic diversification. We compared benthic biting with three other feeding modes: suction feeding, an intermediate group using a mix of both suction and biting, and an uncommon feeding mode we refer to as "ram biting." To determine how the prevalence of benthic biting has changed through time, we reconstructed the history of feeding modes among reef-dwelling teleosts using stochastic mapping on a time-calibrated phylogeny. We then measured the effect of feeding mode on rates of body shape evolution across a broad sample of 1,530 species of reef fishes spanning 111 families of extant teleosts. If biting feeding modes have been a significant stimulus to the diversification of modern reef fishes, we expect to see differences in body shape occupation of morphospace and phenotypic diversification when comparing biters with fish that employ other feeding modes. Our results provide insight into the evolutionary mechanisms underlying the vast phenotypic and ecological diversity of reef fishes.

Results

Evolutionary History of Feeding Modes. We classified 1,530 species of reef fishes by feeding mechanism; 335 (22%) were classified as biters, 277 (18%) were mixed suction and biting feeders, 830 (54%) were suction feeders, and 88 (6%) were ram biters (Dataset S1). We also classified biters and mixed feeders by whether they prey primarily upon algae and detritus ("herbivores/detritivores") or take a larger portion of animal material, such as sponges, corals, or echinoderms. In total, 58% of dedicated biters were herbivores/detritivores, 17% of "mixed" feeders were herbivores/detritivores, and combined, 39% of biters and mixed feeders were herbivores/detritivores.

We used stochastic character mapping to reconstruct the history of feeding mode over the phylogeny. A distribution of 100 stochastic character maps had a mean of 244.5 transitions between feeding modes across reef-dwelling teleosts, with strongly asymmetrical transitions between states (Fig. 1 and *SI Appendix,* Figs. S1 and S2). The mean total time on the phylogeny spent in each state varied dramatically among feeding mode groups (Table 1).

Stochastic character maps indicated a major transformation since the Early Cenozoic in the representation of all three nonsuction modes (Fig. 1). Prior to the end Cretaceous, suction feeding was used by at least 96% of teleost lineages that include species on modern reefs, with the three nonsuction modes accounting for only about 2.8% of all branches at the Cretaceous-Paleogene (K/Pg) boundary. Since that time, the proportion of lineages using biting modes has grown to its peak in the present at 40%. Beginning in the Early Cenozoic, a steady rise was observed in the proportion of lineages that use the three nonsuction modes of feeding, especially the dedicated attached
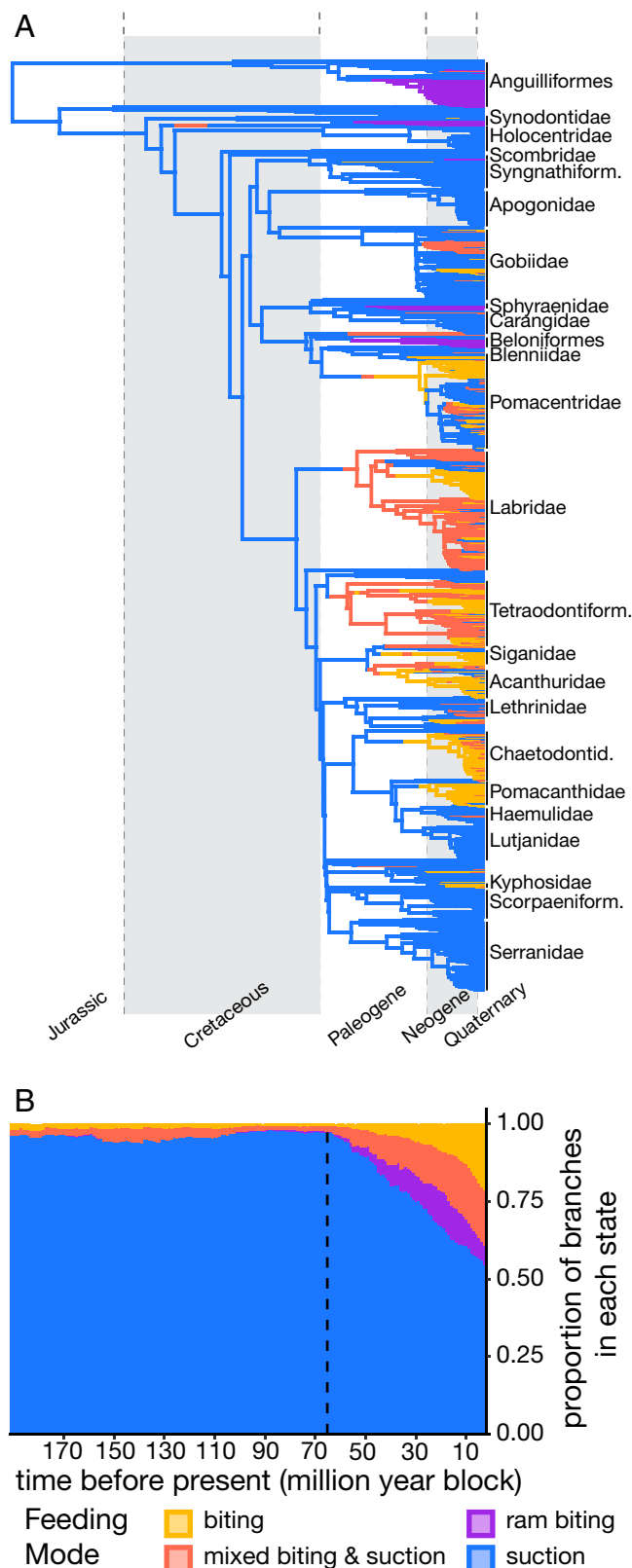
Fig. 1. (*A*) An ancestral-state reconstruction of feeding mode using stochastic character mapping in reef-dwelling teleost fishes. Branches are colored by feeding mode, with selected major lineages labeled to the right. Background bars (white and gray) indicate the geologic time period. (*B*) A bar plot showing the proportion of branches at million-year intervals in each feeding mode state, averaged across 100 stochastic character maps. The proportion of branches in each feeding mode is on the *y* axis, with bars along the *x* axis at million-year intervals starting 192 Ma (*Left*) and progressing rightward toward the present. The dashed line indicates the time of the end-Cretaceous mass extinction event 66 Ma. Note the dramatic increase of biting and mixed feeding modes following the mass extinction event.

Table 1. Comparison of results of multivariate disparity, stochastic character mapping, and evolutionary rate analyses among feeding mode groups

Feeding group	Disparity*	Time on tree,[†] %	Rate[‡]
Biting	0.103	12.1	1.426
Mixed suction and biting	0.121	14.4	0.966
Ram biting	0.324	7.4	0.77
Suction	0.189	66.0	0.838

*Disparity represents multivariate disparity across all eight body shape traits.
[†]Time on tree represents the proportion of the total branch length on the phylogeny reconstructed to be in each state using stochastic character mapping, averaged across 100 reconstructions.
[‡]Rates are calculated as the state-dependent rate of multivariate evolution, which excludes background evolution on each branch.

prey biting category, which clearly accelerated in representation over the past 30 My.

Morphological Disparity and Occupation of Shape Space. We explored how feeding mode affects the morphological diversity of reef fishes, estimating three-dimensional body shape with eight linear measurements of length, depth, and width of the head; body; jaws; and caudal peduncle. When visualizing body shape diversity with a scatterplot of principal components 1 and 2, most species in our dataset were concentrated in an oval-shaped region of morphospace distributed in the upper half of Principal Component Axis 1 (PC1) and across PC2. A low-density spur spanned the majority of PC1, composed of eels and other elongate species, such as pipefishes and needlefishes. Standard length, body depth, and head depth were the major axes of diversity dominating PC1, which accounted for 43.1% of the total variation, with smaller roles for caudal peduncle depth and width (Fig. 2 and *SI Appendix,* Table S1). PC1 defined an axis with elongate, slender bodies with shallow heads on one side and deeper, shorter bodies and deeper heads on the other. PC2, which contained 26.8% of the variation,

was dominated by width and jaw traits: body width, lower jaw length, and mouth width. PC3 and PC4, which each contained ~10% of the variation in the data, were made up of fish width and caudal peduncle traits as well as lower jaw length, caudal peduncle width, and fish width, respectively.

All eight body shape traits differed between feeding mode categories in phylogenetic analyses of variance (ANOVAs) at α = 0.05 and all traits except maximum fish width at α = 0.01 (*SI Appendix,* Fig. S3 and Table S2). All traits had low explanatory power and small effect sizes, except lower jaw length, where feeding mode explained 6% of the variation in the data. Similarly, in a phylogenetic multivariate analysis of variance (MANOVA) including all eight body shape traits, there was a significant effect of feeding mode on body shape ($P < 0.0001$), explaining 2.8% of the overall variance in body shape and an effect size of 5.98. Random forest model fitting identified lower jaw length as the most important trait for discriminating between feeding mode groups, with over threefold higher importance in correctly categorizing species than any other trait (*SI Appendix,* Table S3). We found a trend among feeding mode groups along a gradient of prey evasiveness, where ram biters had elongate, slender bodies with large jaws and species using biting had shorter, deeper heads and bodies with short jaws. Suction feeders typically had intermediate body shapes between ram biters and benthic biters but with substantial variation.

To analytically compare which feeding mode groups had the most variation in body shape, we used multivariate disparity analyses. Body shape disparity was highest in ram biters followed by suction feeders, biters, and mixed biting and suction feeders (Table 1). This pattern was generally repeated among univariate disparity analyses with the notable exceptions of maximum body depth and mouth width, where ram biters had the lowest disparity, and maximum fish width, where there was very little variation between groups (*SI Appendix,* Table S4).

We used hypervolumes to compare the multidimensional morphospace occupation of feeding mode groups. Hypervolumes
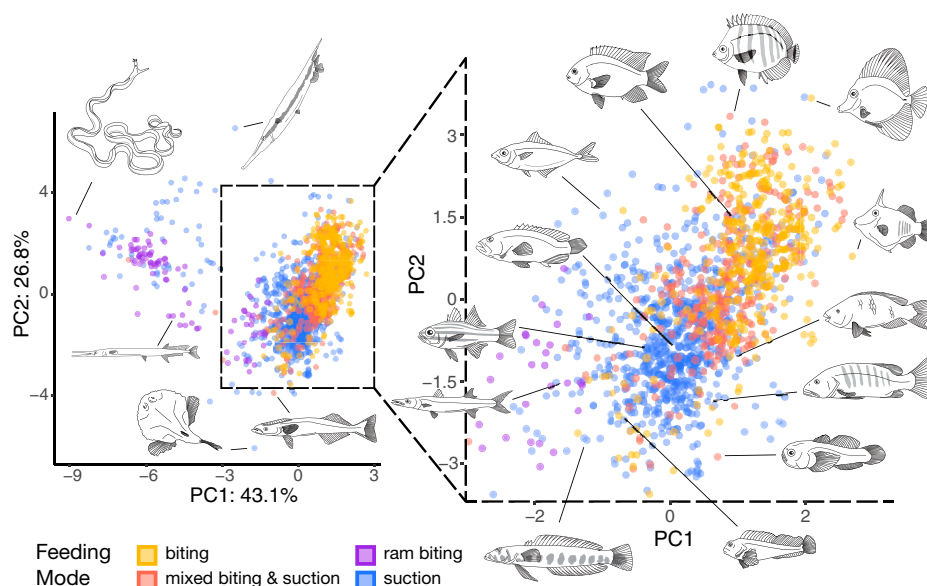

Fig. 2. A plot of 1,530 reef fish species on principal components 1 and 2 based on eight body shape traits, with *Inset* showing a high-density region. Points represent species averages, and each species is colored by feeding mode. Several fishes are drawn to illustrate the shapes of fishes at different regions of morphospace. Main plot (clockwise from the upper right): *Aeoliscus strigatus, Remora remora, Halieutichthys aculeatus, Tylosaurus acus,* and *Rhinomuraena quaesita. Inset* (starting with the upper right): *Zebrasoma scopas, Amanses scopas, Scarus guacamaia, Lutjanus cyanopterus, Paragobiodon modestus, Hypsoblennius hentz, Parapercis millepunctata, Sphyraena jello, Ostorhinchus holotaenia, Cephalopholis cruentata, Equites stercorarius, Stegastes obreptus,* and *Chaetodon multicinctus.* Fish images drawn by K.A.C.

composed of the first six dimensions of a principal component analysis (PCA) revealed modest differences in the amount of unique shape space occupied by feeding mode groups when each was compared with a group containing all other species. However, no comparisons were more extreme than 95% of a "null" distribution of hypervolumes randomly generated from our data (*SI Appendix*, Table S5). Notably, 19% of the space occupied by a composite group of all species using any form of attached prey biting, formed by combining the biting group and the mixed biting and suction group, was unique when compared with a group composed of ram biters and suction feeders (*SI Appendix*, Fig. S4 and Table S5).

Evolutionary Models of Body Shape Diversity. Feeding mode had a strong effect on the multivariate rate of body shape evolution (across body shape traits; posterior probability of state dependence = 1.0) (Fig. 3). Attached prey biters evolved traits 1.5-fold faster than species that use mixed suction and biting, 1.7-fold faster than suction feeders, and 1.9-fold faster than ram biters (Table 1). The substantial variation in background rate of body shape evolution uncovered and accounted for in these models is not surprising given the vast amounts of evolutionary time and taxonomic breadth encompassed by our dataset and *SI Appendix*, Fig. S5.

Discussion

Our results reveal that the end-Cretaceous mass extinction preceded a sustained growth in the preponderance of teleost reef fish lineages that use biting for prey capture. The timing indicated in our reconstruction suggests that the prominence of herbivorous teleosts in the Middle Eocene fossil record (10, 38–40) resulted from a rapid escalation of biting feeding modes among reef fishes, as the frequency of biting had only begun to increase among teleosts in the previous 15 My. These Eocene fossil teleosts show the shortened lower jaws that characterize benthic biters (9, 53), a novel invasion of functional morphospace specialized for feeding on attached prey (38). This rise in benthic biting overlaps with the emergence in the Paleogene and Neogene of lineages that are foundational to modern coral reefs, such as scleractinian corals and crustose coralline algae, and that are major substrates for the feeding activities of benthic biting reef fish (54, 55). Coupled with these novel functional abilities in marine fishes, the evolution of modern reefs in the Early Cenozoic appears to have facilitated a dramatic shift in the distribution of feeding modes used by reef teleosts. We find that the ecological composition of modern reef fish faunas is a relatively recent state and is very different from the historical distribution of feeding modes; the ancestors of modern reef fishes used almost exclusively suction prior to the Cenozoic, but on today's reefs, fully 40% of species use some degree of biting to capture their prey. Furthermore, these benthic feeders are a major driver of reef fish phenotypic diversification as they show substantially elevated rates of body shape evolution when compared with suction feeders despite reduced disparity (Figs. 2 and 3 and Table 1). Taken together, these results suggest that reef biters, which uniquely exploit the flora and fauna that compete for and attach to hard substrates on modern reefs, capitalized on mechanical modifications of the teeth and jaws to diversify around the novel ecological opportunities represented by this resource.

It appears that the expansion of biting in the Early Cenozoic took advantage of already-shifting reef communities. Reefs during the Early Cretaceous were formed by groups of rudist bivalves, bryozoans, corals, and some algae (55–58), and there is little evidence from the fossil record to suggest that teleosts fed on these substrates (38, 39, 55). However, by the Late Cretaceous, a transition was underway to reef structures dominated by grazing-resilient forms of algae and corals that are directly fed on by modern reef fishes and provide substrate for attachment of many other benthic prey (55, 58). The transition to reef structures that succeed despite breakage and excavation, which preceded the expansion of biting in fishes, may have been driven by recently evolved herbivorous urchins and deep-boring limpets (55). Thus, ecological shifts toward grazing-resilient structures in response to invertebrate grazers may have made reef conditions increasingly favorable for biters and able to support larger communities of high-efficiency attached prey feeders (55), such that when fishes began to use biting and evolved functional features adapted for benthic feeding, like shortened jaws and flexible teeth (28, 38, 39, 59), they were extremely successful and were able to diversify within this broad adaptive zone. This pattern could contribute to the previously observed increase in morphological and species diversification of acanthomorph fishes in the Early to Mid-Cenozoic (60). A similar ecological mechanism may explain the dramatic rise of dedicated biting in the last 30 My (Fig. 1), where colonization of highly productive reef flat habitats may have offered new opportunities for intense attached prey feeding by fishes (61); the novelty of reef flats appears to have also stimulated herbivore speciation in this period (43).

Our results demonstrate that biting feeding mechanisms elevate body shape diversification. While we find that dedicated biters evolve body shape most rapidly, we also observe subtly increased rates of body shape evolution of mixed feeders that use both suction and biting (~1.15× faster than dedicated suction feeders). The pairing of a reduced reliance on biting in mixed feeders with a minor rate shift suggests that the magnitude of the role of biting in a fish's feeding repertoire may correlate with the magnitude of increase in evolutionary rate. While reliance on a biting feeding mechanism is not common in the marine realm outside of reef habitats, our results generalize across 111 families of teleost fishes and extend findings from other studies that a biting lineage, the parrotfishes, has the highest rates of evolution of functional morphological traits (12, 62), although this effect is not uniform between and within families as other ecological factors may affect body shape evolution of species (Fig. 3). However, previous studies have found significant but small effects of major habitat transitions on fish body shape diversification (63, 64) that contrast with the significant and stronger results from our phylogenetic MANOVA, suggesting that feeding mode has a relatively strong influence on body shape and its evolution when compared with the effects of other ecological traits.

Among reef fishes, herbivores have been found to evolve functional traits most rapidly, alongside top predators (11). Our results suggest that this effect extends to all fishes that feed by biting benthic prey, as only 39% of species across both our biting and "mixed biting and suction feeders" fed specifically on plant material or detritus. Evolution of biting prey capture mechanisms allowed access to a group of novel trophic niches for fishes (28) involving a diversity of prey types with distinct functional properties. This group includes several lineages that feed on turfs, leafy algae, detritus, and benthic microbial communities that must be scraped, browsed, or yanked off the substrate (65, 66); predators of colonial cnidarians that either scrape the coral surfaces (e.g., many butterflyfishes) or bite off pieces of the colony, complete with bits of the skeleton (e.g.,
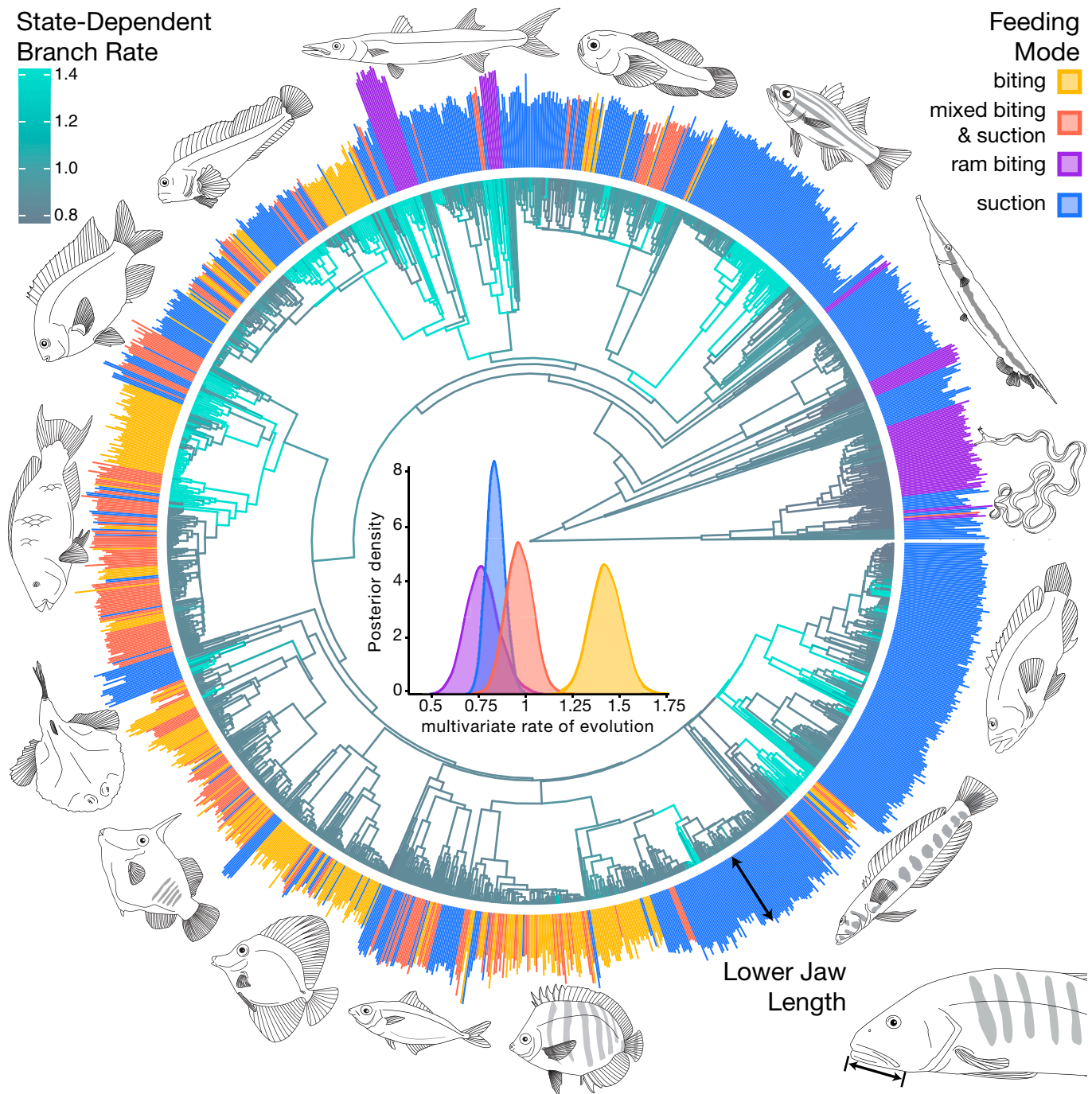
Fig. 3. Results from model fitting for the rate of body shape evolution. The center plot shows the distribution of multivariate, state-dependent rates colored by feeding mode. Branch colors on the phylogeny indicate per branch state-dependent rates of evolution, with gray indicating a lower rate and teal indicating a higher rate. On the outer ring, bars are colored by feeding mode, and the length of bars represents lower jaw length. Selected fishes have been drawn and placed near their clade on the phylogeny (clockwise from *Inset* at bottom right): *L. cyanopterus* (*Inset*), *C. multicinctus*, *E. stercorarius*, *Z. scopas*, *A. scopas*, *H. aculeatus*, *S. guacamaia*, *S. obreptus*, *H. hentz*, *S. jello*, *P. modestus*, *O. holotaenia*, *A. strigatus*, *R. quaesita*, *C. cruentata*, and *P. millepunctata*. Fish images drawn by K.A.C.

some filefishes and pufferfishes); species that scrape encrusted dead coral to feed on the mix of turf algae, detritus, and cyanobacteria that reside on and within the skeleton (e.g., parrotfishes) (23, 27, 29, 67); and even species that grab and extract more mobile invertebrate prey, including urchins and bivalve molluscs, from holdfasts (e.g., some triggerfishes and wrasses). These different prey impose diverse functional requirements on the prey capture apparatus (68), providing the opportunity for functional and morphological diversification. Reliance on biting for prey capture often results in a highly modified feeding apparatus;

indeed, jaw length was the strongest variable in differentiating between feeding mode groups, with biters having shorter jaws on average (*SI Appendix*, Fig. S3). Many biters have evolved substantial novelties that increase access or processing of attached prey, such as a pharyngeal mill (69), an intramandibular joint within the oral jaws (25, 70), or elongated teeth, an innovation that improves access to loosely attached algae and detritus (28). Such novelties may also promote morphological diversification (71–76).

Biters densely populate a region of shape space characterized by shorter jaws and laterally compressed bodies (Fig. 2),

consistent with observations that biters have shortened jaws for improved force transmission during prey capture (38, 53) and predictions that they use a deep body shape for agile maneuvering among the complex reef substrate (77). Biting species with the most extreme body shapes in this region are fully outside the range shown by suction feeding species (*SI Appendix*, Fig. S4). However, the dynamic body shape evolution of attached prey feeders also led to occupation of morphospace that is shared with fishes using other feeding mechanisms, indicating that feeding mode is not a rigid predictor of body shape. The relatively recent proliferation of biting among reef fishes and the elevated rates of biters' body shape evolution suggest that the emergence of biting in the Cenozoic exposed a range of underexploited feeding niches with consequences for both feeding and locomotor functional morphology. We propose that this novel landscape of diverse feeding opportunities, made possible by adept biting, stimulated jaw and body shape evolution.

Our results demonstrate the relative recency of feeding mode diversity among teleost fishes on reefs, dominated by the emergence of the major ecological group of benthic biters that play a prominent role in modern ecosystem processes. We reconstruct the evolution of mechanisms of feeding on attached prey, finding a steady increase in the proportions of reef fishes using biting throughout the Cenozoic. Coupled with evolutionary model-fitting results showing that biters have elevated rates of morphological diversification, our results suggest that ecological changes surrounding the end-Cretaceous mass extinction event set the stage for the diversification of benthic biters, which uniquely took advantage of new more grazing-resilient reefs in the Cenozoic. A major role for feeding on attached prey appears to be one key to the spectacular diversity of modern reef fishes.

Materials and Methods

Morphological Trait Data. Body shape data were drawn from a previously published collection of measurements we made from museum specimens of teleost fishes (63, 78–80). Wherever possible, species values were computed as averages of measurements from three adult specimens. The dataset consisted of eight linear measurements spanning three dimensions: standard length and jaw length; mouth, body, and caudal peduncle width; and head, body, and caudal peduncle depth. We used the R package "rFishBase" (81) to identify 1,530 species from the larger body shape dataset that were both marine and reef associated according to FishBase (82) and extracted these species for use in our analyses. These 1,530 species spanned 486 genera and 111 families, nearly one-quarter of all extant teleost fish families (Dataset S2).

Body shape is a key aspect of morphology that interacts functionally with feeding mode. Although feeding mechanisms have long been linked to the evolution of the feeding apparatus, recent research suggests that motions of the body are integral to successful prey capture across feeding mechanisms. Suction-based prey capture is only effective within approximately one mouth diameter of the jaws (83), and so, suction feeders must swim toward their prey; these forward swimming motions are the major axis of variation among suction kinematics (84), and muscles of the body power the rapid motions of the cranium that produce suction (85). For herbivores and other attached prey feeders, motions of the body and fins are crucial to prey capture as they can be the dominant cause of the forces that detach prey items from the substrate (65).

We conducted most statistical analyses in the R computing environment version 4.0.2 (86). Measurements were size corrected using the preferred method from previous comparisons of size correction with this dataset (78): log shape ratios (87, 88). We created a "size" variable as the geometric mean of standard length, body depth, and body width for each species. Then, we calculated scaled trait values as the ratio of each trait and the new size variable and took the log of those values.

Feeding Mode Categorizations. We categorized fishes into feeding modes based on the prey that each species feed on using a combination of the primary literature, our own field and laboratory-based observations, and FishBase (82) (Dataset S1). We used the functional characteristics of the prey to infer the likely feeding mode required to capture that prey item (further details are provided in *SI Appendix*).

"Suction feeders" were categorized as species where >90% of the prey were free swimming or otherwise nonattached (including but not limited to fishes, many crustaceans, errant polychaetes, and zooplankton). Examples of suction feeders include most grunts (Haemulidae), groupers (Serranidae), and jacks (Carangidae).

A "biter" was a species for whom >50% of the prey require direct contact with the jaws for acquisition in order to graze, scrape, or dislodge the item from a substrate (e.g., many molluscs, hard and soft corals, sponges, algae, hydroids, bryozoans, detritus, and some echinoderms). Examples of biters include parrotfishes (Scarinae), most angelfishes (Pomacanthidae), most surgeonfishes (Acanthuridae), porcupinefishes (Diodontidae), and most triggerfishes (Balistidae). Not all biters are herbivores feeding on plant material or detritivores feeding on detritus; instead, some benthic biters consume higher proportions of metazoan prey, such as sponges, corals, molluscs, echinoderms, or fish scales. We used data on prey type to describe whether biters were herbivores/detritivores or not by categorizing a species as an herbivore/detritivore if 50% or more of its attached prey were plant material and/or detritus.

In classifying feeding modes, we discretized a naturally continuous trait. To accommodate this uncertainty, we added a third category, "mixed biting and suction," for species for which between 10 and 50% of their prey were attached prey items that require direct biting actions to capture, and the remainder of their diet was prey that would likely be captured using suction. For example, we classified many wrasses (Labridae), most porgies (Sparidae), and some pufferfishes (Tetraodontidae) as mixed feeders that rely on both suction and biting.

Our final category was ram biters, which were categorized as species that use direct biting actions of the jaws but minimal suction to capture evasive or free-swimming prey (89–92). This feeding mode was only possible to designate in cases where the literature contained information on the mechanism of prey capture or we had personal observations. Most ram biters are piscivorous, including moray eels (Muraenidae), barracudas (Sphyraenidae), and many lizardfishes (Synodontidae).

Phylogeny of Teleost Fishes. In order to align the time calibration closely with community consensus of divergence times (93–95), we calibrated a pruned phylogram of our 1,530 species (96) by aligning it with a smaller recent phylogeny based on genomic ultraconserved elements for which divergence times had been estimated with fossils (94). We used the R package "geiger" version 2.0.7 (97–99) to "congruify" these trees by identifying nodes shared between both trees and a penalized likelihood program (treePL) to estimate divergence times across the rest of the phylogeny's nodes using the shared nodes as starting calibrations (100–102).

Models of Discrete and Continuous Character Variation. To reconstruct the history of feeding modes along the phylogeny, we used "phytools" version 0.7–80 to generate a distribution of 100 stochastic character maps (103, 104) (further details are in *SI Appendix*). We generated a distribution of character maps to account for uncertainty in the timing and number of feeding mode transitions throughout the evolutionary history of teleost fishes. While using a distribution allows us to alleviate some uncertainty, the reconstructions are confined to the information in our sampled dataset of 1,530 species. It is possible that biases among unobserved speciation and extinction events may also influence our trait reconstructions.

We used a PCA on the correlation matrix of all eight body shape variables to visualize body shape variation in our dataset. We conducted phylogenetic ANOVAs and MANOVA to examine the effect of feeding mode on average body shape in the R package "geomorph" version 3.3.1 (105, 106).

We used random forest models to understand which body shape traits were most powerful in discriminating between feeding mode groups. Random forest models are a machine-learning method of categorization using decision trees that uses combinations of continuous variables (body shape data) to categorize species by feeding mode group (107). We used cforest in the R package "party" version 1.3–5 (108, 109) to fit random forest models using conditional inference trees, which are more robust to interactions between the continuous variables.

We trained the model on a subset of 70% of the data (sampled randomly and without replacement) and then fit the model on the remaining 30% of the dataset, generating a distribution of 5,000 decision trees. We estimated the importance of each continuous variable across the distribution of decision trees as the mean decrease in categorization accuracy when that variable is excluded from the analysis (further details are in *SI Appendix*).

We used geomorph to compute multivariate and univariate morphological variance for each of the four feeding mode groups. To further compare morphospace occupation among feeding mode groups, we generated hypervolumes using the R package "hypervolume" version 3.0.0 (110, 111), which each contained the six-dimensional morphospace that a given set of species occupied. We used the first six axes of a PCA on the correlation matrix, which together accounted for 98.5% of the variance in the data. Hypervolumes were generated for species in each feeding mode group and for sets of species not in each group (e.g., comparing all suction feeders with all species not coded as suction feeders). We compared the overlap of the hypervolumes in order to estimate how much of the morphospace occupied by each feeding mode group was unique. To assess how similar our comparisons were to random groupings of our data, we simulated a null distribution of hypervolumes by permuting group assignments among our species data and compared the percentile of unique space occupation of our data with the distribution of permuted hypervolumes (more details are in *SI Appendix*).

We used MuSSCRat [implemented in RevBayes version 1.0.10 (112, 113)] to compare rates of body shape evolution between feeding mode groups (114). MuSSCRat is a Bayesian model of multivariate Brownian motion that estimates the effect of a discrete character (feeding mode) on rates of continuous character evolution (body shape evolution) while controlling for "background" variation in

rates. We used an uncorrelated log-normal (UCLN) clock to place an independent parameter on each branch to model background rate variation that is not due to the discrete trait of interest (similar to the UCLN relaxed clock model for molecular evolution) (115). The Monte Carlo Markov Chain (MCMC) ran for 200,000 generations. We used Tracer version 1.7.1 (116) to verify convergence of the MCMC and the package "RevGadgets" version 0.1.0 in R to visualize and plot results (117).

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