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FUNCTIONAL INNOVATIONS AND MORPHOLOGICAL DIVERSIFICATION IN PARROTFISH

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The association between diversification and evolutionary innovations has been well documented and tested in studies of taxonomic richness but the impact that such innovations have on the diversity of form and function is less well understood. Using phylogenetically rigorous techniques, we investigated the association between morphological diversity and two design breakthroughs within the jaws of parrotfish. Similar intramandibular joints and other modifications of the pharyngeal jaws have evolved repeatedly in teleost fish and are frequently hypothesized to promote diversity. We quantified morphological diversity within six functionally important oral jaw traits using the Brownian motion rate of evolution to correct for phylogenetic and time-related biases and compared these rates across clades that did and did not possess the intramandibular joint and the parrotfish pharyngeal jaw. No change in morphological diversity was associated with the pharyngeal jaw modification alone but rates of oral jaw diversification were up to 8× faster in parrotfish species that possessed both innovations. Interestingly, this morphological diversity may not have led to differential resource uses as available data suggest that members of this clade show remarkable homogeneity of diet.

KEY WORDS: Adaptive radiation, biomechanics, disparity, Labridae, rates of evolution, Scaridae.

A pattern of innovation and subsequent diversification is observed in complex systems throughout biology from genetics (Ohno 1970; Zhang 2003), genomics, and evo-devo (Crow and Wagner 2006) through to functional morphology (Liem 1973; Vermeij 1973), paleontology, and evolutionary ecology (Williams 2008). Most recent evolutionary studies have focused on developing methods for, and analyzing associations between key character changes and the rate of cladogenesis (e.g., viviparity in vipers, Lynch 2009; nectar spurs in plants, Hodges and Arnold 1995; BiSSE model, Maddison et al. 2007; Fitzjohn et al. 2009), whereas the potentially important role of innovations in shaping patterns of phenotypic diversity across the tree of life has received far less attention.

We focus on the impact of functional innovations on morphological diversity, which we measure directly rather than the older, indirect method of using taxonomic rank as a proxy for morphological distinctiveness (Erwin 2007). Although taxonomic and morphological diversification can be linked under certain conditions (e.g., following key innovations sensu Galis 2001; or during adaptive radiations sensu Gavrilets and Losos 2009), novel traits that allow high rates of morphological evolution will not necessarily influence speciation rate and vice versa. The evolution of some morphological or functional traits can increase a lineage's potential to diversify morphologically by opening up previously inaccessible niches (Simpson 1944) and/or by increasing the degrees of freedom within a structural system (Vermeij 1973). However, the actual occurrence of diversification is ultimately determined by ecological circumstances, developmental constraints, and genetic variation (Liem 1990). For example, there is evidence that geographic constraints play a significant role in the realization of disparity following innovations in mid-Jurassic Ammonoidea (Navarro et al. 2005). Consequently, the expectation of finding general or consistent patterns between the evolution of a character and diversification may be unreasonable as many factors can inhibit the realization of diversity, an observation that has been made frequently within the speciation literature (e.g., Vermeij 2001; Moore and Donoghue 2007). Therefore, if we find no link between our hypothesized innovation and morphological diversity, it may be due to factors inhibiting diversification not due to the lack of evolutionary potential generated by the innovation.

Innovations that open up new adaptive zones for exploitation act as design breakthroughs for the organism and substantially change the adaptive landscape thus increasing the potential for novel functional diversity (e.g., Simpson 1944; Wainwright 2007). Additionally, there are a variety of ways for innovations to increase the degrees of freedom within a structural system, such as adding new structures, increasing the complexity of the structure, duplicating structures, or decoupling previously linked features or functions (Lauder 1990; Wainwright 2007). Increasing the degrees of freedom within the morphospace increases the number of possible mechanical solutions (Vermeij 1973) and can reduce selective constraints and trade-offs placed on individual elements in a mechanical system providing opportunities for increased evolutionary change (Arnold et al. 1989; Lauder 1990). For example, it has been shown that the hind limbs of birds are more disparate than those of nonavian theropods, which supports the hypothesis that the evolution of wings in birds decoupled the hind limbs, tail, and fore limbs permitting a radiation of hind-limb structures (Gatesy and Middleton 1997).

It is important to recognize that morphological diversity does not necessarily have functional or ecological consequences and therefore may not be associated with the occupation of new niches. For example, Foote (1999) found that Paleozoic crinoids were more morphologically diverse than post-Paleozoic crinoids but that the latter exploited a wider range of ecological niches. The lack of correspondence between morphological and ecological diversity may be explained by genetic or developmental constraints (Foote 1999) or within complex mechanical systems, many-to-one mapping of form to function (Alfaro et al. 2005; Wainwright 2007). An innovation that increases the degrees of freedom within a mechanical system may facilitate such functionally synonymous changes, as there are often several ways to combine individual elements within a complex structure to achieve the same functional property (i.e., many-to-one mapping of form to function, Alfaro et al. 2005; Wainwright et al. 2005).

Despite innovations being a central theme in the discussion of morphological diversity (Liem 1973; Vermeij 1973), studies that address the link between innovations and morphological diversity, which also take into account the potentially confounding effects of time and phylogeny on the calculation of disparity, are rare. The scarcity of such studies is perhaps explained by the recent development of the statistical methods to incorporate phylogeny into the measures of morphological diversity (Foote 1997; Hutcheon and Garland 2004; O'Meara et al. 2006) and the time and effort needed to measure a variety of morphological traits across a large number of species (with and without the innovation) and to generate a time-calibrated phylogeny.

In this article, we concentrate on two major innovations within the feeding mechanisms of parrotfish and their connection to the diversification of the oral jaws in this important group of reef fish. Parrotfish are a monophyletic group of 96 species of ecologically prominent reef fish (Bellwood 1994) phylogenetically nested within the diverse Labridae (wrasses, weed-whitings, and parrotfish; see Fig. 1). The two innovations of interest are the novel pharyngeal jaw apparatus shared by all parrotfish and the intramandibular joint possessed by a sub-clade of parrotfish. Pharyngeal jaw and intramandibular joint innovations are frequently hypothesized to promote morphological diversity as well as cladogenesis within labrids and other teleost fish.

Structural innovations within the pharyngeal jaws of cichlids and labrids have been linked to the rapid speciation and trophic diversification of these clades (Liem 1973; Liem and Sanderson 1986; Galis and Drucker 2002; Hulsey et al. 2006), although the association with trophic or morphological diversity has never been explicitly tested within a phylogenetic framework. All parrotfish share a complex set of changes to the general labrid pharyngeal jaws (Gobalet 1989 and see Fig. 2A) that enable them to pulverize the mixture of sand, coral skeleton, algae, detritus, and benthic infaunal invertebrates that they all consume. These changes include enlarged branchial muscles which connect the lower pharyngeal jaw to the neurocranium, including a novel anterior coupling not present in other labrids as well an enlarged lower pharyngeal jaw that increases the grinding surface.

Parrotfish, feeding actions are unique among reef fish and reflect their unusual morphology; many species feed by scraping or gouging the reef substratum with their beak-like oral jaws. As grazing herbivore/detritivores parrotfish shape benthic reef

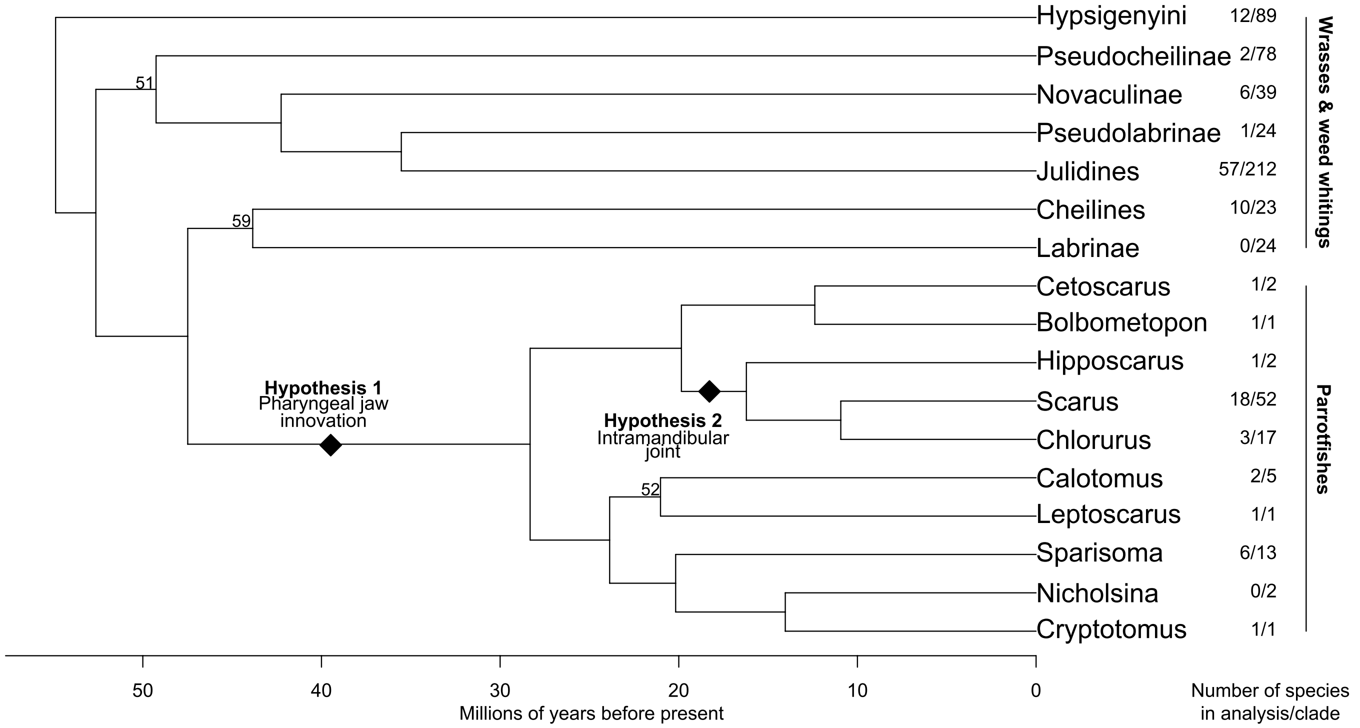

Figure 1. **A phylogeny of the major clades of Labridae including all parrotfish genera, based on a maximum likelihood tree by Kazancioglu et al. (2009) built using a multi-gene dataset and time-calibrated phylogeny using relaxed molecular clock methods. Nodes with <75% bootstrap support are labeled on the tree. The number of species used in the analysis compared to the total extant species in each clade is indicated next to the clade names and diamonds denote the branches along which each innovation is inferred to have occurred.**

communities by clearing space for competitively inferior coral species (Hughes 1994; Hixon and Brostoff 1996; Nystrom et al. 2000; Bellwood et al. 2004) and some species act as major bioeroders and producers of sand on coral reefs (Bellwood 1995; Bellwood et al. 2003, 2006a). We hypothesize that the parrotfish' pharyngeal jaw is a major design breakthrough that may allow further diversification of the oral jaws as it allows them to access food in a manner that no other group of reef fish are known to exploit. This opening up of the herbivorous/detritivorous niche is predicted to have provided the opportunity for oral jaw specialization to more effectively collect food from particular types of reef substrata, from the algal matrix (turfs), large fleshy algae, and live corals (Randall 1967; Bellwood and Choat 1990; Rotjan and Lewis 2006; Alwany et al. 2009), although wrasses are also noted for their trophic diversity (Randall 1967; Wainwright et al. 2004). We quantitatively test the hypothesis, taking into account the effects of phylogeny, that oral jaw diversity is higher within parrotfish than wrasses.

Intramandibular joints have evolved multiple times in coral reef clades including butterflyfish (Chaetodontidae), angelfish (Pomacanthidae), and surgeonfish (Acanthuridae), where they are hypothesized to promote trophic diversity by enhancing the potential range of biting strategies (Konow et al. 2008). Within parrotfish, the evolution of an intramandibular joint between the dentary and articular bones of the lower jaw occurred within a clade comprised of the genera *Scarus*, *Chlorurus* and *Hipposcarus* (Fig. 2B). This joint, together with the standard articular-quadrate joint, permits more complex motions of the mandible during the scraping actions of feeding parrotfish (Wainwright et al. 2004). The ability to modulate the dentary-articular joint may allow parrotfish to maintain a constant orientation of the scraping surface of the jaw throughout the sweep of the bite, and may also permit a wider vertical gape and therefore a longer scraping action. The intramandibular joint increases the degrees of freedom within the oral jaws, and hence the mechanical complexity, and may also represent a breakthrough that promotes subsequent diversification. We therefore hypothesize that oral jaw morphological disparity is highest within the parrotfish that possess the pharyngeal jaw innovation and the novel intramandibular joint. It is, however, important to note that most of the functional and dietary diversity currently described in parrotfish resides within the group of parrotfish that do not possess the intramandibular joint (Randall 1967; Bruggemann et al. 1994). For example, the genus *Sparisoma* is particularly diverse with excavating and scraping detritivores as well as browsing herbivores (Randall 1967). Thus, if there is increased morphological diversity within *Scarus*, *Chlorurus*, and *Hipposcarus*, it may not have led to obvious niche divergence and the variation may be functionally synonymous.

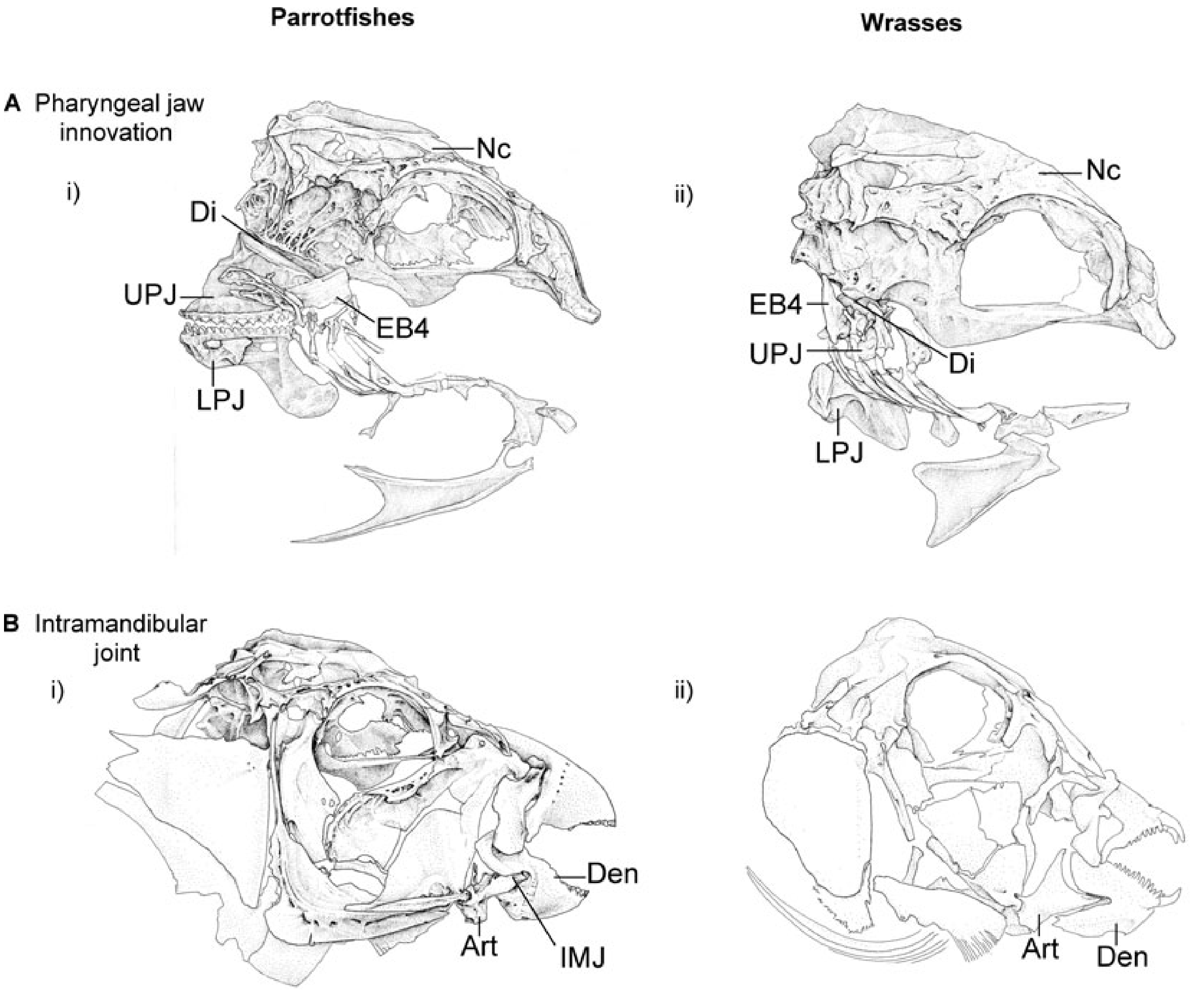

Figure 2. Illustrations of the pharyngeal jaw innovation (A) and intramandibular joint (B) in parrotfish (i) compared to the general labrid (wrasse) condition (ii). The illustrations of the pharyngeal jaw (A) are detailed deep views with the superficial bones removed, whereas the intramandibular joint illustrations (B) depict the superficial exterior bones and are adapted from Figure 2 in Wainwright et al. (2004). The neurocranium (Nc), diarthrosis (Di), upper pharyngeal jaw (UPJ), lower pharyngeal jaw (LPJ), and 4th epibranchial (EB4) are illustrated in A. The intramandibular joint (IMJ) as well as the articular (Art) and dentary (Den) bones are illustrated in B. Ai, the parrotfish *Chlorurus sordidus*; Aii, the wrasse *Bodianus axillaris*; Bi, the parrotfish *Cetoscarus bicolour*; Bii, the wrasse *Xyrichtys martinicensis*. Scale bars are 10 mm.

Despite the interest in pharyngeal jaw and intramandibular joint innovations and their impact on fish diversification, there have been no phylogenetically rigorous tests of the connection between them and the accumulation of disparity. We provide two such tests, by comparing the phylogenetically corrected estimates of disparity in clades that do and do not possess the two innovations. If we find a connection between each functional innovation and increased morphological diversity, it will support our hypotheses. If we find no relationship, it will falsify the hypothesis that the innovation leads to oral jaw diversity but it will not falsify the hypothesis that it provided the potential to diversify morphologically, as morphological diversification may have been inhibited by ecological or genetic conditions (Liem 1990).

Methods

MORPHOLOGICAL DATA

We characterized the functional diversity of jaw mechanics across labrids using species averages of eight functionally rich morphological traits (as described in Wainwright et al. 2004; Collar et al. 2008). The specific traits were mouth-closing lever ratio (Close), mouth-opening lever ratio (Open), kinematic transmission coefficient of the oral jaws four-bar linkage (Jaw KT), adductor mandibulae (AM) muscle mass, premaxillary protrusion distance (Prot), gape width (Gape), levator posterior (LP) muscle mass, sterno-hyoideus (SH) muscle mass as well as adult body mass (Body mass). The first six traits listed are oral jaw traits, which are predicted to be affected by the two functional innovations. The LP and SH muscles function primarily outside the oral jaws; LP is the main adductor of the pharyngeal jaws in labrids and the major function of SH is to depress the floor of the buccal cavity although it does secondarily depress the mandible which is part of the oral jaws (Wainwright et al. 2004). Therefore, if both LP and SH also exhibit an elevated rate of evolution we cannot ascribe this increase to either of the two innovations. Body mass was added as it can have a significant effect on trophic diversity even when jaw mechanics are similar. The collection and measurement procedures for these data have previously been published along with the data in Wainwright et al. (2004). Measurements of all nine traits were available for 122 species (34 parrotfish and 88 wrasses) represented in the Kazancioglu et al. (2009) phylogeny, which is used throughout the paper to take into account shared evolutionary history amongst taxa.

To ensure that the magnitude of character change was unrelated to the trait value (larger changes are less likely when trait values are small) we log transformed all linear measurements, masses were log transformed after cube-root transformation. Our initial analyses indicated that all morphological traits had a strong association with size with no evidence of strong clade-specific allometric differences or grade-shifts. We therefore calculated size-corrected values across labrids by first calculating independent contrasts (Felsenstein 1985) of the log-transformed traits and performing a regression through the origin of body mass contrasts and the contrasts of each trait. The slope from this regression was then fitted to the original log-transformed species data and the residuals from the regression line calculated. Hereafter when we refer to a particular trait we are actually referring to the phylogenetically size-corrected estimate. All dataset manipulations and statistics were done in "R" (R Development Core Team 2008) and the ape package (Paradis et al. 2004) was used for generating independent contrasts. Contrasts were standardized using branch lengths equivalent to time, using the time-calibrated phylogeny of Kazancioglu et al. (2009).

COMPARING MORPHOLOGICAL DIVERSITY

Morphological diversity or disparity of continuous traits can be measured as the variance, range or average pair-wise distance between species. However, both time and shared evolutionary history can confound these measures (see review by Foote 1997). The rate of phenotypic evolution, calculated using a time-calibrated phylogeny, can take into account both of these confounding factors to give a phylogenetically correct estimate of morphological diversity as it relates directly to all three common metrics of disparity (Hutcheon and Garland 2004; O'Meara et al. 2006). Maximum likelihood estimates of the rate of evolution for each trait were calculated using the censored rate test implemented in Brownie (O'Meara et al. 2006). Using the Akaike Information Criterion (AIC) and likelihood ratio (LR) tests we compared models that fit a single rate of morphological evolution across the whole tree to a 2-rate model that allowed the clades with and without the innovation to have different rates. Due to small sample sizes AICc was used (Burnham and Anderson 2002) and the LR test was modified so that the null distribution of the LR statistics was given by a parametric bootstrapping procedure, using 1000 pseudoreplicates. This avoids inflation of Type 1 errors associated with using the χ^2 distribution when sample sizes are small (see O'Meara et al. 2006). A difference between AICc scores (ΔAICc) of 4 or more was taken as support for one model over the other following Burnham and Anderson (2002), strong support is indicated by ΔAICc > 10. Results from the LR tests are not explicitly discussed in the article but can be found in Appendix S1.

Hypothesis 1: enhanced oral jaw diversification followed the evolution of the novel pharyngeal jaw mechanism in parrotfish. We tested this hypothesis by comparing a model that fitted a single rate of evolution across labrids to one that allowed parrotfish and wrasses to have different rates of phenotypic evolution. To ensure that any rate-shift we saw at the more inclusive parrotfish node was really occurring at that node and not caused by a change in rate at the second innovation nested within parrotfish at the *Scarus*/*Chlorurus*/*Hipposcarus* (hereafter S/C/H) node, we removed the S/C/H parrotfish and re-ran the analyses. A strong trickle-down effect (sensu Moore et al. 2004) from the S/C/H node will cause the results of these two analyses to be very different.

Hypothesis 2: diversification of oral jaw mechanics followed the evolution of an intramandibular joint in the jaws of the parrotfish genera Scarus, Chlorurus, and Hipposcarus. As *Scarus*, *Chlorurus,* and *Hipposcarus* all share the derived pharyngeal jaw form, as well as the intramandibular joint and both innovations are hypothesized to effect the oral jaws we are really examining the effect that the combination of these two innovations have on diversification. We tested this second hypothesis using two different taxon sets. To take into account the possible confounding effects of the pharyngeal jaw innovation we compared a model that fitted a single rate of evolution across parrotfish to one that allowed parrotfish species with (S/C/H parrotfish) and without (hereafter non-S/C/H parrotfish) the novel joint to have different rates. However, if the pharyngeal jaw innovation does not appear to affect the diversification of oral jaw mechanics, a more appropriate test of the prediction that the intramandibular joint increases oral jaw diversity is to compare S/C/H parrotfish with the novel joint to all other labrids without it. Thus, we also tested a model that fitted a single rate of evolution across labrids to one that allowed S/C/H parrotfish to have a different rate of phenotypic evolution compared to all other labrids (wrasses plus non-S/C/H parrotfish).

TESTING THE APPROPRIATENESS OF THE BROWNIAN MOTION MODEL

The method we used to calculate phylogenetically correct estimates of morphological disparity assumes that the traits of interest fit a Brownian motion (BM) model of continuous character evolution as described by Felsenstein (1985). However, if traits are under selection and evolving toward a fitness peak an Ornstein–Uhlenbeck (OU) model might be more appropriate (Hansen 1997; Butler and King 2004). To test whether a BM or OU model was more appropriate we compared the fit of the two models for all traits across each clade of interest. For example, when testing Hypothesis 1 by comparing the rate of evolution in parrotfish to wrasses there are three clades of interest: parrotfish, wrasses, and the combination of these two clades, which in this case represents Labridae. When every clade used to test a hypothesis fit a single model of evolution the Brownie analyses were run once, either using the original branch lengths in the Kazancioglu et al. (2009) tree if the trait fit a BM model (e.g., gape when parrotfish and wrasses are compared) or if it fitted an OU model (e.g., Jaw KT when parrotfish and wrasses are compared), using the branch lengths transformed by the OU α parameter from the most comprehensive partition. When clades involved in a comparison were best fit by different models (e.g., jaw closing when parrotfish and wrasses are compared, parrotfish and wrasses fit an OU model but when combined into the Labridae they fit a BM model), the analyses were run twice using both the original branch lengths and those transformed using the OU α parameter from the most comprehensive clade. After any OU transformation a check was performed to ensure that all clades subsequently fit a BM model. For a few analyses (indicated by a * in Appendix S1) branch lengths transformed using the α parameter from the most comprehensive clade was not sufficient to ensure that all partitions fitted a BM model. In this case the largest α parameter estimated from one of the less inclusive partitions was used to transform the branch lengths, which resulted in all clades fitting a BM model. All analyses and branch length transformations were done in the R package GEIGER (Harmon et al. 2008).

Results

Hypothesis 1: enhanced oral jaw diversification followed the evolution of the novel pharyngeal jaw mechanism in parrotfish. Two of the six oral jaw traits evolved faster within parrotfish, whereas the other oral jaw traits and SH mass evolved at similar rates in both clades (see Fig. 3 and Appendix S1). However, when the analyses were repeated using only the parrotfish species that do not possess the second intramandibular joint innovation (non-S/C/H parrotfish) the results were very different, two of the six oral jaw traits evolved faster within wrasses whereas the other traits evolved at similar rates in both clades.

The rate of evolution of the jaw opening lever ratio was 3× faster in parrotfish than wrasses (ΔAICc 14.4) and Jaw closing lever ratio was 4.5× faster than wrasses (ΔAICc 21.1). In contrast the rate of levator posterior (LP) muscle mass evolution was higher in wrasses (3.4× faster than parrotfish ΔAICc 13.9). These results were not qualitatively altered when branch lengths were OU transformed. Similarly when the rate of evolution within non-S/C/H parrotfish was compared to wrasses the majority of traits fit a single-rate model but for this comparison jaw opening evolved 5.5× faster in wrasses than non-S/C/H parrotfish (ΔAIC 8.9) and jaw KT evolved 3.3× faster in wrasses (ΔAIC 3.7), which increased to 5.9× when branch lengths were OU transformed (ΔAICc 8.7). Body mass and LP were the only two traits to show similar patterns in the two different tests of Hypothesis 1. Body mass evolved faster within parrotfish and within non-S/C/H parrotfish relative to wrasses, whereas LP evolved faster in wrasses regardless of whether they were compared to parrotfish or just non-S/C/H parrotfish.

Protrusion was the only oral jaw trait to show any suggestion of a faster rate of evolution in non-S/C/H parrotfish (2.8× faster than wrasses ΔAICc 3.4) although when branch lengths were OU transformed a 1-rate model fit just as well (ΔAICc 0.12). Since there is no evidence that oral jaw mechanics evolved at faster rates within parrotfish that do not possess the novel intramandibular joint, the appearance of elevated rates at the parrotfish node cannot be connected to the pharyngeal jaw innovation but instead may be attributed to trickle-down from the S/C/H parrotfish.

Hypothesis 2: diversification of oral jaw mechanics followed the evolution of an intramandibular joint in the jaws of the parrotfish genera Scarus, Chlorurus, and Hipposcarus. Both tests of Hypothesis 2 gave similar results: four of the six oral jaw traits evolved at higher rates within S/C/H parrotfish (see Fig. 3 and Appendix S1) regardless of whether they were compared to non-S/C/H parrotfish or the combination of wrasses and non-S/C/H parrotfish. AM, jaw KT, jaw closing, and opening lever ratios all evolved at higher rates within S/C/H parrotfish when branch lengths were untransformed, however support for the two-rate model within several of these traits decreased (ΔAICc < 4) when transformed branch lengths were used.

Protrusion showed slightly faster rates of evolution in S/C/H parrotfish when compared to all other labrids (S/C/H parrotfish

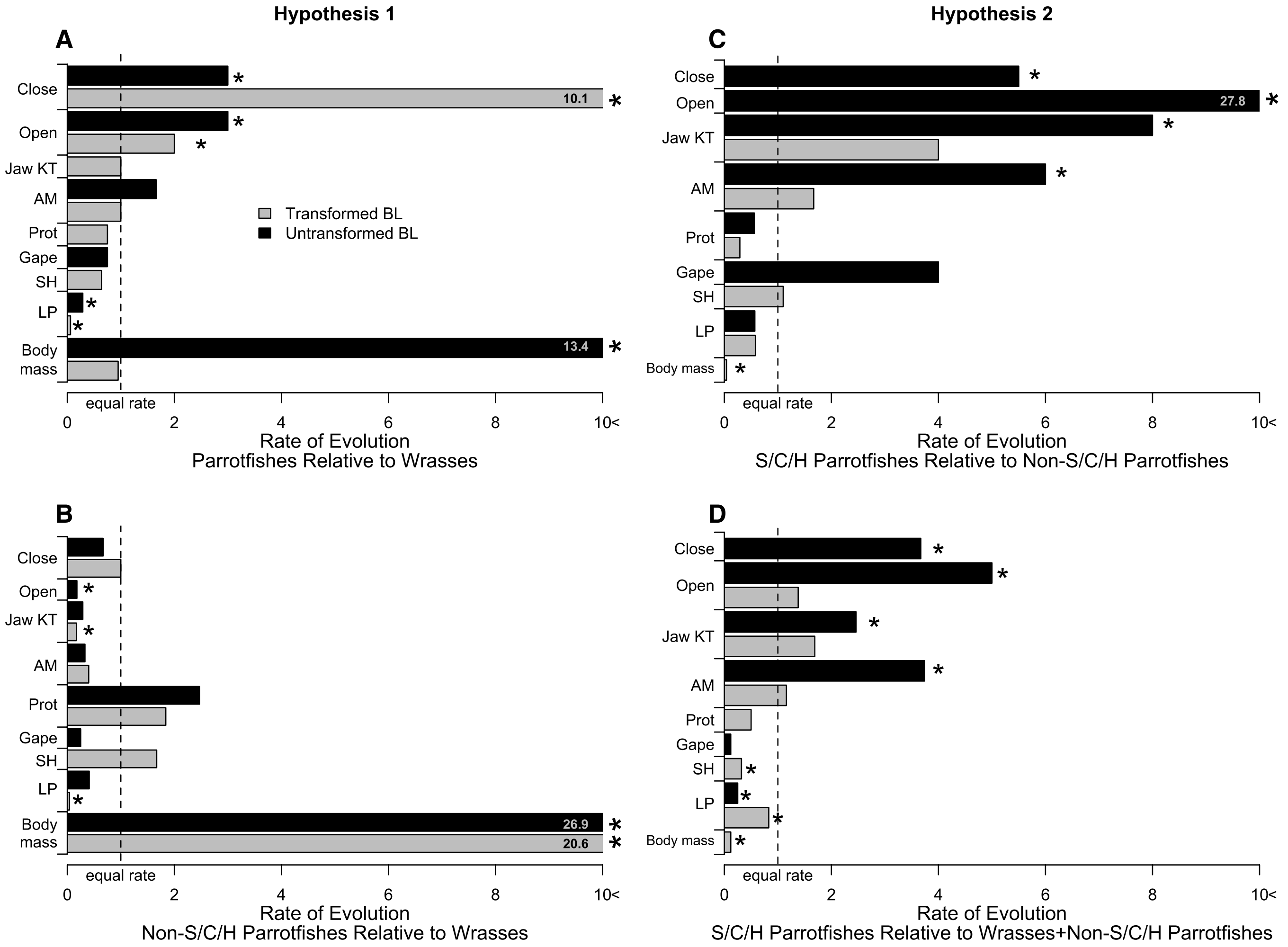

Figure 3. Relative rates of morphological evolution in clades with the innovation of interest compared to those without it, substantial support for different rates of evolution in the two clades (ΔAICc > 4) are indicated by *. Relative rates >1 indicate evolution is faster in the clade with the innovation of interest and <1 slower. Black bars indicate results are from an analysis that used untransformed branch lengths (untransformed BL) and gray bars OU transformed branch lengths (Transformed BL), numbers within the bars give the rate of evolution when it is greater than 10-fold. The impact of each innovation is evaluated using two different clade comparisons. Tests of Hypothesis 1, that *enhanced oral jaw diversification followed the evolution of the novel pharyngeal jaw mechanism in parrotfish,* first compare (A) parrotfish to wrasses that do not have the innovation and then to ensure that the second intramandibular innovation does not bias the results, (B) parrotfish without this joint (non-S/C/H) are compared to wrasses. Tests of Hypothesis 2, that *diversification of oral jaw mechanics followed the evolution of an intramandibular joint in the jaws of the parrotfish genera Scarus, Chlorurus, and Hipposcarus*, first compare (C) parrotfish with the joint (S/C/H) to parrotfish that do not have the joint (non-S/C/H) and additionally compare (D) S/C/H parrotfish to all labrids that do not have the joint (wrasses plus non-S/C/H). These comparisons reveal that the origination of the parrotfish' pharyngeal jaw is not associated with elevated oral jaw diversity as any increase in the rate of evolution at the parrotfish node is lost when S/C/H parrotfish are removed. However, the possession of both the pharyngeal jaw and intramandibular joint within the sub-clade *Scarus*/*Chlorurus*/*Hipposcarus* is associated with oral jaw diversification.

rate 2.3× wrasses + non-S/C/H parrotfish ΔAICc 2.9) but not when compared to the other parrotfish (ΔAICc 1.3). Gape and the two traits not primarily associated with oral jaw mechanics (LP and SH) evolved considerably faster in the paraphyletic wrasse and non-S/C/H parrotfish clade (gape: 8.5× faster than S/C/H parrotfish ΔAICc 23.8; LP 3.3× faster than S/C/H parrotfish ΔAICc 12.1; SH 3.3× faster than S/C/H parrotfish ΔAICc 6.8).

ABSOLUTE RATES OF EVOLUTION ACROSS LABRIDS

When the absolute rates of evolution were compared across the three different groups a clear pattern emerged (see Appendix S1): the fastest rates of evolution across all oral jaw traits were exhibited by S/C/H parrotfish, whereas the slowest rates were found in non-S/C/H parrotfish. Gape evolved equally fast within wrasses and S/C/H parrotfish. It should be noted that the rate parameters can only be compared across models that use the untransformed branch lengths, that is, fit BM, as rates are not comparable across models that use different branch lengths because the interpretation of the rate parameter differs in clades best fit by the stationary peak OU model and clades evolving under BM.

TESTING THE APPROPRIATENESS OF THE BROWNIAN MOTION MODEL

The appropriateness of a BM versus an OU model was tested across all traits and data partitions: labrids, wrasses, parrotfish, S/C/H parrotfish, non-S/C/H parrotfish and finally the paraphyletic clade consisting of wrasses and non-S/C/H parrotfish. Body mass, SH, and gape consistently fit a single model of evolution across all partitions of interest: body mass and SH fit an OU model whereas gape fitted a BM model. The other traits fit a mix of BM and OU models (see Appendix S2), for example, AM mass fitted an OU model across labrids, parrotfish, and wrasses+non-S/C/H parrotfish and a BM model across S/C/H parrotfish, non-S/C/H parrotfish, and wrasses. When no single model was appropriate, analyses were performed using both transformed and untransformed branch lengths, this sometimes leads to conflicting results which are illustrated in Figure 3 and can be seen in full in Appendix S1. Conflicting results between OU and BM models indicate that a cautious interpretation is required when drawing conclusions about changes in the rate of evolution as it depends on the evolutionary model.

Discussion

Our analyses reveal that no change in oral jaw diversity was associated with the pharyngeal jaw modification alone. However, following the evolution of the intramandibular joint in a subclade of parrotfish, rates of oral jaw diversification were up to 8× faster. Remarkably, the S/C/H clade exhibits 1.4 times more standing morphological disparity in their oral jaws (calculated as the average-squared Euclidean distance) compared to non-S/C/H parrotfish even though the S/C/H parrotfish encompass only 16 million years of evolutionary history compared to the 28 million years spanned by non-S/C/H parrotfish.

THE PHARYNGEAL JAW INNOVATION IS NOT ASSOCIATED WITH INCREASED DIVERSITY

The elevated rates of morphological evolution observed within two oral jaw traits of parrotfish can be attributed to trickle-down effects from the nested intramandibular joint innovation. This is because the pattern is reversed when parrotfish species with the novel intramandibular joint (S/C/H parrotfish) are removed from the comparison; wrasses exhibit significantly faster rates of evolution in two oral jaw traits and the rest fit a single-rate model. Furthermore the estimated BM rate parameters show that the fastest rates of oral jaw evolution occur within S/C/H parrotfish and the slowest within non-S/C/H parrotfish, with the exception of jaw protrusion (see Appendix S1). Combined these results provide strong evidence that trickle-down effects from the S/C/H node are responsible for the appearance of elevated rates of morphological evolution at the parrotfish node.

An analogous trickle-down effect is evident when testing the hypothesis that the pharyngeal jaw modification leads to higher lineage diversification rates within parrotfish (Alfaro et al. 2009). These results do not mean, however, that the pharyngeal jaw innovation was of little consequence for the evolution of parrotfish, only that the innovation alone was not sufficient to immediately drive morphological or lineage diversification. Although the origin of the novel pharyngeal jaw in parrotfish was associated with a dramatic shift in feeding habits other factors may have constrained oral jaw diversification within this new adaptive zone. In fact it may actually be rare to find synchrony between the origin of innovations and the diversity they make possible due to the numerous possible ecological and genetic inhibiting factors (Liem 1990; Galis 2001). Indeed, the synergy between the pharyngeal jaw modifications and the novel intramandibular joint likely facilitated the rapid morphological diversification in the S/C/H parrotfish.

Although none of the oral jaw traits appear to evolve faster within parrotfish when trickle-down is taken into account, there is an indication from the estimated BM rate parameters that the rate of jaw protrusion increased within parrotfish. Wrasses have the slowest rate of jaw protrusion evolution with rates increasing in non-S/C/H parrotfish and becoming the fastest in S/C/H parrotfish (see Appendix S1). This result is interesting as wrasses are well known for their jaw protrusion abilities, an extreme example of which is the slingjaw wrasse (*Epibulus insidiator*) that can protrude its jaw an incredible 20% of its body length, although the majority of wrasses in this study exhibit protrusion distances of between 1% and 3% of body length (Wainwright et al. 2004). The rate of evolution is faster within parrotfish as they have had less evolutionary time over which to accumulate a similar amount of variance in log jaw protrusion (28 million years for parrotfish and 54 for wrasses). This rapid change in jaw protrusion ability within parrotfish may be due to a relaxation of selective pressure associated with suction feeding, as jaw protrusion is strongly mechanically linked to the forces exerted on prey by suction feeding fish (Holzman et al. 2008) and parrotfish no longer use protrusion for prey capture by suction.

THE INTRAMANDIBULAR JOINT IS ASSOCIATED WITH INCREASED DIVERSITY

Rates of oral jaw evolution were higher within S/C/H parrotfish relative to all other labrid species, including other parrotfish, although for some traits this was occasionally lost when using OU branch length transformations. S/C/H parrotfish share a novel intramandibular joint between the dentary and articular bones, an innovation which has evolved multiple times in major lineages of biting reef fish (Konow et al. 2008) and in biting dischodontine characoid fish (Vari 1979), indicating that it is a major functional innovation that enhances biting strategies (Konow et al. 2008). Within S/C/H parrotfish the intramandibular joint likely supports a scraping mode of detritivory by maintaining a constant orientation of the scraping surface of the jaw and permitting a wider vertical gape. Therefore, the herbivorous/detritivorous diet facilitated by the pharyngeal jaw innovation was necessary for the evolution of the intramandibular joint within S/C/H parrotfish so it is the combination of these two innovations that facilitates diversification of oral jaw mechanics within S/C/H parrotfish.

The intramandibular joint allows motion between two bones within the oral jaw apparatus; this increases mechanical complexity by allowing force and motion transfer to be modified by changes in the angle between the dentary and articular bones. This additional complexity potentially reduces the trade-offs and/or constraints placed on the individual elements within this system, and along with the increased degrees of freedom within the oral jaw morphospace, provides increased potential for evolutionary change.

MORPHOLOGICAL AND ECOLOGICAL DIVERSITY WITHIN S/C/H PARROTFISH

The lack of data concerning niche differentiation in parrotfish means the precise relationship between morphological and ecological diversity within S/C/H parrotfish remains to be determined. However, the available evidence from the feeding ecology of the S/C/H parrotfish suggests that the morphological diversity seen within this clade does not translate to trophic diversity. The S/C/H clade are all described as detritivores (Crossman et al. 2001; Choat et al. 2002); the only significant trophic transition known within this group occurs along the branch leading to *Chlorurus*. Species of *Scarus* and *Hipposcarus* feed by scraping the surface of dead coral rock where detritus-loaded turf algae communities predominate, whereas some species also feed on bacterial/detritus mats that occur on sand (Bellwood and Choat 1990). In contrast, species of *Chlorurus* are excavators that take deeper bites from the reef increasing the proportion of inorganic carbonate material that is ingested (Bellwood and Choat 1990). The morphology of these two groups is distinct, with the excavating *Chlorurus* having larger jaw adductor muscles and more massive oral jaw elements than the scraping *Scarus* and *Hipposcarus* (Bellwood and Choat 1990). Nevertheless, quantitative analysis of diet revealed similar dietary profiles in two species of *Chlorurus* and one *Scarus* (Choat et al. 2002; Crossman et al. 2005), indicating that mechanical differences in the feeding mechanism may have little impact on diet in this group.

The constancy of diet within the S/C/H parrotfish that has been demonstrated in prior studies is remarkable in light of the diversity found among non-S/C/H parrotfish. This group includes the 25-kg *Bolbometopon muricatum* that takes deep bites out of the reef, consuming live coral and other invertebrates in addition to algae and detritus (Bellwood et al. 2003), the 45-mm *Cryptotomus* and at least one species of *Sparisoma* that feed on the epiphytes that occur on seagrass blades (P. Wainwright, pers. obs.), *Calotomus* that feed on fleshy algae (Bellwood and Choat 1990; McClanahan et al. 2002) and the larger species of *Sparisoma* that appear to function as excavating reef detritivores (Randall 1967; Bruggemann et al. 1994). Thus, compared to non-S/C/H parrotfish there is very little inter-specific diversity in the food eaten by species in the S/C/H clade. In addition, most feed in mixed-species schools and have broadly overlapping patterns of habitat use (Bellwood and Choat 1990). It therefore appears that the high rates of oral jaw evolution and the associated high diversity of these structures in S/C/H parrotfish are not associated with high trophic diversity and may possibly be functionally synonymous. However, more studies are needed on the fine-scale niche partitioning of parrotfish to determine whether the morphological diversity observed within the S/C/H parrotfish does or does not lead to ecological diversity.

INCREASED DIVERSITY IN THE PHARYNGEAL JAW MUSCLES OF WRASSES

The LP muscle is the only trait in our study that consistently exhibited faster rates of evolution within wrasses. This muscle is the primary adductor of the pharyngeal jaw, providing most of the pharyngeal biting force (Wainwright 1987; Clements and Bellwood 1988; Gobalet 1989) and may exhibit decreased diversity within parrotfish as all species use the pharyngeal jaw apparatus to grind algae and coral (Gobalet 1989). In wrasses, a wide variety of dietary strategies put a diversity of demands on the prey processing capabilities of the pharyngeal jaw (Liem and Sanderson 1986; Wainwright 1988) and this muscle shows considerably greater diversity within wrasses than either the sternohyoideus muscle or the oral jaw-closing adductor mandibulae muscle (Wainwright et al. 2004). Wrasse food items range in hardness from heavy-shelled gastropods, bivalves, and echinoderms to very soft items such as zooplankton and coral mucous.

TESTING INNOVATION HYPOTHESES

One of the many aspects of understanding the evolution of biodiversity is identifying what drives the uneven distribution of disparity across the tree of life; why are some lineages so morphologically diverse whereas others are not (Erwin 2007)? Although there are many internal and external factors that can inhibit diversification (Liem 1990; Vermeij 2001) it is still possible to detect traits or environmental conditions that, on a case-by-case basis, appear to have facilitated morphological diversification in a particular clade. Within parrotfish we have found that the opening up of the herbivorous/detritivorous niche through the changes in the pharyngeal jaw did not result in oral jaw diversification, in fact if anything it may have led to a reduction in diversity as the rates of morphological diversification are slower within the more basal non-S/C/H clade. The question whether the pharyngeal jaw changes provided potential for morphological change is left unanswered but these changes were probably a prerequisite for the second intramandibular joint innovation in S/C/H parrotfish. Future work that encompasses multiple independent evolutionary origins of intramandibular joints and pharyngeal jaw modifications will hopefully enable the investigation of the genetic and ecological circumstances that interact with these novel design features to drive the generation of disparity.

Although the increased evolutionary rates within S/C/H parrotfish are consistent with predictions based on Hypothesis 2, that is, diversification following the formation of the intramandibular joint, we cannot definitively conclude that the rapid evolutionary change observed within this clade was caused by the intramandibular joint adding complexity to the oral jaws, as we have only shown correlation not causation. Additionally the precise synchrony of the intramandibular innovation and the increase in rates of jaw evolution cannot be determined. Unfortunately, because the nearby nodes only differ in the placement of a few species (the node directly below includes two additional species and the node above excludes a single species), it is impossible to distinguish between the scenario that the rate shift occurred at one of these neighboring nodes rather than at the S/C/H node.

CONCLUSION

Our results demonstrate that although the modification of the pharyngeal jaw (Gobalet 1989) undoubtedly allowed parrotfish to exploit an abundant niche there was no immediate increase in oral jaw diversity. This result does not imply that the innovation did not generate evolutionary potential only that diversification was not realized, possibly due to environmental or genetic constraints. However, the estimated rate parameters indicate oral jaw diversification may have slowed down during the early evolution of parrotfish. Therefore, if there was a rapid diversification into specialized herbivorous/detritivorous niches within parrotfish after the new trophic zone was opened up by the pharyngeal jaw modifications, it is highly unlikely to have involved the oral jaws. It is possible, however, that initial dietary diversification within parrotfish involved changes in body mass as rates are elevated within non-S/C/H parrotfish relative to wrasses and S/C/H parrotfish. Size can affect diet even if the jaw mechanics are similar (Mittelbach 1981; Wainwright 1988; Bellwood et al. 2006b) and may explain why non-S/C/H parrotfish appear to have diverse diets but show little oral jaw diversity. After the initial slowdown, rates of oral jaw evolution increased significantly within parrotfish following the evolution of the intramandibular joint. This pattern is consistent with the prediction of increased oral jaw diversification following the addition of complexity to the oral jaw mechanical system introduced by this novel joint. It is not clear whether the resulting morphological diversity within the oral jaw system led to ecological diversity due to the lack of detailed information concerning parrotfish diets, however, the data currently indicate that S/C/H parrotfish show remarkable consistency in feeding on turf algae and the detritus that is held within its canopy.

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Supporting Information

The following supporting information is available for this article:

Appendix S1. Brownian rate estimates for 1 and 2-rate models including a model fit comparison with and without branch length transformation.
Appendix S2. Model comparison using ΔAICc comparing the fit of a Brownian motion model and an Ornstein–Uhlenbeck model for each trait in every data partition used in the analysis.

Supporting Information may be found in the online version of this article.