

Herbivory Promotes Dental Disparification and Macroevolutionary Dynamics in Grunters (Teleostei: Terapontidae), a Freshwater Adaptive Radiation

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ABSTRACT: Trophic shifts into new adaptive zones have played major (although often conflicting) roles in reshaping the evolutionary trajectories of many lineages. We analyze data on diet, tooth, and oral morphology and relate these traits to phenotypic disparification and lineage diversification rates across the ecologically diverse Terapontidae, a family of Australasian fishes. In contrast to carnivores and most omnivores, which have retained relatively simple, ancestral caniniform tooth shapes, herbivorous terapontids appear to have evolved a variety of novel tooth shapes at significantly faster rates to meet the demands of plant-based diets. The evolution of herbivory prompted major disparification, significantly expanding the terapontid adaptive phenotypic continuum into an entirely novel functional morphospace. There was minimal support for our hypothesis of faster overall rates of integrated tooth shape, spacing, and jaw biomechanical evolution in herbivorous terapontids in their entirety, compared with other trophic strategies. There was, however, considerable support for accelerated disparification within a diverse freshwater clade containing a range of specialized freshwater herbivores. While the evolutionary transition to herbivorous diets has played a central role in terapontid phenotypic diversification by pushing herbivores toward novel fitness peaks, there was little support for herbivory driving significantly higher lineage diversification compared with background rates across the family.

Keywords: phenotypic disparification, herbivory, dentition, carnivory, trophic shifts.

Introduction

Adaptive radiation is the rapid evolution from a common ancestor of an array of species as a consequence of adaptations to distinct ecological niches. It is typically triggered

by an ecological opportunity in the form of underutilized resources, such as the colonization of a new habitat, the extinction of ecological antagonists, or the evolution of a novel phenotypic trait—an evolutionary key innovation (Schluter 2000; Gavrillets and Losos 2009; Losos 2010). Whatever circumstances initiated an adaptive radiation, a strong link always exists between adaptively relevant traits and the habitat and/or foraging niche (a phenotype-environment correlation; Schluter 2000; Gavrillets and Losos 2009; Losos 2010). Dietary changes and exposure to new selective regimes have long been suggested to play a major role in phenotypic divergence across a range of vertebrate and invertebrate radiations (Grant 1986; Mitter et al. 1988; Albertson et al. 1999; Vitt et al. 2003). However, the frequency with which particular dietary modes have evolved varies considerably across vertebrate lineages (Price et al. 2012).

Diversification in dentition is of particular evolutionary interest, as tooth shape and arrangement play a key role in food procurement and processing, with teeth literally on the cutting edge of ecomorphological adaptation and evolution (Bellwood et al. 2014). Comparative odontology has been a cornerstone of research in mammalian evolution, where dentition pattern, individual tooth and crown shape, and dental interlocking are frequently used as markers for deciphering ecological adaptation, particularly in plant-based diets (Sues 2000; Mihlbachler et al. 2011). Together with jaw structure, oral teeth are also critical components in the trophic machinery of fishes, with often striking differences between carnivorous and herbivorous species (Bellwood et al. 2014). The teeth of nonmammalian jawed vertebrates are thought to have originated as simple monocuspid, conical teeth, with significant increases in complexity evolving from this plesiomorphic condition (Rücklin

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et al. 2012; Jackman et al. 2013). A limited number of species-rich fish clades, such as cichlids, are textbook exemplars of the evolution of tooth form variation and its role in resource exploitation and trophic variation (Fryer and Illes 1972; Liem 1980; Rüber et al. 1999); however, comparatively little is known about the link between diversity and potential radiations in other fish clades. While herbivory is broadly distributed across mammals (>25% of species) and frequently associated with pronounced evolutionary diversification (Sues 2000; Price et al. 2012), this trophic strategy has a much more restricted occurrence (2%–5% of species) among other vertebrate groups, such as reptiles and fishes (Choat and Clements 1998; Espinoza et al. 2004). Despite their numerical and biomass dominance in many communities, fishes feeding primarily on plant material make up <5% of the 426 recognized families of teleostean fishes, with herbivorous representation even less pronounced at the species level (Choat and Clements 1998; Horn 1998). Herbivorous-detritivorous fishes, such as cichlids and cypriniforms, are paradoxically some of the most successful and diverse vertebrate clades (Nelson 2006).

As in mammals, the evolution of novel plant-based diets in fishes is associated with distinct morphological innovations. Rows of closely spaced multicuspidate or flattened, chisel-like, and spatulate cutting teeth are prevalent in herbivorous fishes (Rüber et al. 1999; Sibbing and Witte 2005; Streelman et al. 2006; Bellwood et al. 2014). High jaw lever ratios permitting high-force transmission (but constraining velocity) are also common among many herbivorous fishes (Bellwood 2003; Sibbing and Witte 2005). Although much attention has focused on the diet and adaptations of specific fish species, the role played by herbivory in driving macroevolutionary patterns of large-scale phenotypic diversification remains undetermined. Selective pressures associated with trophic shifts and evolution of novel or specialized trophic niches have, however, produced contrasting effects, alternatively promoting rapid morphological diversification in several fish clades (Martin and Wainwright 2011; Price et al. 2011; Frédérich et al. 2013) but constraining disparification in others (Collar et al. 2009).

A species-rich and trophically diverse Australasian fish family, the terapontid grunters (Terapontidae) exemplify one of the most important freshwater adaptive radiations in a region biogeographically distinct from that of most other studied fish clades (Davis et al. 2012). Evolving from ancestrally carnivorous marine ancestors, freshwater terapontids in particular acquired feeding habits that span piscivorous, insectivorous, omnivorous, herbivorous, frugivorous, and detritivorous trophic strategies (Davis et al. 2011). In a continental ichthyofauna exhibiting relatively restricted trophic diversity, terapontids are especially notable for the prevalence of herbivorous and detritivorous feeding habits, wherein plant and/or detrital material make up the domi-

nant proportion of the diet for approximately two-thirds of the freshwater species (Davis et al. 2012). Marked variation in oral anatomy (fig. 1) provided key diagnostic characters in taxonomic treatments of the family (Mees and Kailola 1977; Vari 1978) but received only cursory treatment in comparative studies of the nature and tempo of intrafamilial species and phenotypic diversification (Davis et al. 2014).

We quantify tooth form disparity and gauge relationships to diet in terapontids using a suite of recently developed comparative methods to address several questions. We test the hypothesis that ecological novelty in the form of transitions to plant-based diets is associated with phenotypic disparification into new morphospace (Bellwood et al. 2014). In addition, we assess whether ecological novelty is linked to elevated rates of both morphological disparification and lineage diversification in the Terapontidae. Specifically, we predict that the shift from carnivory resulted in increased rates of disparification toward novel fitness peaks in herbivorous clades, a phenomenon seen in many adaptive radiations (Ackerly 2009; Glor 2010).

Material and Methods

Terapontid Phylogeny, Taxon Sampling, and Molecular Markers

A framework for the comparative study is based on a phylogenetic analysis of 38 terapontid species (of 53 valid species) using combined nuclear (nDNA) and mitochondrial (mtDNA) DNA sequences from our previous study (Davis et al. 2012) as well as others obtained from GenBank. This included all but one valid genus, 12 marine-euryhaline species, 23 of the 25 species of Australian freshwater terapontids, and three species endemic to New Guinea (fig. 2). For rooting purposes, the new analysis also included a comprehensive representation of 48 out-group taxa in four other families in Terapontoidei (see Betancur-R. et al. 2013). The concatenated data set consisted of 8,471 sites of three mitochondrial and four nuclear loci. Sequences from each gene were aligned using MAFFT (ver. 7.017; Katoh and Standley 2013), and the resulting gene alignments were concatenated in Geneious (ver. 8.1; Biomatters). Ten partitions and models were selected using PartitionFinder (ver. 1.1.1; Lanfear et al. 2012) and used as input for downstream Bayesian analyses.

To address uncertainty in tree topology, branch lengths, and the evolutionary history of dietary evolution, we generated a collection of trees using the Bayesian method in BEAST (ver. 2.1.3; Bouckaert et al. 2014). The analysis used an uncorrelated lognormal relaxed molecular clock with rate variation following a tree prior using a birth-death process for speciation. Because the fossil record of Terapontidae is scarce, we used a secondary prior calibration of 74 (± 5) Ma

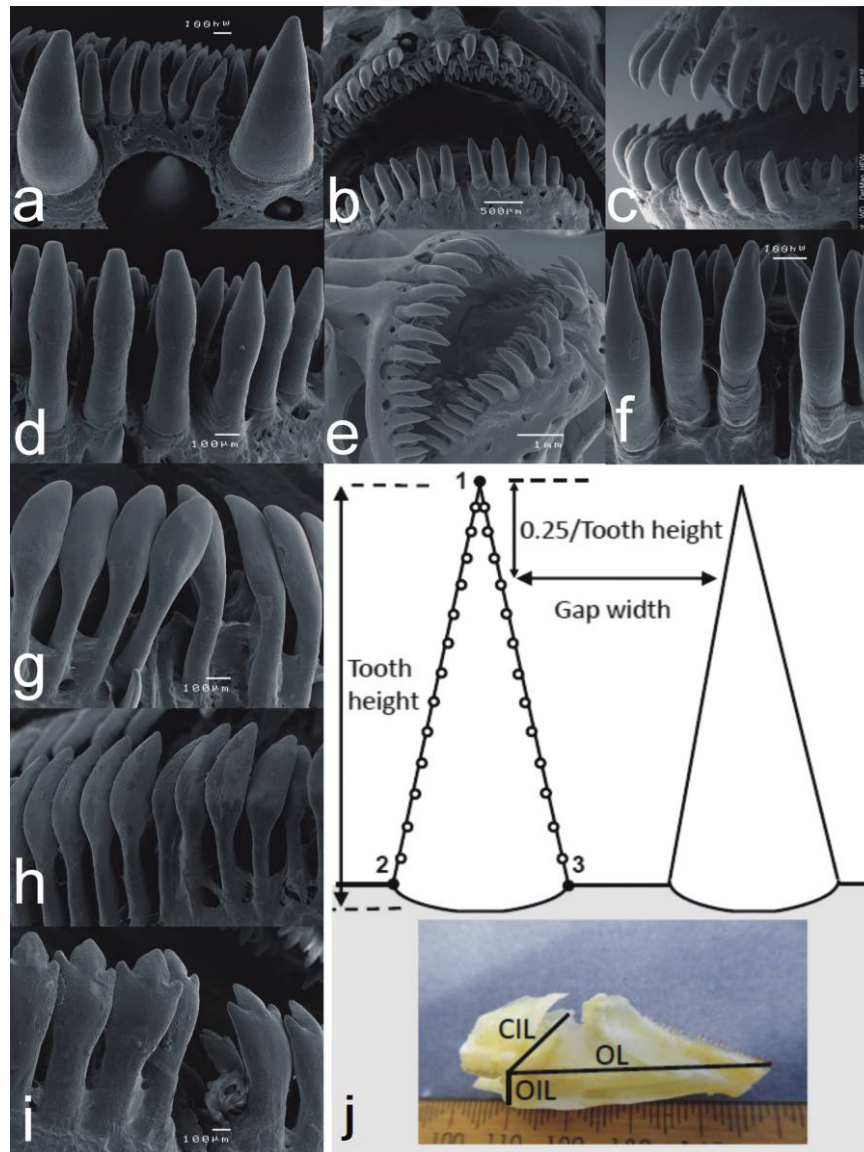


Figure 1: Example oral dentition patterns in Terapontidae (not at same scale): a, *Terapon jarbua* (carnivore-lepidophage); b, *Hephaestus carbo* (carnivore); c, *Leiopotherapon plumbeus* (carnivore); d, *Amniataba percoides* (omnivore); e, *Variichthys lacustris* (omnivore); f, *Leiopotherapon aheneus* (omnivore); g, *Pingalla gilberti* (algivore-detritivore); h, *Syncomistes trigonicus* (algivore-detritivore); i, *Helotes sexlineatus* (herbivore). j, Morphometric quantification of tooth shape: landmarks (filled circles), sliding landmarks (open circles), tooth height, and gap width, including lower jaw of *Hephaestus epirrhinos*, showing the dentary and articular bones that form the jaw and the measurements taken to calculate jaw ratios. OL = out-lever; CIL = closing in-lever; OIL = opening in-lever. Closing ratio is CIL/OL, and opening ratio is OIL/OL.

for the root age following a normal distribution ($\sigma = 3.0$). This age prior is based on the most recent phylogenetic study of ray-finned fishes using multiple fossil calibrations (Betancur-R. et al. 2015). BEAST analyses were run in duplicate for 500 million generations, with parameters logged every 20,000 generations. A maximum clade credibility tree with mean nodal heights was also estimated using Tree-Annotator (ver. 2.2.0; figs. 2, A1; figs. A1–A6 are available online). Extended phylogenetic methods are given in the

appendix (available online). The maximum clade credibility tree and 500 BEAST-generated trees are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.sj8vk> (Davis et al. 2016).

Dietary Classification and Quantification

The diet of the Australasian Terapontidae is reasonably well documented using volumetric stomach content analy-

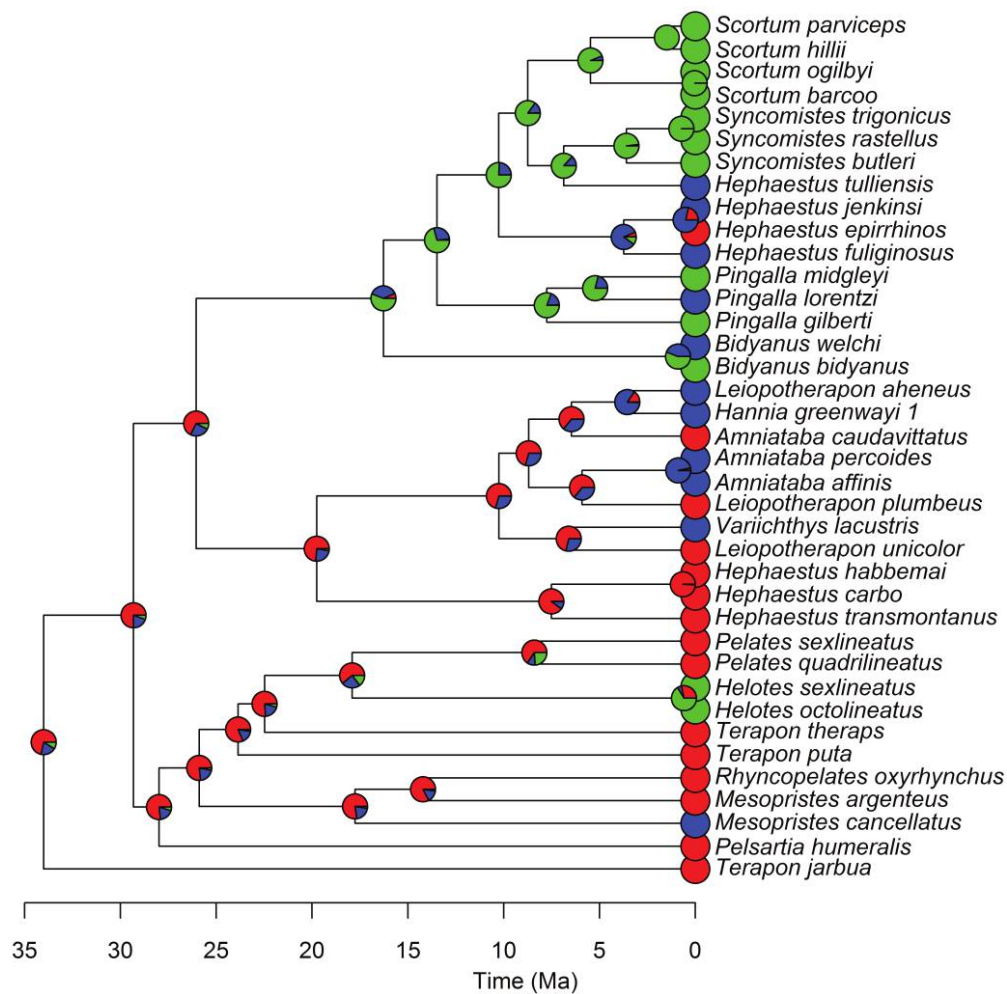


Figure 2: Maximum clade credibility tree for terapontid phylogeny. Species are coded by discrete trophic designation (red = carnivore; blue = omnivore; green = herbivore). Pie charts at nodes indicate proportion of discrete dietary states reconstructed at the node from 500 BEAST-generated trees subject to stochastic character-mapped SIMMAP reconstructions of foraging behavior.

ses (table A3; tables A1–A8 are available online) in several recent studies conducted by the authors (Davis et al. 2011, 2012). The 38 species encompass all major trophic habits among Australo-Papuan freshwater and marine terapontids: invertivores, generalist carnivores, omnivores, herbivores, and algivores-detritivores (Davis et al. 2011, 2012). We defined three main trophic groups (fig. 2; table A3) by transforming proportionate dietary data into a discrete variable that describes each species' degree of carnivory, as follows: carnivore (consumed $\geq 80\%$ animal prey), omnivore (animal prey $> 20\%$ and $< 80\%$), and herbivore-detritivore ($\leq 20\%$ animal prey).

Anatomical Preparation and Trait Quantification

To clear jaws of flesh, they were dissected out of adult specimens and put into a solution of enzyme-based laun-

dry presoaker until most tissue could be removed. Samples were passed through an ascending series of ethanol solutions to absolute ethanol, dried, mounted on specimen stubs, sputtered with gold, and viewed with a scanning electron microscope (SEM).

Morphological integration of complex, multidimensional tooth shape was quantified via measurements taken directly from anterior and lateral SEM images of the largest anterior-most tooth of the lower jaw. Tooth shape was quantified using 2-D geometric morphometrics (Bookstein 1991) in TpsDig2 (Rohlf 2006), with 30 points including three homologous landmarks (the two basal points and the tooth base and tip) and 27 including sliding semilandmarks (Gunz and Mitteroecker 2013; fig. 1). The configurations of points were then subjected to a generalized Procrustes analysis in MorphoJ (Klingenberg 2011), which aligns the specimens to a common coordinate system and removes positional, rotational, and

size information from the data set but retains shape variation (Rohlf and Slice 1990).

Several variables relating to tooth size and arrangement typically associated with diet (Bellwood et al. 2014) were also generated from SEM imagery (fig. 1). Tooth length was calculated from tooth tip to insertion in the jaw, and gap width (tooth spacing) was calculated as the distance between teeth 25% below the tooth tip. Values were log transformed followed by regressions of each morphological tooth variable against standard length to provide phylogenetic size correction (Revell 2012). Jaw-opening and jaw-closing lever ratios were also measured to provide a simple biomechanical model of species' potential bite force and jaw velocity (Wainwright and Richard 1995).

Trait Evolution

We analyzed trait evolution using (1) the geometric morphometric data on tooth shape and (2) the orthogonal measurements on combined tooth and jaw biomechanics data. For the geometric morphometric data set, the Procrustes residuals resulting from the superimposition were analyzed using a principal component analysis (PCA) in the R package GEOMORPH (Adams and Otárola-Castillo 2013) to represent shape variation on a few synthetic axes. Because evolutionary change in complex, multidimensional traits such as shape correspond to a shift in the position of species in a multivariate trait space, we used recent methods (see Adams 2014) to test for changes in the tempo of terapontid tooth shape evolution (from both anterior and lateral perspectives). Under the expectation of a Brownian motion process, this test allows comparison of shape evolutionary rates by simulations ($n = 999$ iterations) along the phylogeny using all principal components (PCs) of shape variables. The net rate of phenotypic evolution over time (σ^2) was estimated and statistically compared among carnivorous, omnivorous, and herbivorous terapontids in GEOMORPH. To examine tooth shape evolution, we treated the main PC axis (PC1) from anterior and lateral perspectives as continuous traits, from which we calculated ancestral states for tooth shape under maximum likelihood (Schluter et al. 1997) in Phytools (Revell 2012), including 95% confidence intervals on ancestral state estimates.

A combined data set of geometric (the first two axes of anterior and lateral tooth shape) and orthogonal (tooth length, spacing, and jaw biomechanics) measurements was subjected to phylogenetically corrected PCA (PPCA; Revell 2009) to eliminate multicollinearity and to synthesize the main axes of integrated terapontid tooth and jaw morphology variation. The PPCA used the evolutionary correlation matrix of the maximum clade credibility tree, with species' scores on the main PC axes used as character values in subsequent morphological analyses. To avoid constraining the

analysis to a Brownian motion model, we used λ optimization to set the most appropriate value in the model and find correlation structure. The significance of any dissimilarity in the multivariate dispersion of species' tooth morphologies between the three a priori trophic habits was tested using a nonparametric, permutation-based, one-way analysis of similarity (ANOSIM; 999 permutations) in PRIMER (Clarke and Gorley 2007). The ANOSIM used species' PPCA scores for PC1 and PC2.

Temporal Macroevolutionary Dynamics

Several evolutionary models were assessed to find the best fit to explain the evolution of trophic morphology (species' scores on the first two morphological PPCA axes) in terapontids. We used an a priori assessment of selective regimes, building stochastic character-mapped reconstructions of foraging behavior (SIMMAP; Nielsen 2002) based on the three trophic groups (i.e., carnivore, omnivore, and herbivore-detritivore). To integrate uncertainty in tree topology, branch lengths, and the evolutionary history of diet, stochastic maps were estimated using the 500 trees sampled from the posterior distribution of the BEAST analysis.

First, we fit single-rate Brownian motion (BM1) to each PC axis, a time-homogeneous process in which morphological disparity varies at random and increases uniformly as a function of time. A three-rate BM model (BMS; O'Meara et al. 2006) was also assessed in which carnivores, omnivores, and herbivores exhibit different rates of BM evolution. Second, we fit a single-optimum Ornstein-Uhlenbeck (OU) adaptive model (Hansen 1997) with one parameter for the variance of random walk (σ^2) and strength of selection (α) toward a global optimum for all terapontids (OU1). Third, we assessed the fit of OU models with separate morphological (PC) optima for each trophic habit but global σ^2 and α parameters for the different carnivorous (θ_c), omnivorous (θ_o), and herbivorous (θ_h) selective regimes (OUM; Beaulieu et al. 2012) as well as the fit of a three-optimum OU model with separate random walk variances for carnivores, omnivores, and herbivorous selective regimes (σ^2) and one global selection parameter (α ; OUMV). We also assessed the fit of an early-burst model to assess whether terapontid morphology followed a classic adaptive radiation trajectory of initial rapid morphological evolution (as lineages enter new adaptive zones and rapidly fill vacant ecological space) followed by a slowdown in rates of phenotypic evolution (Harmon et al. 2010).

Adaptive models were fit with OUwie (Beaulieu et al. 2012) and GEIGER (Harmon et al. 2008), and the relative fit of models was assessed using a model-averaging approach where we calculated the Akaike weights (AIC_w) for each model (i.e., the relative likelihood of each model) by means of the second-order Akaike information criterion using re-

duced sample-size corrections (AIC_c). The parameter estimates for each model were then averaged together to identify their corresponding AIC_w , that is, the proportion of support a model receives relative to the total support for all models (Burnham and Anderson 2002). The utility of PCA to reduce multivariate data dimensionality to univariate trait models has recently been demonstrated to sometimes introduce undesirable statistical artifacts into evolutionary model fitting (Uyeda et al. 2015). To assess this effect, we also utilized raw trait data for several of the traits loading most strongly on PC axes and subjected each trait to the same model fitting analysis.

Because of the element of circularity in modeling a priori designation of ecomorphs and a limited capacity to detect substantial rate variation within broader a priori-defined trophic groups (i.e., within-clade trickle-down rate divergence effects; Moore et al. 2004), we also assessed whether the terapontid phylogeny has been shaped by a mixture of macroevolutionary processes using Bayesian analysis of macroevolutionary mixtures (BAMM; Rabosky 2014; Rabosky et al. 2014). This platform can infer mixtures of time-dependent and clade-specific lineage or phenotypic rate regimes on phylogenetic trees. Shifts in rates of lineage or phenotypic evolution are detected automatically, with no a priori designations, and can occur at nodes or along branches. BAMM simulates posterior distributions of rate-shift configurations and does not estimate a single best-fit configuration of rate shifts (Rabosky et al. 2014), with the set of rate-shift configurations simulated using BAMM analogous to the credible set of tree topologies sampled using Bayesian inference software in phylogenetics. After computing tree-appropriate rate priors using the `setBAMMpriors` function in `BAMMtools` (Rabosky et al. 2014), we ran BAMM for 100 million generations on the maximum clade credibility tree, sampling every 20,000 generations. We explored the Markov chain Monte Carlo (MCMC) output using tools from the `coda` package (Plummer et al. 2006) and, after checking for convergence, removed the first 10% of generations as burn-in, which resulted in effective sample sizes of >500 for each estimated parameter. We used functions in the `BAMMtools` package (Rabosky et al. 2014) to calculate posterior odds ratios for the most likely number of rate shifts and to identify the shift configurations with the highest posterior probability.

Testing the Phenotype-Environment Correlation

We used phylogenetic generalized least squares (PGLS; Freckleton et al. 2002) to examine correlations between oral morphology and diet, independent of similarity due to phylogeny. The response variable (logit-transformed proportion of animal prey in diet) was regressed against species' scores from the first two morphological PPCA axes on

the consensus terapontid tree, using CAPER (Orme et al. 2013). We included the scaling parameter λ (Pagel 1999) estimated by maximum likelihood (Orme et al. 2013) to the most appropriate value in our PGLS regressions to model differences in tempo and mode of trait evolution. At present, no formal model exists that can specifically accommodate compound models of diversification rate variation across phylogenies, although PGLS offers a reasonable compromise.

Relationship between Lineage Diversification and Trait Evolution

To assess whether net diversification (speciation minus extinction) rates are associated with the dietary classifications for each species (carnivore, omnivore, and herbivore) or are a function of diet or morphology as a continuous variable, we implemented state-dependent diversification (SSE) analyses using the multistate speciation and extinction (MuSSE) and the quantitative-state speciation and extinction (QuaSSE) approaches implemented in the R package `DIVERSITREE` (FitzJohn 2012). For the QuaSSE analyses, we separately evaluated the relationship between lineage diversification rates on the consensus terapontid tree and diet (logit-transformed proportion of animal prey) and the relationship between these rates and oral morphology (PC1 and PC2 scores) as continuous analytical framework.

While SSE approaches are widely used, their posterior probability estimates of diversification rate have been demonstrated to be inflated under some circumstances, leading to frequent type I errors (Rabosky and Goldberg 2015). To assess this potential effect (following Rabosky and Goldberg 2015), we simulated neutral, continuous traits—under a Brownian motion model, without any specified influence on diversification—30 times on the terapontid phylogeny using the `fastBM` function for quantitative trait simulation on a phylogeny in `Phytools` (Revell 2012). We then assessed whether these simulated continuous traits correlated significantly with speciation rate. Full methodological details on the SSE analyses are provided in the appendix.

To assess for shifts in lineage diversification rates within Terapontidae with no a priori designations for rate heterogeneity in relation to trophic habit, we also used BAMM following the same methodology in setting priors, convergence assessment, and posterior odds calculation as used to assess shifts in oral disparification. To account for non-random incomplete sampling, we estimated sampling fractions on a genus-by-genus basis following the list of valid species in Terapontidae (from Eschmeyer and Fong 2013); sampling fractions were assigned to the sampled tips in the phylogeny as species-specific sampling probabilities.

All phylogenetic comparative analyses were performed using R (ver. 2.15.0; R Development Core Team 2013), with

data manipulations conducted using functions from R packages Phytools (Revell 2012), Ape (Paradis et al. 2004), and Geiger (Harmon et al. 2008).

Results

Trait Evolution

The first two PC axes captured the dominant proportion of anterior tooth shape variation in the geometric morphometrics data set (76% and 16%, respectively). Variation in PC1 tooth shape related primarily to tooth-base width, ranging from species with robust, hypertrophied (mammiliform) tooth bases to species with spatulate teeth (narrow bases; fig. 3A). PC2 related mainly to overall tooth width, spanning species with relatively fine, villiform dentition to the broader, tricuspidate teeth in *Helotes*. From the perspective of lateral shape, PC1 (53% of variance) mainly captured tooth robustness, with robust, hypertrophied base teeth and conversely narrow, slender teeth in the lateral dimension occupying morphospace extremes (fig. 3B). Variance captured in PC2 (33% of variance) from a lateral perspective related predominantly to degree of lingual tooth curvature. The maximum likelihood estimate of tooth shape suggested that the ancestral terapontid had relatively simple caniniform dentition similar to that in the majority of carnivorous-omnivorous species (fig. 3), although with large confidence level estimates (fig. A2). Tests of evolutionary rates of change in tooth shape revealed significant differences in net evolutionary rates over time for different trophic strategies. Specifically, the rate of anterior tooth shape evolution was more than four times faster in herbivores relative to carnivores and omnivores ($\sigma_{\text{herbivores}}^2 = 3.7 \times 10^{-5}$, $\sigma_{\text{carnivores}}^2 = 7.8 \times 10^{-6}$, $\sigma_{\text{omnivores}}^2 = 8.6 \times 10^{-6}$; $P < .001$), with even more rapid evolutionary rates in herbivores from a lateral perspective ($\sigma_{\text{herbivores}}^2 = 1.2 \times 10^{-4}$, $\sigma_{\text{carnivores}}^2 = 1.7 \times 10^{-5}$, $\sigma_{\text{omnivores}}^2 = 1.3 \times 10^{-5}$; $P < .001$).

In the PPCA of combined morphological traits (shape and orthogonal measurements), PC1 (the primary axis of morphological variation) explained ~38% of total data set variance (table A4). As a synthetic measure of morphological variability in terapontids, tooth shape (anterior and lateral dimensions), tooth spacing, and jaw-opening lever ratios were all positively correlated with PC1. The PC1 summarily quantifies a transition from the widely spaced, robust, caniniform teeth and high-velocity jaw-opening capacities characteristic of many generalist carnivores and invertivorous species to the closely packed incisiform or tricuspidate teeth in macroalgal feeders and algal-aufwuchs scrapers (fig. 1). PC2 explained ~18% of the variance and loaded heavily onto traits such as lateral tooth robustness and higher jaw-closing lever ratio (with the first four PC axes together explaining ~82% of the total variance).

The phylomorphospace plot of PC1 versus PC2 (fig. A3) illustrates that the adoption of specialized herbivorous-detrivorous diets resulted in a substantial character shift in terapontids, with these dietary strategies occupying essentially an entirely new functional morphospace. This phenotypic shift was also supported by ANOSIM, which identified that the area of tooth morphospace occupied by herbivorous-detrivorous fishes was significantly different from other trophic strategies (global $R = 0.308$, $P \leq .01$). There was, however, no significant difference in the dispersion of carnivorous and omnivorous species (i.e., significant overlap; global $R = 0.07$, $P = .13$).

Temporal Macroevolutionary Dynamics in Morphology

The OU models received most support for both PC axes (table 1), suggesting that the evolution of both PC axes oscillated, at least in part, around one or more phenotypic optima. In OU models, estimated PC optima for different trophic strategies were found in all cases within the values realized for studied species (fig. A4), suggesting that the models were a realistic description of current morphology. There was substantial support for the OUM model of evolution ($AIC_w = 0.87$; table 1) for PC1, and with the exception of OUMV (which suggested faster disparification rates for carnivores), all alternative models received low support ($AIC_w < 0.001$). Model fitting for PC2 identified a single peak morphological optimum (OU1) as the best model, although OUM and OUMV models (with different optima for each trophic designation) received some support. This suggests that although the evolutionary dynamics for herbivores on PC1 were driven toward a significantly different phenotypic optimum, this dynamic was not at significantly different evolutionary rates relative to carnivores and omnivores. There was little support of multiple phenotypic optima or differing rates of phenotypic evolution according to trophic strategy for PC2. Similarly, early-burst models received the lowest support for both PC axes, suggesting that the process of terapontid disparification bears little resemblance to classical early-burst adaptive radiation (see also Harmon et al. 2010). Evolutionary model fitting of raw trait data for several traits loading most strongly on the first two PC axes (anterior and lateral tooth shape, tooth spacing, jaw-opening and jaw-closing lever ratios) produced outcomes for most variables similar to the analysis based on PPCA axis scores. Raw trait-based modeling identified the same best-fit models, or the identified model was not a significantly better fit ($\Delta AIC < 4$) than the model favored using PPCA axis scores as traits (table A5). This suggests that the subsequent PPCA process used to synthesize the main axes of morphological variation was not unduly biasing modeling outcomes.

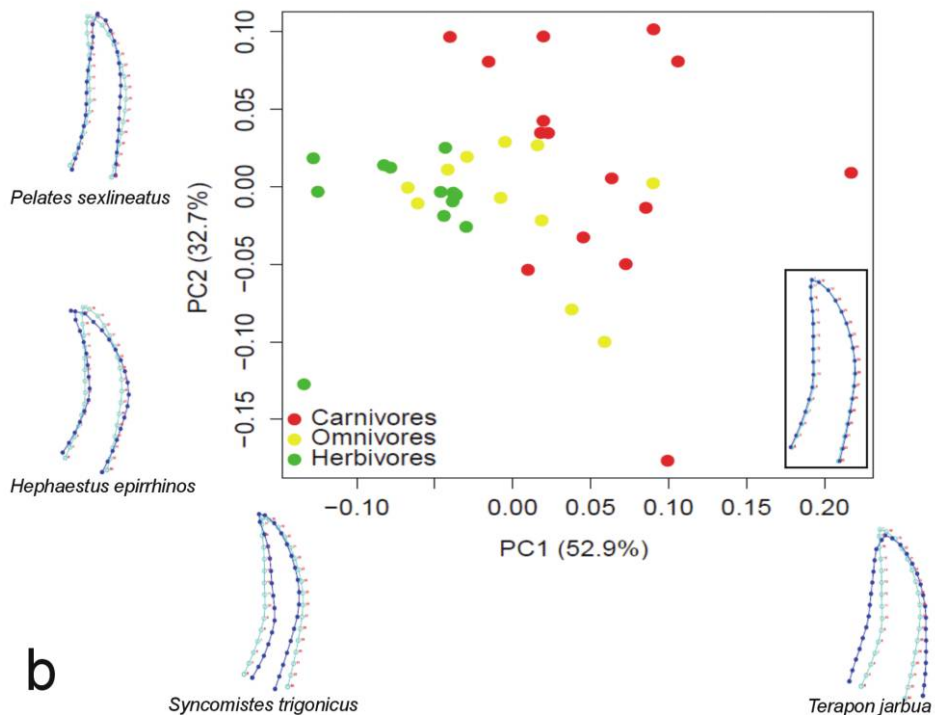
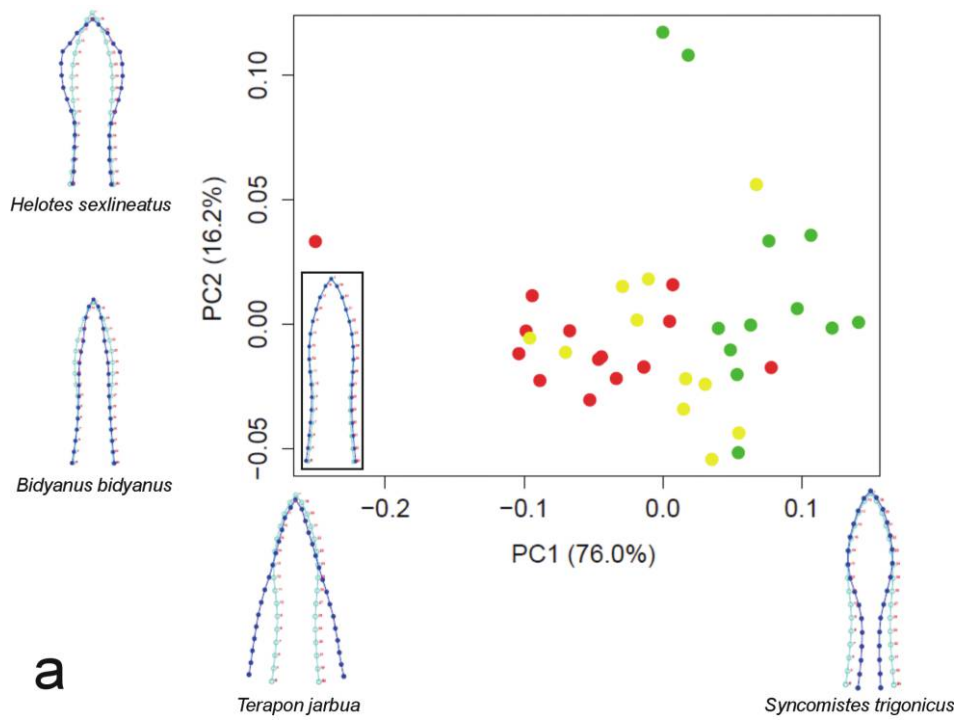


Figure 3: Principal component (PC) analysis of terapontid tooth shape (PC1 vs. PC2) from the anterior (*a*) and lateral (*b*) perspectives. Tooth shapes from species representing PC extremes on each axis are indicated. Ancestral character-state reconstructions for both PC1 axes are inserted within each graph. Species are coded by discrete trophic designation (red = carnivore; yellow = omnivore; green = herbivore).

Table 1: Average Akaike weights (AIC_w) representing the relative likelihood of each of the six evolutionary models (fitted over 500 reconstructions of foraging strategy) investigated on the combined morphological data set for PC1-PC2 axes

Model	lnLik	AIC_c	ΔAIC	Average AIC_w	Phenotypic optima			Rate of phenotypic evolution		
					C	O	H	C	O	H
PC1:										
BM1	-133.69	271.73	20.89	.00
BMS	-128.24	265.69	14.85	.00
OU1	-130.24	267.18	16.34	.00	1.99*	15.77	15.77	15.77
OUM	-119.48	250.84	.00	.87	-2.96	2.00	17.29	85.16	85.16	85.16
OUMV	-118.46	254.65	3.81	.13	-3.09	2.27	18.02	110.49	75.59	67.28
EB	-133.69	274.09	23.25	.00
PC2:										
BM1	-125.44	261.91	17.59	.00
BMS	-121.77	252.75	8.43	.01
OU1	-118.81	244.32	.00	.83	-2.07*	60.92	60.92	60.92
OUM	-118.32	248.52	4.20	.10	-2.75	-2.00	-1.00	56.68	56.68	56.68
OUMV	-115.89	249.51	5.19	.06	-2.95	-1.76	-.45	31.13	18.65	64.15
EB	-132.41	271.53	27.22	.00

Note: Boldface type indicates the model with the highest support. lnLik denotes the natural logarithm of likelihood. Lower AIC_c scores indicate a better fit. Higher AIC_w values indicate better support (shown in boldface type). Asterisks indicate the value of a single adaptive optimum for all taxa regardless of dietary habit. AIC_c = second-order estimator of the Akaike information criterion.

Evolutionary modeling using the data-driven BAMM platform with no a priori designation of trophic habit found considerable support for shifts to a higher rate of phenotypic evolution in the Australasian terapontid radiation. For PC1, there was considerable collective posterior support for detectable among-clade heterogeneity in phenotypic rates, specifically, increased phenotypic evolution for both traits concentrated around the *Syncomistes-Pingalla-Scortum-Hephaestus-Bidyanus* subclade (fig. 4a). No particular model with a specific shift time occurred at high frequency, suggesting that rate shifts could not be reduced to a single event at a strictly specified time. Constant-process phenotypic evolution did receive some support (posterior probability of ~0.2). For PC2, there was similar support for detectable increases in phenotypic rates also concentrated on the *Syncomistes-Scortum-Hephaestus* subclade (fig. 4c) and minor support for a single time-varying process of trait evolution (posterior probability of ~0.09). Plotting of the phenotypic evolutionary rate in the nodes subtending these clades suggested that disparification in both PCs was approximately three times faster than background rates across the rest of the tree (fig. 4b, 4d). This clade contains some of the most divergent ecotypes in phylogenetic morphospace (see fig. A3) and exhibits a large component of terapontid trophic diversity (table A3), including cropping herbivores (*Scortum* species), macrocarnivores (*Hephaestus epirrhinos*), omnivores (*Hephaestus* species), and scraping algivore-detritivores (*Syncomistes* and some *Pingalla* species), a trophic strategy unique to this clade.

The Phenotype-Environment Correlation

PGLS analyses revealed highly significant diet-morphology associations in the form of negative correlations between increasing species scores for morphological PC1 (closely packed, flattened dentition; slower jaw-opening velocity) and PC2 (finer, laterally compressed teeth; slower, more forceful jaw closing) and increasing logit-transformed proportions of animal prey in diet (fig. 5). The significant correlation between PC1 and diet particularly aligned with earlier evolutionary model testing, suggesting that herbivorous species had separate adaptive optima compared with omnivores and carnivores.

Lineage Diversification

The MuSSE model assessment of lineage diversification suggested that net diversification (speciation minus extinction) rates varied as a function of dietary habits. Higher net diversification rates were evident for herbivores (0.31) relative to omnivores (0.062) and carnivores (0.049), although the MCMC plots (fig. A5; table A6) overlap considerably, presumably due to power issues (e.g., Davis et al. 2013). All QuaSSE models that included diet-dependent speciation received significantly higher support compared with a model of constant treewide speciation (table A7). The strongest support was for a model in which speciation rate decreased with increasing proportion of animal prey in species' diets, following a linear function—that is, speciation increased as

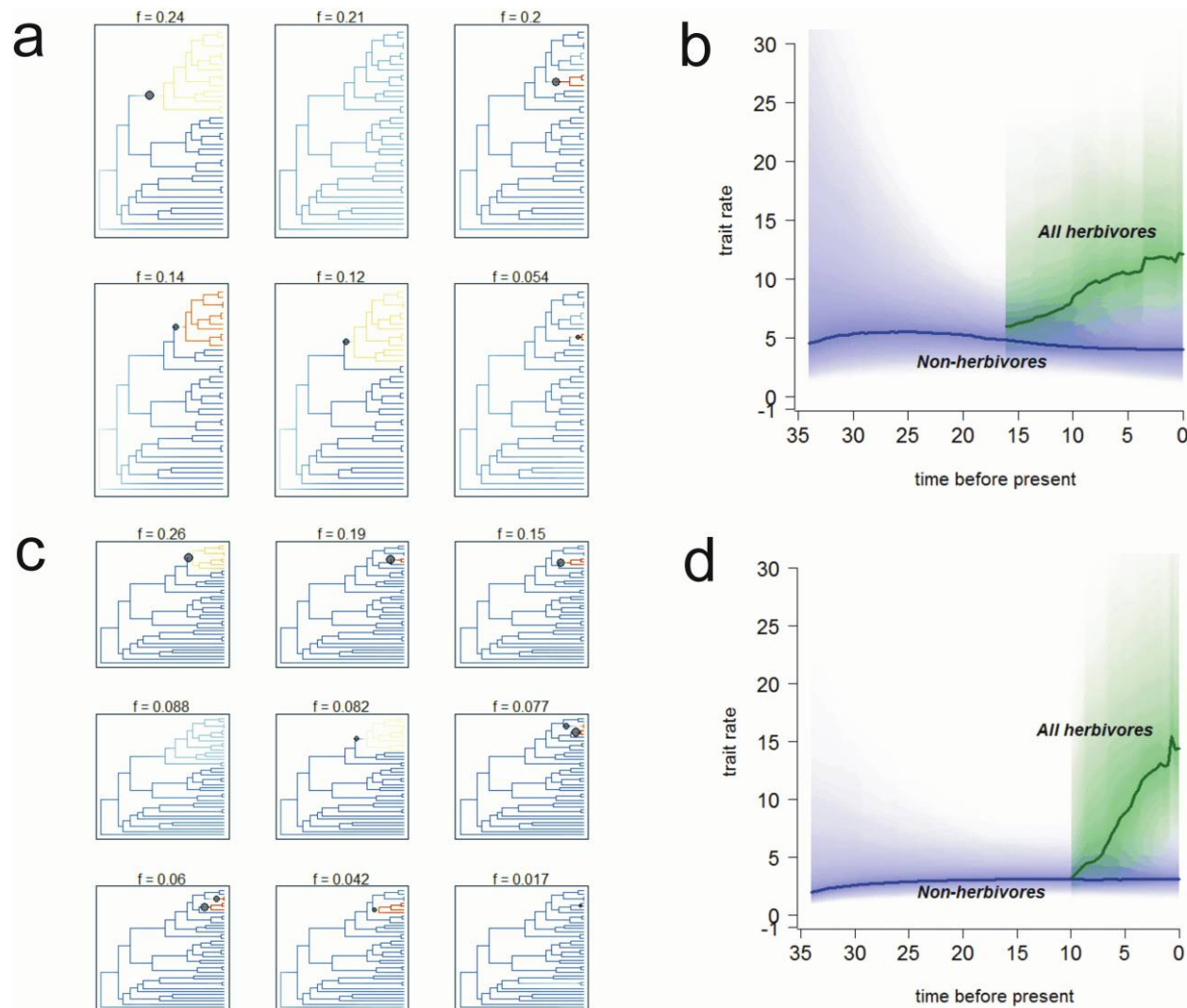


Figure 4: Rates of phenotypic evolution, estimated by Bayesian analysis of macroevolutionary mixtures, on the first and second morphological principal components during the radiation of Australasian terapontid fishes. Smaller multipanel phylogenies (*a*, *c*) show the distinct rate-shift configurations with the highest posterior probability. For each distinct shift configuration, the locations of rate shifts are shown as red (rate increases) and blue (rate decreases) circles, with circle size proportional to the marginal probability of the shift. Text labels (e.g., $f = 0.25$) denote the posterior probability of each shift configuration. Also shown are rate-through-time plots (*b*, *d*) for phenotypic evolution rate, with 95% confidence intervals indicated by shaded areas. Blue indicates the rate across the phylogeny without the shift clade (background rate; nonherbivores), and green indicates the rate of the nested *Syncomistes*, *Pingalla*, *Scortum*, *Bidymanus*, and *Hephaestus* clade (all herbivores).

species became more herbivorous (fig. A5). Under the morphological trait-based speciation analyses, the best QuaSSE model for PC1 was one in which the speciation rates were inferred to linearly increase with increasing PC1 scores (i.e., as species evolved toward morphologies more characteristic of herbivores and some omnivores). Unimodal models received the dominant support for the relationship between speciation rate and species' scores for morphological PC2 (fig. A5), indicating that axis extremes, which contain morphotypes considerably divergent from other species, have lower speciation rates.

For continuous-character data sets simulated on the terapontid phylogeny and subjected to QuaSSE analysis, however, a considerable proportion revealed a significant association between character state and diversification despite no such association being specified in the simulation model (table A8). Of the 30 character sets analyzed, 21% showed a significant ($P < .05$) association between character state and speciation rate, and 13% rejected the character-independent model with great confidence ($P < .01$). This suggests that the tendency for high type I error rates inherent to binary-state speciation and extinction models (Rabosky and Goldberg

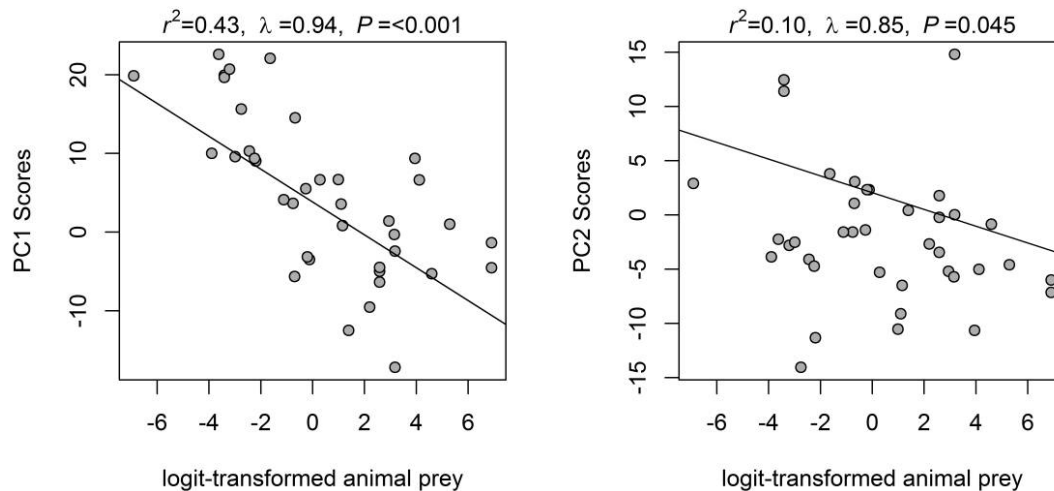


Figure 5: Relationship between terapontid species principal component (PC) scores for PC1 (left), PC2 (right), and diet for 38 terapontid species. Data were fitted using phylogenetic generalized least squares (PGLS) with Pagel's correlation structure. Graph legends indicate the maximum likelihood estimate of Pagel's λ for phylogenetic signal, model R^2 , and P value; 95% confidence intervals of Pagel's λ were 0.772–0.998 for PC1 and 0.515–0.965 for PC2. The regression line is the fit of the PGLS regression model.

2015) may also extend to the QuaSSE model. Additional details on SSE analyses are given in the appendix.

Our BAMM diversification analysis converged after a few generations, and the effective sample size values were high (>500). This analysis found dominant support for minimal rate heterogeneity within the family (fig. A6), with the speed of diversification slowing down gradually toward the present (i.e., a constant-rate model without any significant shift in net diversification rates). This suggests that the significant increase in phenotypic disparification rate concomitant with the evolution of a herbivorous diet in terapontids was not coupled with similarly significant increases in lineage diversification.

Discussion

Our study demonstrates that the shape and arrangement of terapontid dentition and jaw structure exhibit significant disparification closely associated with dietary habits, in particular the evolution of specialized herbivorous-detritivorous diets. Species exhibiting this dietary strategy evolved to a new functional morphospace and significantly different phenotypic optima relative to those in carnivores and omnivores (which overlap considerably in phenotypes). The evolutionary history of terapontids is marked by a transition from widely spaced, robust, caniniform teeth with rapid jaw-opening velocities in many carnivorous species to closely packed incisiform, spatulate, or tricuspidate teeth with slower opening velocities in herbivorous-detritivorous species. This diversity of individual tooth shapes in herbivores (whose dentition evolved at significantly higher rates than in carnivores)

likely reflects the different functional demands associated with several distinct herbivorous feeding habits, such as macrophyte cropping and biofilm-aufwuch scraping (Davis et al. 2012). These terapontid tooth types all apparently evolved from a relatively simple conical tooth shape, replicating at a smaller scale the evolution of tooth diversity seen across fishes as a whole, wherein caniniform dentition is regarded as plesiomorphic (Jackman et al. 2013). There was little evidence for our hypothesis of faster overall rates of integrated tooth shape, spacing, and jaw biomechanical evolution in herbivorous terapontids in their entirety compared with other trophic strategies. Data-driven tests did, however, identify acceleration in phenotypic evolution in a morphologically and trophically diverse freshwater clade containing several herbivorous genera, including acquisition of biofilm-scraping strategies unique within the family.

While BAMM (with no prior designation of trophic habits) detected no significant shifts in Terapontidae, state-dependent diversification analyses suggested that terapontid lineages with greater degrees of omnivory-herbivory showed higher speciation rates. This suggested that shifts away from predominantly carnivorous diets (the ancestral trophic habit in terapontids; fig. 2) may have catalyzed intrafamilial speciation. Although it is possible that dietary variation underlies subtle, heterogeneous speciation dynamics across terapontids, simulation results clearly show that this phylogeny possesses properties such that even neutral characters, which do not influence diversification, will frequently be statistically linked to differential speciation, and our results should be treated with considerable caution. The utility of multi- and sister-clade meta-analyses offer some potential for methodo-

logical refinement of state-dependent analyses (see Huang and Rabosky 2014; Rabosky and Goldberg 2015), but these are beyond the taxonomic scope of this study.

Our results align at several levels with previous research wherein evolution of herbivorous-detritivorous diets prompted the expansion of reef fishes into entirely novel areas of functional morphospace (Price et al. 2011; Bellwood et al. 2014). While we currently lack direct quantitative comparison, terapontid oral morphology does bear striking similarities to a range of marine and freshwater fishes exploiting analogous feeding modes (Fryer and Illes 1972; Vari 1979; Clements and Choat 1997; Sibbing and Witte 2005; Bellwood et al. 2014). The closely packed, flattened teeth (often with narrow, slender tooth “stalks”) seen in herbivorous terapontids likely offer a relatively continuous “tooth band” that can more effectively scrape or crop algal or biofilm material from hard surfaces than would widely spaced, caniniform teeth (Fryer and Illes 1972). These morphological parallels across these often distantly related groups reflect the common challenge in procuring aquatic plant-detrital material from a hard substratum, whether it is the epilithic algal matrix on reefs or biofilm-aufwuchs in African rift lakes or northern Australian freshwaters.

Whereas we detected a significant relationship between terapontid oral anatomy and diet, this explained only ~43% of data set variation, likely reflecting the challenge of defining the specific nutritional targets in fish diet, particularly for nominal omnivores. In contrast to the nutritional ecology approaches so informative to the study of terrestrial herbivory, the assimilatory targets, food composition, and associated digestive functioning of many herbivorous-detritivorous fish remain poorly defined (Choat and Clements 1998).

In addition to implications for the evolutionary trajectories of specific clades, major transitions in feeding mode (such as herbivory/detritivory) also mark profound shifts in the nature of fish-benthos interactions and overall aquatic community ecosystem function (Bellwood 2003; Bellwood et al. 2014). In a continental fauna dominated by carnivorous and omnivorous fishes (Davis et al. 2012), the evolution of relatively specialized herbivory-detritivory would have marked a major ecological breakthrough for terapontids, opening up abundant trophic resources (see Cebrian 1999) only indirectly utilized by most other fishes. Previous studies highlighted the importance of the historic macrohabitat transition from marine to freshwater environments in triggering greater rates of lineage and phenotypic diversification in freshwater terapontid clades (Davis et al. 2014) as well as in ariid catfishes (Betancur-R. et al. 2012). This study documents further evidence that much of the morphological diversification in freshwater terapontids following this adaptive zone shift is driven by evolutionary trajectories toward morphological optima suited to exploitation of non-animal diets. These trophic optima are shared across the

family regardless of habitat affiliation but are more frequently expressed in freshwater species, likely due to the greater ecological opportunity afforded in Australia’s relatively species-poor freshwater environments (Betancur-R. et al. 2012; Davis et al. 2012).

Conclusion

While large clades have been the focus of much attention, smaller families can provide valuable context to the underlying dynamics and drivers of phyletic evolution. Study results demonstrate that much of the phenotypic disparification evident in the terapontid radiation revolved around increasing consumption of a variety of plant and/or detrital materials (i.e., a novel morphospace to match a novel diet). The critical importance of morphological breakthroughs in fishes (particularly for herbivory) as well as their role in unprecedented diversification and the appearance of radical new forms is a long-standing theme in studies of fish evolution (Bellwood 2003). While we demonstrated the ecological and phenotypic divergence that is widely recognized as a requisite component of adaptive radiation, we did not identify any early burst in ecological novelty and disparate morphological diversification rates in integrated oral morphology, often regarded as a common feature of many classic adaptive radiations (Ackerly 2009; Glor 2010; Harmon et al. 2010; Martin et al. 2011), nor were any rate shifts in lineage diversification clearly associated with herbivory in the family. Bursts of accelerated disparification were, however, evident in specific freshwater herbivorous-detritivorous clades, including those evolving biofilm-scraping diets unique in the family. Clades like Terapontidae that are exceptionally diverse phenotypically but exhibit unexceptional species diversity are generally neglected in studies of adaptive radiation and pose definitional challenges (Losos and Mahler 2010), but they may provide critical insights into the role played by speciation in adaptive radiation.

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