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Evolutionary biology

Body shape convergence driven by small size optimum in marine angelfishes

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Convergent evolution of small body size occurs across many vertebrate clades and may reflect an evolutionary response to shared selective pressures. However it remains unclear if other aspects of phenotype undergo convergent evolution in miniaturized lineages. Here we present a comparative analysis of body size and shape evolution in marine angelfishes (Pomacanthidae), a reef fish family characterized by repeated transitions to small body size. We ask if lineages that evolve small sizes show convergent evolution in body shape. Our results reveal that angelfish lineages evolved three different stable size optima with one corresponding to the group of pygmy angelfishes (*Centropyge*). Then, we test if the observed shifts in body size are associated with changes to new adaptive peaks in shape. Our data suggest that independent evolution to small size optima have induced repeated convergence upon deeper body and steeper head profile in *Centropyge*. These traits may favour manoeuvrability and visual awareness in these cryptic species living among corals, illustrating that functional demands on small size may be related to habitat specialization and predator avoidance. The absence of shape convergence in large marine angelfishes also suggests that more severe requirements exist for small than for large size optima.

1. Introduction

Body size is among the most significant of morphological traits because of its critical influence on performance and many ecological factors (e.g. [1]). Evolutionary impacts of transitions to large body size are well-documented (e.g. [2]), yet trends towards miniaturization are also characteristic of many branches in the tree of life [3]. However, the scarcity of rigorous phylogenetically controlled tests of macroevolutionary effects from miniaturization limits our understanding of its role in generating morphological diversity. As exemplified by the rise of birds from Theropoda [4], an evolutionary trend to small body size may promote phenotypic diversity and lead to higher rates of morphological evolution. Shifts to small body size may be driven by various factors, such as predation pressure and resource competition [3,5], and convergent evolution of small body size would thus be due to a shared response to those drivers. Miniaturization may lead to new adaptive peaks, and lineages evolving towards small size might converge upon similar morphologies [3,6].

Here we explore the evolution of marine angelfishes (Pomacanthidae), an iconic reef fish family of approximately 88 species, wherein small body size has led to a traditional classification that assigns 34 species to the genus

Table 1. Results from fitting shape diversification models (summarized as median values across the 5000 character maps). Models are specified by their parameters and ranked from best to worst, according to AICc (small-sample corrected AIC) scores and Akaike weights (AICcWt). Δ AICc scores indicate differences between the candidate model and the best-fitting model.

model specification					
model	rate parameter (σ)	optimum (θ)	AICc	Δ AICc	AICcWt
OUM_size	a diagonal σ matrix	separate θ for size groups	−837.97	0	0.93
OU1	a diagonal σ matrix	one single θ for all species	−832.73	5.24	0.07
BMM_size	separate σ for size groups	—	−776.79	61.19	4.82×10^{-14}
BM1	one single σ for all species	—	−671.32	166.65	6.05×10^{-37}

Centropyge, the so-called ‘pygmy angelfishes’ [7]. Recent molecular phylogenies suggest that this genus is paraphyletic and constitutes at least three lineages currently considered as subgenera [8]. The disparity of body size within Pomacanthidae (from 7 to 60 cm in total length, TL) with potential convergent evolutionary miniaturization presents an opportunity to explore the impact of size variation on the pattern of phenotypic evolution. Using molecular phylogenetics, morphometrics and comparative methods on a dataset of approximately 75% of the extant angelfish species, we asked if body size evolved to different stable optima in Pomacanthidae. To probe the hypothesis that similar factors may drive small body size to an adaptive peak, we tested if pygmy lineages have converged upon a similar body shape, suitable for cryptic lifestyles.

2. Material and methods

(a) Phylogenetic analyses

Our molecular dataset includes six genes for 67 angelfish species, representing all described genera, and seven outgroups (see analyses details in electronic supplementary material, appendix S1 and table S1). We performed maximum likelihood and Bayesian inference phylogenetic analyses, producing a phylogeny consistent with earlier studies [8,9] (electronic supplementary material, appendix S1). From the Bayesian posterior distribution generated by BEAST v. 1.8 [10], we randomly sampled 100 trees to account for uncertainty in tree topology and branch length in our comparative analyses.

(b) Morphological data

We compiled information on maximum body size (TL) from the literature (electronic supplementary material, table S1) and obtained X-ray images of adult specimens ($N = 186$) representing 57 species (electronic supplementary material, table S1). Overall body shape, an ecologically relevant character directly related to habitat partitioning [11], was quantified by geometric morphometrics [12] using 18 two-dimensional landmark coordinates (electronic supplementary material, figure S1). A generalized Procrustes analysis was used to align specimens, and a shape variable dataset was obtained for each specimen. A principal component analysis on shape variables was performed to summarize the major axis of shape variation.

(c) Comparative analyses

All analyses were conducted in R v. 3.2.2 [13]. To test if lineages have evolved to different body size optima, we ran an

exploratory analysis of size evolution (log-transformed TL) in SURFACE v. 0.4.1 [14]. This method fits Ornstein–Uhlenbeck (OU) models [15] with accumulating adaptive peaks to data, using a stepwise Akaike information criterion (AIC) model selection procedure. We also inferred the ancestral body size of angelfishes (see details in electronic supplementary material, appendix S2).

The evolutionary interaction between size and shape was assessed using a phylogenetic regression based on Procrustes distances [16]. Then mvMORPH v. 1.0.7 [17] was used to compare the fit of four models of shape evolution (table 1). These models included Brownian motion (BM) and OU models differing by the number of rate parameters (σ) or optima (θ) associated with size groups inferred from SURFACE (see details about modelling shape evolution in electronic supplementary material, appendix S3). We expect OUM_size to best fit our data if body size drives evolution to different shape optima. Conversely, BMM_size should fit better if size mainly influences the rate of shape evolution. We fitted these models using (i) mean species scores and associated variance along the first three PC axes on shape variables to reduce the number of parameters and (ii) 5000 character maps produced by stochastic character mapping [18] to include possible histories of body size. We finally compared the models based on *a priori* biological hypotheses with the SURFACE method using data-driven algorithm.

3. Results

SURFACE found three body size optima: 1.04 (=11.1 cm TL for pygmy angelfishes), 1.31 (=20.6 cm TL for medium-sized species) and 1.60 (=40.2 cm TL for large-sized species), consistent with the observed size range of extant lineages (figure 1 and electronic supplementary material, figure S2). Ancestral state reconstruction suggested that small body size is a derived state (electronic supplementary material, appendix S2).

Phylogenetic regression revealed a non-significant linear association between body size and shape in Pomacanthidae ($F = 1.26$; $p = 0.11$; $R^2 = 0.49$). Most body shape variation (78%) occurred along the three first PC axes, which detected divergence in relative body height (PC1) and head shape (PC2 and PC3; figure 2). Taking Δ AICc > 4 as strong indication of support for the best model over other candidate models [19], the OUM_size model, allowing the three size categories to form around separate optimal body shapes, received most support whereas all other models performed relatively poorly (table 1). SURFACE results refined this pattern (AICc improved from −837 to −938), revealing three convergences on body shape in the small-sized *Centropyge* (figure 2).

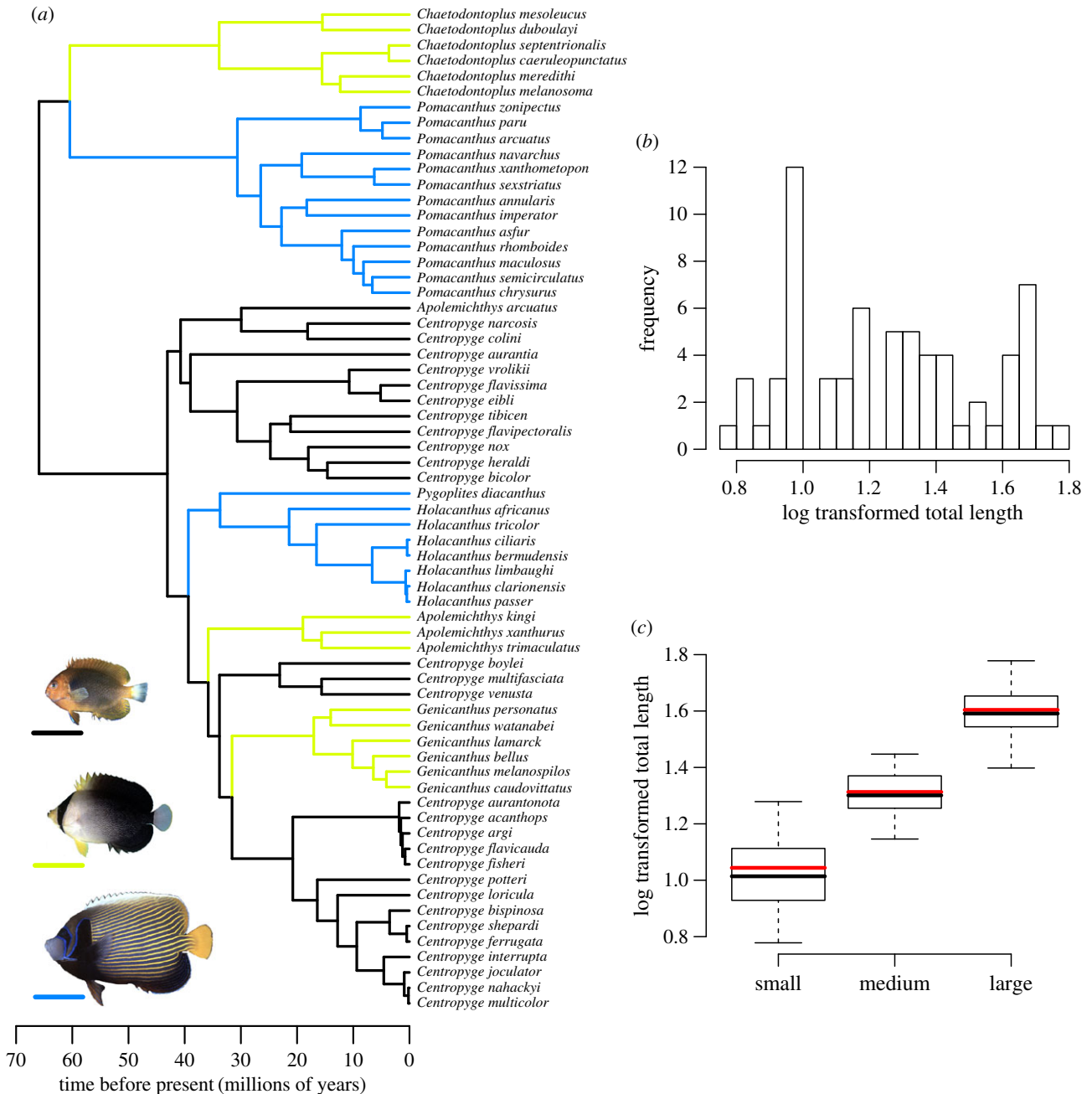


Figure 1. Body size diversification in Pomacanthidae. (a) Consensus time-tree illustrating three size regimes detected by SURFACE. (b) Log transformed body size for all pomacanthids. (c) Log transformed body size variation within each optimum detected by SURFACE. Red bars indicate optima and black bars indicate the mean value. Fish images modified under Creative Commons licence from original photographs by J. E. Randall (retrieved from <http://pbs.bishopmuseum.org/images/JER/>).

These pygmy angelfishes mainly differed from larger taxa by having a higher and more vertical forehead (+PC2; figure 2).

4. Discussion

We found support for three different optimal sizes in marine angelfishes. These adaptive peaks likely correspond to ecomorphs and there might be multiple underlying drivers for this observed pattern. Predatory avoidance and ecological specializations may have operated on angelfish size evolution. Most pygmy angelfishes (*Centropyge*) live cryptically in corals or coral rubble, whereas large-sized *Holacanthus* and *Pomacanthus* species defend wide home ranges around shelters [20]. Angelfishes obtain attached, benthic prey by biting (except the zooplanktivorous *Genicanthus*) and their size diversification is likely driven by biomechanical constraints related to prey

robustness: *Pomacanthus* feed on firmly attached, resilient invertebrates (e.g. sponges, tunicates), whereas pygmy angelfishes consume delicate foods (e.g. hydrozoans and filamentous algae) [21]. Bite force is positively related to head size among vertebrates [22], so it might be expected that specialization on robust prey may have selected for large size and powerful bite.

Evolutionary change in body size may be viewed as a key innovation that produces ecological opportunity and induces changes in the tempo and mode of phenotypic evolution [23]. We show that pomacanthid miniaturization induces repeated convergence on body shape (figure 2) rather than shifts in diversification rate, consistent with the idea that evolution towards small size acts as a morphological novelty that permits the colonization of new adaptive zones [23]. Convergent evolution upon similar body shapes in pygmy lineages suggests more severe requirements on small than on large size optima. Functional demands in small-sized angelfishes

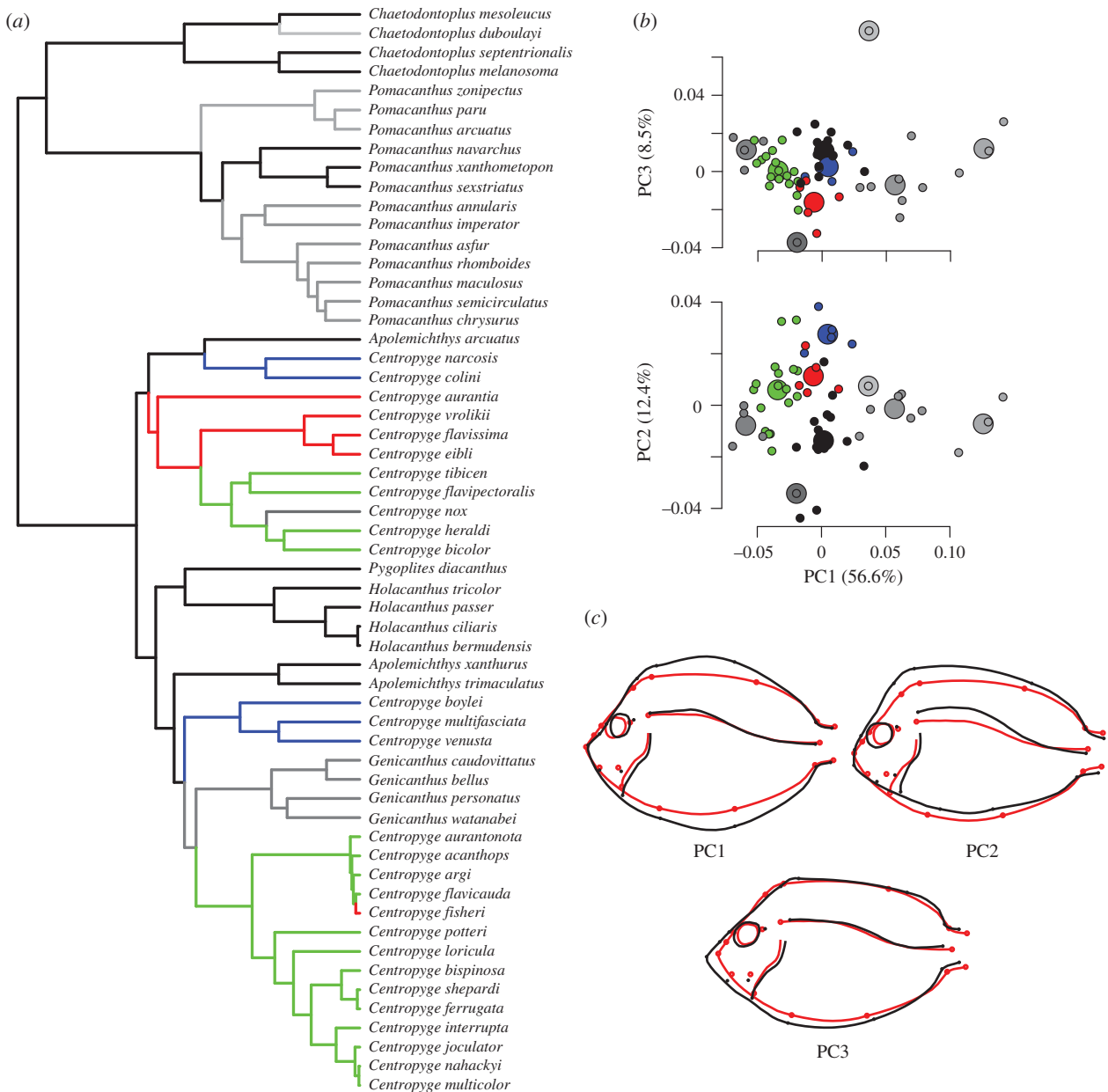


Figure 2. Pomacanthid body shape convergence on the macroevolutionary adaptive landscape. (a) Consensus phylogeny drawn to show body shape evolution based on SURFACE results. Convergent peaks are colour-mapped whereas non-convergent peaks are in grey-scale. (b) Morphospace constructed on principal component scores for shape variables illustrating species (small circles) and inferred adaptive peaks (large circles) from SURFACE. (c) Illustrations of shape variation along PC axes. Red (minimum) and black (maximum) curves illustrate shapes at the most extreme PC scores.

are probably related to habitat partitioning and predator avoidance [21]. The deeper anterior body part and higher head profile of *Centropyge* favour manoeuvrability in structurally complex habitats [11] and optimize feeding on benthic prey while maintaining visual awareness of predators [24].

Our results reveal a pattern of imperfect body shape convergence in pygmy angelfishes (figure 2), consistent with results from small frogs illustrating that numerous miniaturized lineages have not responded identically to reduced size [6]. Convergent ecomorphs may vary in behaviour, exploit a common resource or share habitat in different ways, and thus may have experienced selection on morphology differently [25]. Our data from marine angelfishes add to the growing evidence that morphological convergence can be imperfect even if similar selective demands operate on pygmy lineages.

Ethics. Experimental procedures were approved by the University of Liège Institutional Animal Care and Use Committee (protocol n 1154).

Data accessibility. Data supporting this article are available as electronic supplementary material and in the Dryad Digital Repository (Dryad: <http://dx.doi.org/10.5061/dryad.5br8k>) [26].

Authors' contributions. B.F. and M.E.A. conceived the study. B.F. performed research, analysed data and drafted the manuscript. F.S. and J.S. helped with phylogenetic analyses and comparative methods, respectively. N.K. and D.L. contributed raw data. All authors contributed to manuscript revisions, approved publication and agreed to be accountable for this work.

Competing interests. We declare we have no competing interests.

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