RESEARCH ARTICLE

Breaking constraints: The development and evolution of extreme fin morphology in the Bramidae

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Abstract

The developmental process establishes the foundation upon which natural selection may act. In that same sense, it is inundated with numerous constraints that work to limit the directions in which a phenotype may respond to selective pressures. Extreme phenotypes have been used in the past to identify tradeoffs and constraints and may aid in recognizing how alterations to the Baupläne can influence the trajectories of lineages. The Bramidae, a family of Scombriformes consisting of 20 extant species, are unique in that five species greatly deviate from the stout, ovaloid bodies that typify the bramids. The Ptericlinae, or fanfishes, are instead characterized by relatively elongated body plans and extreme modifications to their medial fins. Here, we explore the development of Bramidae morphologies and examine them through a phylogenetic lens to investigate the concepts of developmental and evolutionary constraints. Contrary to our predictions that the fanfishes had been constrained by inherited properties of an ancestral state, we find that the fanfishes exhibit both increased rates of trait evolution and differ substantially from the other bramids in their developmental trajectories. Conversely, the remaining bramid genera differ little, both among one another and in comparison, to the sister family Caristiidae. In all, our data suggest that the fanfishes have broken constraints, thereby allowing them to mitigate trade-offs on distinctive aspects of morphology.

KEYWORDS
Bramidae, comparative methods, geometric morphometrics, historical contingency, modularity

1 | INTRODUCTION

Development must be flexible enough to create variation upon which natural selection acts, but also rigid enough to limit the phenotype from deviating into a maladaptive space (Darwin, 1859; Huxley, 1942; Maynard Smith et al., 1985; Waddington, 1942, 1956; Wright, 1932). Systems that constrain, maintain, or promote phenotypic variation occur at numerous biological levels, including genetic (Crump et al., 2004; Swartz et al., 2012; Uller

et al., 2018), developmental (Cheverud, 1984; Green et al., 2017; Klingenberg, 2005; Uller et al., 2018; Wagner, 1988), behavioral (Holekamp et al., 2013), morphological (Evans et al., 2021; Larouche et al., 2018), physiological (Briffa & Sneddon, 2007; Glass, 2003), and evolutionary (Conway, 2003; Jacob, 1977; Pigliucci & Preston, 2004; Schwenk & Wagner, 2004). Constraints, however, regardless of their position in these various biological levels, can be broken (Galis & Metz, 2007; Minelli & Fusco, 2019). A consequence of breaking a constraint may include increased variability, which in turn may allow the population to fluctuate more freely in phenotypic space (McGhee, 2007; Sheftel et al., 2013), providing new variants for selection to act on.

As with most complex biological phenomena, constraints range from rigid and unbending, lest a lethal phenotype is expressed, to flexible, forgiving, and holistically adaptive (Jacob, 1977; Klingenberg, 2005; Wagner & Misof, 1993). Constraints may also be viewed on a different, but not mutually exclusive, spectrum from universal to local. In this view, universal constraints are a result of the laws of physics or the physical, chemical, or functional properties of a material (Jacob, 1977; Maynard Smith et al., 1985). Alternatively, local constraints are limited to some taxonomic level, such as the organization of a Bauplän (Maynard Smith et al., 1985), which result from biases in development that limit the variants that it can express (Cheverud, 1984; Emlen, 2000; Gould, 1980; Maynard Smith et al., 1985). Modularity of traits can affect evolution, limiting or facilitating, depending on the pattern/strength of modularity and the axis of selection upon which it acts by allowing particular traits to be modified to varying degrees without affecting surrounding traits (Larouche et al., 2018; Parsons et al., 2012; Schluter, 2000; Zelditch & Goswami, 2021). Thus, evolution requires a delicate balance between the generation of sufficient levels of variation for selection to act upon but limiting it enough so that function is not compromised (Pigliucci & Preston, 2004; Schwenk & Wagner, 2004). The history of evolutionary biology has largely been dominated by seeking out mechanisms that precipitate change. However, despite billions of years of evolution, there remain obvious lacunae in morphological space that can provide invaluable insights into the flip side of the evolutionary coin (Arnold, 1992; Gould & Lewontin, 1979; Gould, 1980; Holekamp et al., 2013; Maynard Smith et al., 1985; Schwenk & Wagner, 2004).

It is increasingly recognized that characterizing constraints inherent in developmental processes can contribute to a better understanding of evolutionary processes (Gould, 1980; Holekamp et al., 2013; Pigliucci & Preston, 2004; Schlichting & Pigliucci, 1998; Schwenk & Wagner, 2004). A notable challenge in doing so,

however, is differentiating constraints that are imposed by the developmental process from those that arise due to selection (Gould, 1980; Maynard Smith et al., 1985). This difficulty is further exacerbated due to the paradoxical nature of constraints, as constraints limit the phenotypes that natural selection may act upon, but they are themselves products of natural selection (Schwenk & Wagner, 2004). Nevertheless, routinely used methods for identifying developmental constraints include documenting evolutionary stasis over time, as well as identifying unoccupied regions of theoretical morphospace (Maynard Smith et al., 1985; Schwenk & Wagner, 2001, 2004; Spurway, 1949; Vavilov, 1922; Wagner & Schwenk, 2000). Further, it has been suggested that by comparing ontogenetic trajectories within a clade, one can garner evidence for developmental constraint, which has been predicted to manifest as parallel trajectories (Gould & Lewontin, 1979; Gould, 1980; Maynard Smith et al., 1985; Schwenk & Wagner, 2004).

The study of constraints can be assisted by examining "extreme" traits, because they are often the product of breaking one or more constraints and precipitating additional constraints. Such traits may therefore be viewed through the lens of trade-offs. For example, bats (Chiroptera), being the only extant mammals to have evolved powered flight, exhibit substantial constraints in body size (Jones, 1994; Moyers Arévalo et al., 2020). Other trade-offs in bats include those between the energetic demands associated with both echolocation and vision (Thiagavel et al., 2018). Similarly, beetle weaponry (i.e., horns and extreme mandibles) has evolved several times across the Coleoptera, and are generally used for male sparring (Emlen, 2000). The size of beetle mandibles and horns varies greatly, and can force trade-offs in other energetic systems, such as flight (Goyens et al., 2015), which ultimately constrains the weight such weaponry can attain. Beetle weaponry also influences the size at which eyes (Nijhout & Emlen, 1998), or wings (Kawano, 1997), can develop. While observations at adult stages can provide insights into trade-offs (e.g., negative correlations between traits), evaluating ontogenetic pathways can inform hypotheses as to *how* (mechanistically) specific traits are correlated with others (Emlen, 2000). Here, we aim to explore the ontogeny and evolution of an array of ecomorphological traits in a group of open water, marine fishes, in which an extreme morphology has evolved.

Bramidae, while modest in species diversity ($n = 20$), is a relatively understudied group of fishes that offer unique opportunities to investigate evolutionary constraints, and how the development of extreme morphologies can influence evolvability of other traits (Gilbert et al., 2021). The "fanfishes" refer to a bramid lineage, the

Pteraclinae, that includes two genera (*Pterycombus* and *Pteraclis*; Figure 1), characterized by an extreme exaggeration of the medial fins (Gilbert et al., 2021). Ontogenetic trajectories of select traits have been previously studied in this group (Mead, 1972), but data were unable to be interpreted through a phylogenetic lens, rendering hypotheses about evolutionary relationships and constraints untestable. Here, we expand on this previous work (e.g., Gilbert et al., 2021; Mead, 1972) by comparing anatomical divergence across the Bramidae at early and adult life-history stages in a phylogenetic context. Specifically, we will assess the degree to which the evolution of extreme fin morphologies has limited the evolution of other ecomorphological traits. We will first compare juvenile and adult morphospace with respect to patterns and magnitudes of variability. Similar morphospaces between juveniles and adults would demonstrate that species-specific bramid morphologies arise early in ontogeny, suggesting that constraints that determine body shape are acting on early developmental processes. Next, we will compare ontogenetic trajectories for specific traits among bramid taxa. Divergent (i.e., nonparallel) trajectories would suggest constraints arising later in development. Finally, we will compare rates of morphological evolution across the same functionally and ecologically relevant traits, to assess the degree to which any putative developmental constraints are associated with evolutionary patterns. Collectively, these results will provide insights into how an unusual trait, in this case, extreme exaggeration of the medial fins, has influenced the development and evolution of the Bramidae.

2 | MATERIALS AND METHODS

2.1 | Morphometric data acquisition

We collected specimens from the Harvard Museum of Comparative Zoology (MCZ) and Smithsonian National Museum of Natural History (NMNH) with additional larval samples from the MCZ, as well as numerous adult specimens from the National Museum of Nature and Science (NMNS) and the Australian Museum (AMS) that we could not have otherwise acquired in the United States. In total, our sampling covered all seven bramid genera for the adult analyses and six for the juvenile ($n = 163$, Supporting Information: Table 1).

Methods for acquiring both geometric morphometric data and linear measures are described in detail in Gilbert et al. (2021). In short, the left lateral surfaces of specimens were imaged and then digitized using STEREOMORPH (Olsen & Westneat, 2015) in R (R Core Team, 2018). The landmark scheme used was identical to that used in Gilbert et al. (2021) to cross reference results and expand on testable hypotheses concerning the evolution of the Bramidae (Supporting Information: Figure 1). Raw landmark were subjected to generalized Procrustes analyses before statistical comparisons (GPA; Boas, 1905; Goodall, 1991; Sneath, 1967) and then the aligned data were subjected to numerous statistical tests. Linear measures were then taken on anatomical units of interest using those same two-dimensional images through MorphoJ (Klingenberg, 2011).

2.2 | Analysis of developmental trajectories

To assess differences in shape trajectories throughout ontogeny, we used geometric morphometric methods designed to assess changes in phenotypes and compare differences among group phenotype trajectories (Collyer & Adams, 2013; Collyer et al., 2015). While we were able to perform this analysis with previously published data, the current and much-expanded data set included the addition of numerous difficult to acquire specimens (e.g., genus *Pteraclis*), allowing for a much deeper and holistic dive into the nuances of bramid shape trajectories. Differences in trajectories among genera were quantified

FIGURE 1 Digital photographs of representatives of *Ptericlis aesticola* (AMS I.43350-001; left) and *Taractichthys steindachneri* (AMS I. 34633-001; right). *Source*: Photographs taken by Kerryn Parkinson at the Australian Museum, Sydney (AMS).

using the trajectory.analysis function (Collyer & Adams, 2013; Collyer et al., 2015) in GEOMORPH v3.3.6 (Adams et al., 2015, 2018). This function utilizes analysis of variance (ANOVA) and an RRPP v0.4.1 (randomized residual permutation procedure; Collyer & Adams, 2018) to calculate differences in trajectory path distances. Our final ANOVA model (Shape ~ Genus * Stage ~ Size) used genus and developmental stage, as well as the interaction between genus and developmental stage, as a factor against shape and included size as a covariate. The residuals of the ANOVA model were then subjected to a total of 10,000 random permutations. To visualize the degree of morphological change from the juvenile to adult stages in all genera, we plotted the first two axes of a principal component analysis (PCA) of all genera across the two stages of development.

2.3 | Phylogenetic comparative methods

By pruning the tree created by Gilbert et al. (2021), we produced two smaller trees, one to include genera available in juvenile data set and another that would include all seven bramid genera and a representative of the closely related sister taxa from Caristiidae, *Caristius*. These two topologies served as the foundation for subsequent comparative analyses for both linear measures and geometric morphometric data and allowed us to assess trends in both the juvenile and adult data sets independently for when genera were not available for both (e.g., *Xenobrama*). For more details, see Gilbert et al. (2021).

To create a phylomorphospace for both the juvenile and adult data sets, we utilized both GEOMORPH v3.3.6 (Adams et al., 2014, 2018) and PHYTOOLS v0.6-60 (Revell, 2012) to map principal component data derived from morphology to the associated phylogenetic relationships. We then calculated mean PC1 and PC2 scores for whole body shape morphology, independently in both adults and juveniles to determine rates of body shape evolution in both stages. This was accomplished using the Bayesian analysis of macroevolutionary mixtures (BAMM) software package (Rabosky, 2014; Rabosky, Grundler, et al., 2014). Each analysis utilized four reversible MCMC simulations for 1×10^7 generations with sampling occurring every 1000 generations. Prior distributions were estimated via BAMMtools (Rabosky, Grundler, et al., 2014) in R (R Core Team, 2018). This was repeated for both PC1 and PC2 means for the juveniles (βInitPrior = 1506.443 and 2401.617, βShift-Prior = .020 and 0.020) and adults (βInitPrior = 419.192 and 2399.823, βShiftPrior = 0.020 and 0.020). BAMMtools (Rabosky, Grundler, et al., 2014) was then used to analyze outputs.

2.4 | Linear measures

In total, we regressed against standard length the linear measurements of nine traits that we predicted would be constrained or directly altered by extreme medial fin morphology to calculate the phenotypic trajectories of each trait across and among the genera. Using the package emmeans (Lenth, 2020) in R (R Core Team, 2018), we then tested for differences in slopes between genera for each of the nine traits of interest. The R package lattice v0.20-35 (Sarkar, 2017) was then used to map the resulting p-values in a visually representative way to observe instances of significance. Due to our inability to acquire juvenile *Xenobrama* specimens, *Xenobrama* data were excluded from these analyses.

Lastly, we wanted to determine if noticeable differences in evolutionary rates across the nine traits were detectable in the adult data set. To this end, we utilized the same methods in the previous section to assess evolutionary rates in PC1 and PC2 scores by first calculating mean ratios of each trait against standard length. Using those mean ratios, we used BAMM (Rabosky, 2014; Rabosky, Grundler, et al., 2014) to calculate rates of trait evolution across the Bramidae, each implementing 1×10^7 generations and sampling once every 1000 generations. Prior distributions for each of the nine traits were determined via BAMMtools (Rabosky, Grundler, et al., 2014). Priors were as follows: anal fin length (βInitPrior = 407.215, βShiftPrior = 0.020), body depth (βInitPrior = 1391.950, βShiftPrior = 0.020), breast length (βInitPrior = 8264.754, βShift-Prior = 0.020), dorsal fin length (βInitPrior = 340.709, βShiftPrior = 0.020), head length (βInitPrior = 2615.804, βShiftPrior = 0.020), lower jaw length (βInitPrior = 9972.032, βShiftPrior = 0.020), nape length (βInitPrior = 1002.481, βShiftPrior = 0.020), orbit diameter (βInit-Prior = 53675.542, βShiftPrior = 0.020), pelvic to anal fin length (βInitPrior = 2129.310, βShiftPrior = 0.020). BAMMtools (Rabosky, Grundler, et al., 2014) was used to analyze outputs. We then quantified differences in evolutionary rates between the fanfishes and remaining bramids for all nine linear measures. To accomplish this, we calculated the Brownian rate of evolution (σ^2) for all traits under a null model that fixed the rate across the tree and compared this to a model that allowed the fanfishes to exhibit a different rate of trait evolution to the remaining bramids. We statistically assessed differences in log-likelihood scores between the single and multigroup models via a χ^2 test (O'Meara et al., 2006). To compare rates we used the brownie.lite function from the R package phytools v0.6-60 (Revell, 2012), and gained a distribution of output parameters by running the analysis over a previously generated posterior distribution of 1000

phylogenetic trees (Gilbert et al., 2021) to account for phylogenetic uncertainty. To assign taxa to bramid and fanfish groups we used the Stochastic Mutational Mapping on Phylogenies (SIMMAP) tool (Bollback, 2006) from phytools and simulated one map for each of the 1000 trees. We illustrate the distribution of σ^2 parameters as a violin plot and report the median values given their skewed distributions.

3 | RESULTS

3.1 | Differences in whole body shape morphology are detectable during early stages of ontogeny and largely mirror adult patterns

We initially sought to assess and compare patterns of shape variation in juvenile and adult bramids. For juveniles, size ($Z = 4.631$, $p \le .0001$), genus ($Z = 7.536$, $p \le .0001$), and the size:genus interaction ($Z = 4.231$, $p \le .0001$) were significant. While size explained a substantial percentage of the variation ($R^2 = .162$), it explained much less than the effect of genus ($R^2 = .497$). The interaction term explained the least amount of variation ($R^2 = .043$). For the adults, a similar pattern was

revealed, with size ($Z = 5.183$, $p \le .0001$), genus ($Z = 8.964$, $p \le .0001$), and the interaction ($Z = 6.263$, $p \le .0001$) being significant, genus ($R^2 = .724$) also had greater explanatory power than size alone ($R^2 = .122$). Like juveniles, the interaction term was the weakest for adults ($R^2 = .018$).

Subsequent pairwise comparisons of juvenile shape data across genera revealed that 15/21 comparisons were significantly different (Table 1). All comparisons to the fanfishes, *Pterycombus* and *Pteraclis*, were significantly different (including to one another; $p = .005$) and all but one comparison to the sister group, *Caristius*, was significant (comparison with *Brama*; $p = .236$). The greatest differences in morphological shape were always between the fanfishes and the other bramids, with the comparison between *Pteraclis* and *Taractes* being the most substantial ($Z = 8.458$). With the adult data, we found a comparable number of significant comparisons, at 13/21 (Table 1). Like the juvenile data, all comparisons to fanfishes were significant, apart from the comparison between *Pterycombus* and *Caristius* ($p = .065$), and the strongest morphological differences (based on Z-scores) were found in the comparisons with *Pteraclis*, with the most notable comparisons being against *Taractichthys* ($Z = 14.397$), *Brama* ($Z = 13.263$), and *Taractes* ($Z = 13.710$). Unlike the juvenile data, however, only 1/6 comparisons were significant with

TABLE 1 Results of procrustes MANOVA across all bramid juveniles (above) and adults (below).

	Brama	Caristius	Eumegistus	Pteraclis	Pterycombus	Taractes	Taractichthys
Juveniles							
Brama		**2.7059**	−.4984	**7.2863**	**5.9423**	**1.8385**	.4412
Caristius	**.0139**		.64802	**2.7324**	**2.1407**	**2.7261**	**2.0124**
Eumegistus	.6400	.2362		**4.10256**	**2.3850**	.0659	−.5665
Pteraclis	**.0001**	**.0150**	**.0002**		**3.4702**	**8.4578**	**7.7505**
Pterycombus	**.0002**	**.0382**	**.0280**	**.0050**		**7.8091**	**6.3575**
Taractes	.0585	**.0130**	.4057	**.0001**	**.0001**		−.0455
Taractichthys	.2738	**.0459**	.6724	**.0001**	**.0001**	.4413	
Adults							
Brama		1.0114	−.0109	**13.2629**	**5.7131**	**3.6393**	**2.4933**
Caristius	.0716		.3642	**3.2191**	1.4545	1.0068	.9614
Eumegistus	.3321	.2121		**5.8061**	**2.6351**	.0534	.3484
Pteraclis	**.0001**	**.0236**	**.0011**		**3.2501**	**13.7096**	**14.9737**
Pterycombus	**.0003**	.0646	**.0277**	**.0087**		**5.9612**	**5.9631**
Taractes	**.0051**	.0763	.3182	**.0001**	**.0001**		**4.4957**
Taractichthys	**.0245**	.0759	.2080	**.0001**	**.0003**	**.0018**	

Note: MANOVA was conducted with 10,000 permutations of residual values (randomized residual permutation procedure [RRPP]). Effect sizes (z-scores) are above, and p values are below the diagonal. Bolded p values and z scores indicate significant differences in mean shapes between species. For significance testing, $\alpha = .05$.

Caristius, suggesting that bramid shape diverged from that of its sister taxon over ontogeny. However, given that we only have a single specimen for juvenile and adult *Caristius* data, we are limited in what can be confidently said regarding comparisons to the outgroup.

To summarize, body shape differences between the genera are detectable at the early stages, a trend that is followed by the adult sample population. These statistics suggest that constraints acting on body shape in the Bramidae are acting early in the developmental process.

3.2 | Patterns of morphological variation are similar between juvenile and adult stages

We next wanted to see if patterns of morphological variation held between early and late ontogenetic windows in a phylogenetic context. To this end, we conducted a PCA of both juvenile and adult body shapes, which revealed that much of the variation, at both stages, was limited to the first two axes (PC1 55.1/71.6%, PC2 12.2/15.3%—juveniles and adults, respectively; Figure 2a,b). These PC scores were then utilized for two purposes. First, to estimate rates of whole-body shape evolution across the Bramidae, and

second, to qualitatively assess distribution of genera in a phylomorphospace.

For PC1, rates of body shape evolution across taxa were similar between stages (Figure 2a), with relatively higher rates of morphological evolution observed in the fanfishes and *Caristius* compared to other lineages; however, the difference in rates between adult fanfishes (notably *Pteraclis*) and the other bramids was an order of magnitude higher in adults than juveniles, which indicates that divergent body shapes in fanfishes are elaborated over ontogeny. For PC2, rates of body shape evolution across taxa were distinct between stages. Among juveniles, rates of morphological evolution were relatively low and similar across bramid species. The one exception to this being *Caristius*, which showed a greatly elevated rate of morphological evolution. In adults, PC2 rates were higher in adult fanfishes, specifically *Pterycombus*, compared to most other bramids, which is similar to what was observed for PC1. Unlike PC1 rates, however, the difference in PC2 between fanfishes and other bramid genera was not as striking. Given the Bramidae comprise a relatively small number of genera, uncovering the evolutionary processes that produced the distribution of our trait data is challenging, and difficult to infer from rate data alone. Recent assessments into the sensitivity of the Ornstein–Uhlenbeck
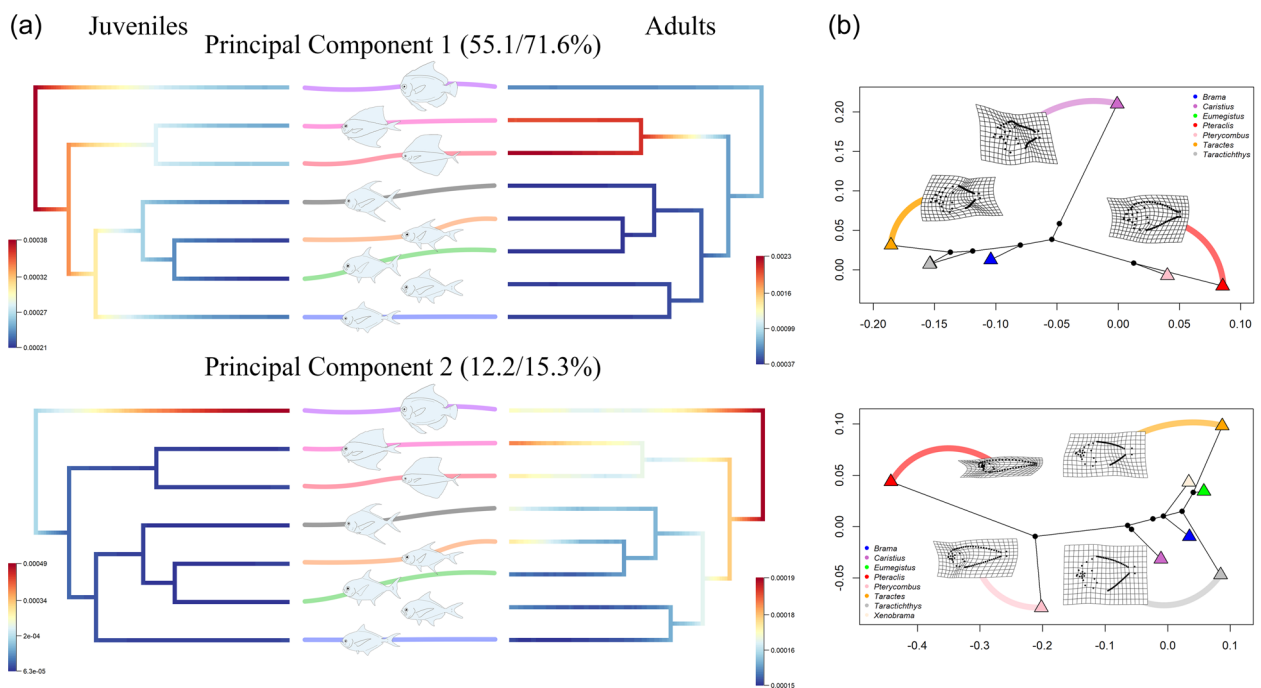
FIGURE 2 (a) Left column portrays the juvenile rates across the phylogeny and are aligned with corresponding adult rates on the phylogeny to the right. Curved, colored lines connect the two sides and colors are representative of the genera throughout the manuscript. Genera read, from top to bottom, *Caristius, Pterycombus, Pteraclis, Taractichthys, Taractes, Eumegistus, Xenobrama* (not present in juvenile analyses), and *Brama*. Warm colors represent faster rates of morphological evolution while cool colors represent slower. (b) Phylomorphospace of whole-body shape morphology and the transition of morphospace through ontogeny. Deformation grids are provided for the extremes. Triangles represent overall group means.

evolutionary model has demonstrated that low sample size (<200 tips) can result in an increase in the Type I error rate (Cooper et al., 2016). Similarly, simulation studies have found an increased propensity for traits to look like they follow Early Burst (EB) models of evolution when surveying at lower taxonomic levels (Harmon et al., 2010), yet when sampling is expanded, the EB trend disappears and rate heterogeneity is observed across the tree (Puttick, 2018). Lastly, others have found that quantifying evolutionary rates by using the initial principal component axes can bias the results to mirror an EB evolutionary model (Uyeda et al., 2015). We, therefore, urge caution in these interpretations and refer to our previous paper (Gilbert et al., 2021) for other results supporting an EB model.

The distribution of bramid genera across morphospace showed a clear phylogenetic signal for both juveniles and adults (Figure 2b). In both instances, the major axis of variation (i.e., PC1) described difference in medial fin length, and separated fanfishes from the other bramids, with the sister group, *Caristius*, occupying an intermediate position. As juveniles, bramid species exhibited little variation along PC2, and this axis separated bramids from their sister group, *Caristius*, a pattern that is reflected in estimates of evolutionary rates (Figure 1a). As adults, genera became more disparately distributed throughout morphospace, especially along PC2, which described variation in body depth, with *Taractes* and *Tarachtichthys* showing extreme shapes along PC2.

3.3 | The fanfishes exhibit divergent ontogenetic trajectories in body shape

We next combined the juvenile and adult data sets to compare the phenotypic trajectories of each genus. The results of pairwise comparisons of trajectory path

distances revealed that *Pteraclis* had a significantly greater distance (|0.2466|) than any other genera, except the sister group, *Caristius* (|0.1751|; Table 2). Of the bramids, *Pteraclis* exhibited twice the distance as any other genus, with *Pterycombus* and *Taractichthys* exhibiting the second greatest distances (|0.1266| and |0.1261|, respectively). The greatest difference in distance was between *Pteraclis* and *Taractes* ($Z = 7.2094$), with the comparison between *Pteraclis* and *Brama* being close behind ($Z = 6.9291$). Despite exhibiting the second greatest distance in morphospace, *Caristius'* ontogenetic trajectory was not significantly different from any bramid genus, likely due to very low sample size.

We next wanted to visualize these genera-specific developmental trends in morphospace. Using the first two PC scores from a PCA, we plotted the juvenile and adult specimens, along with their general trajectories, in morphospace (Figure 3). Juvenile morphologies, while separate in morphospace, generally occupied the upper right quadrant. In many instances, juvenile morphologies overlapped with one another and with the regions of morphospace occupied by certain adults. While differences in paths can be observed between many genera, path distance in *Pteraclis* was clearly distinct, moving from the upper right to bottom left of morphospace. The other fanfish genus, *Pterycombus*, exhibited a similar path toward the bottom left of morphospace, albeit to a lesser extent relative to *Pteraclis*. Consistent with previous observations (i.e., Figure 2b), *Caristius* moved from a fanfish region of shape-space at the juvenile stage, towards a generalized bramid phenotype at the adult stage.

In summary, these results further support that the early parsing of morphospace in juveniles sets the foundation for a stark divergence in the overall adult body plan for bramids that possess exaggerated dorsal fins.

TABLE 2 Pairwise comparisons of trajectory path distances from trajectory.analysis

	Brama	*Caristius*	*Eumegistus*	*Pteraclis*	*Pterycombus*	*Taractes*	*Taractichthys*
Brama		.4476	−.6371	**6.9291**	**1.4562**	−.6045	.8271
Caristius	.2221		.1629	.3577	−.3468	.3592	−.1183
Eumegistus	.7303	.2983		**1.9509**	−.8960	−.7594	−.6846
Pteraclis	**.0001**	.2311	**.0404**		**4.1031**	**7.2094**	**5.0424**
Pterycombus	**.0889**	.5759	.869	**.0010**		.4189	−1.1508
Taractes	.6734	.2455	.8153	**.0001**	.2715		.3712
Taractichthys	.1614	.4291	.7663	**.0008**	.9830	.2631	
Absolute distances	.0873	.1751	.1101	.2466	.1266	.0971	.1261

Note: MANOVA was conducted with 10,000 permutations of residual values (randomized residual permutation procedure [RRPP]). Effect sizes are above, and p values are below the diagonal. Bolded p values and z scores indicate significant differences in mean shapes between species. For the purpose of significance testing, $\alpha = .05$.
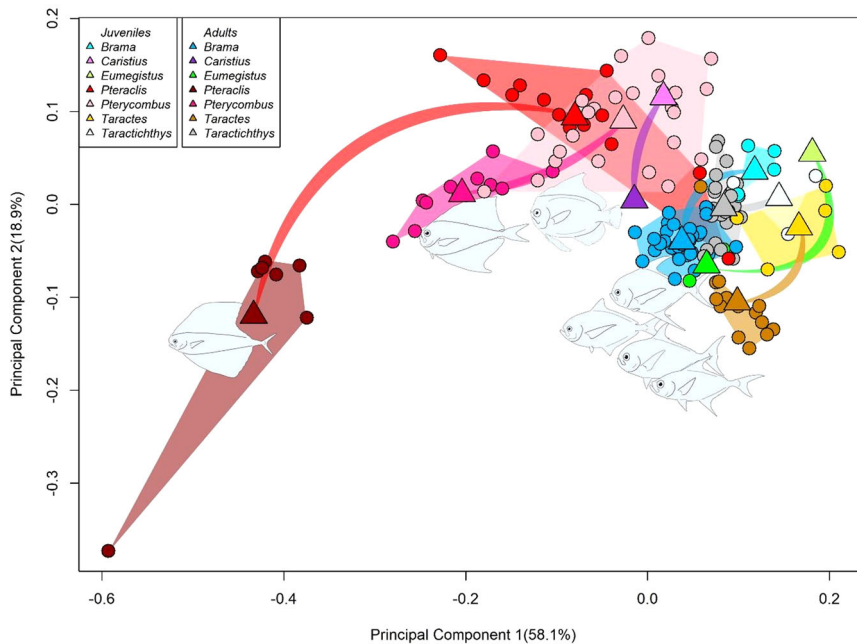
3.4 | Fanfishes exhibit unique ontogenetic trajectories for specific traits

We next compared specific, ecologically relevant, aspects of morphology. Nine linear measures were regressed against standard length, and we conducted an ANOVA to test for differences in slopes between genera (Figure 4). We found few significant differences in slopes for cranial traits, including lower jaw length, breast length, orbit diameter, or head length. The significant differences in slopes that occurred within these four traits were generally limited to comparisons that involved the fanfish, *Pteraclis*. The change in these traits appears to be constrained across the Bramidae. Orbit diameter is particularly interesting as the only significant difference was between the two fanfish genera, which exhibited the smallest (*Pteraclis*) and largest (*Pterycombus*) orbits (S2). Thus, while orbit size may be constrained among most bramids, it appears to be more variable in fanfishes.

Analyses of the other five traits (body depth, dorsal fin length, pelvic to anal fin length, nape, and anal fin length) revealed several pairwise differences in the slopes of nonfanfish bramids; however, one or both fanfish genera exhibited statistically distinct trajectories for all these traits. Taken together, these patterns document divergent growth of several traits within the fanfishes compared to other bramid lineages.

To summarize, the majority of bramid taxa express ontogenetic trajectories that are parallel to one another, suggesting that constraints are present and likely exist from some ancestral state. However, the fanfishes routinely differ from all other bramids, having very different ontogenetic trajectories across 6/9 trait comparisons. The statistics from these data suggest that the Ptericlinae have broken a, or a series of, biological constraints that have allowed them to deviate away from their bramid relative into a novel region of phenotypic space.

3.5 | Fanfishes exhibit increased rates of trait evolution in medial fin morphology and other traits

We previously reported that fanfishes experienced rates of whole-body shape (a highly multivariate trait) evolution ~2.9 times faster than their bramid relatives (Gilbert et al., 2021). Given that numerous univariate traits appeared to differ in ontogenetic trajectory across the family (Figure 4), and especially between fanfishes and other bramids, we wanted to test whether evolutionary rates across those same traits had experienced divergent rates of morphological evolution. Across the nine traits of interest, we found that only four did not differ between the two clades. Using median values for comparison (Figure 5), our analyses showed greater rates of trait evolution in the fanfishes for lower jaw length ($p = .009$), orbit diameter ($p = .004$), dorsal fin length ($p = .002$), nape (premaxilla to dorsal fin insertion; $p = .002$), and anal fin length ($p = .009$). While no significant differences in breast, pelvic to anal fin distance, body depth, and head length were detected, they were trending in the same direction with fanfishes exhibiting greater rates on average.
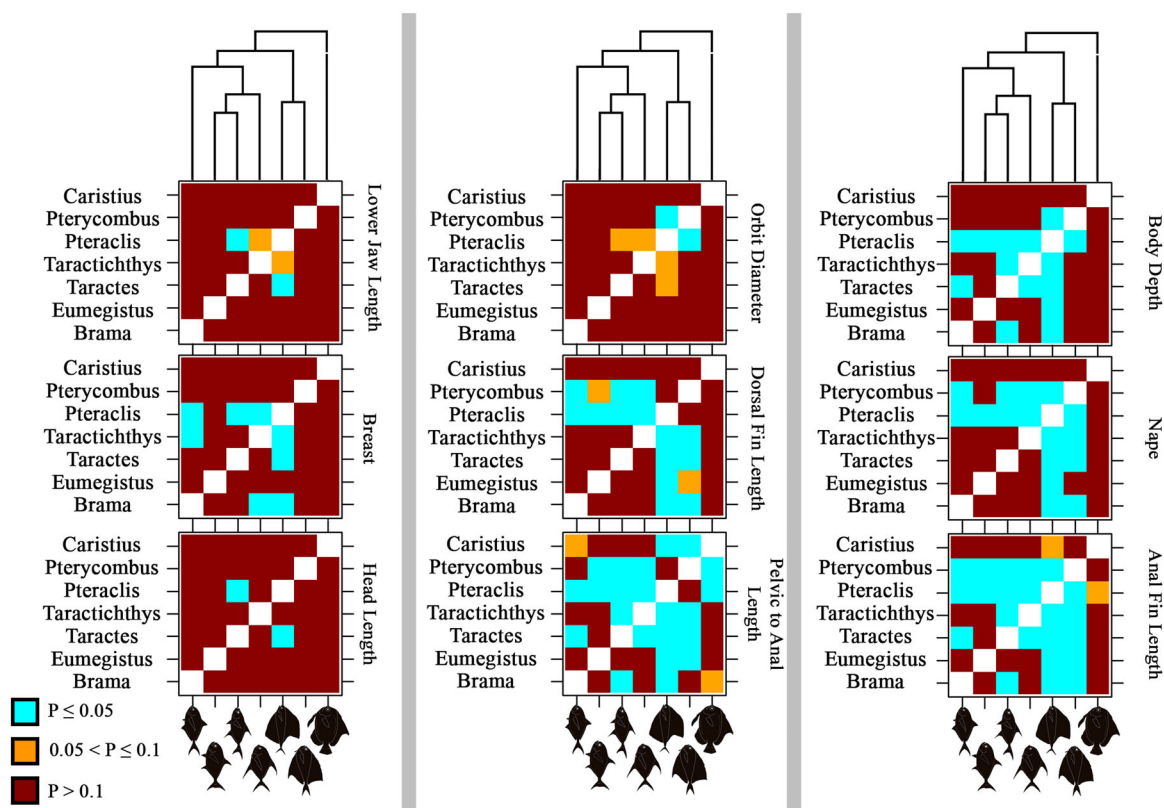
FIGURE 4 Pairwise matrix of *p* values illustrating significant differences in slopes between and among genera. Genera are ordered to reflect the branching order of the phylogeny depicted above, and a phylogenetic tree demonstrates evolutionary relationships at the top of each column. Typical body shape morphologies are found at the base of each column and are phylogenetically ordered. The white diagonal represents comparisons with self and a *p* value of 1. Significant comparisons are cyan, borderline significant comparisons are orange, insignificant comparisons are dark red.

In summary, fanfishes exhibit greater rates of morphological evolution than the other bramids. While these rates of evolution do not consistently track with degrees of morphological shape change, a small group like the Bramidae could create biases in the interpretation of these statistics. Therefore, we recommend caution in interpretations from data sets that contain few tips, such as ours.

4 | DISCUSSION

The evolution of extreme morphologies often involves the breaking of one or more constraints, but at the same time their integration into developmental systems can lead to new, or bolster other undefined, constraints. Fanfishes possess exceptionally exaggerated medial fins, as well as many associated putative adaptations to accommodate this structure (Gilbert et al., 2021). In this paper, we sought to assess the degree to which the evolution of elaborated medial fins may constrain morphological variability in other traits within the bramid lineage.

4.1 | Did the ancestral state of elaborated dorsal fins constrain the evolution of cranial traits in bramids?

In a previous paper, we showed that exaggerated dorsal fin morphology is likely ancestral in bramids and described changes in the skull of fanfishes that likely arose to support this structure. Specifically, we reported substantial decreases in supraoccipital crest size in the Pteraclinae (Gilbert et al., 2021), a region that had become fully occupied by a deep groove, providing an area for the attachment of associated dorsal fin musculature and architecture. Given that the mechanical space available to any given trait is limited and that the supraoccipital crest is an important craniofacial element required for adequate suction feeding (Camp & Brainerd, 2014; Carroll et al., 2004), we posited that the evolution of an exaggerated dorsal fin had constrained feeding ecology across the Bramidae by influencing other crucial anatomical elements. Our work here supports this assertion by showing that most cranial (and some postcranial) traits exhibit parallel developmental trajectories across the
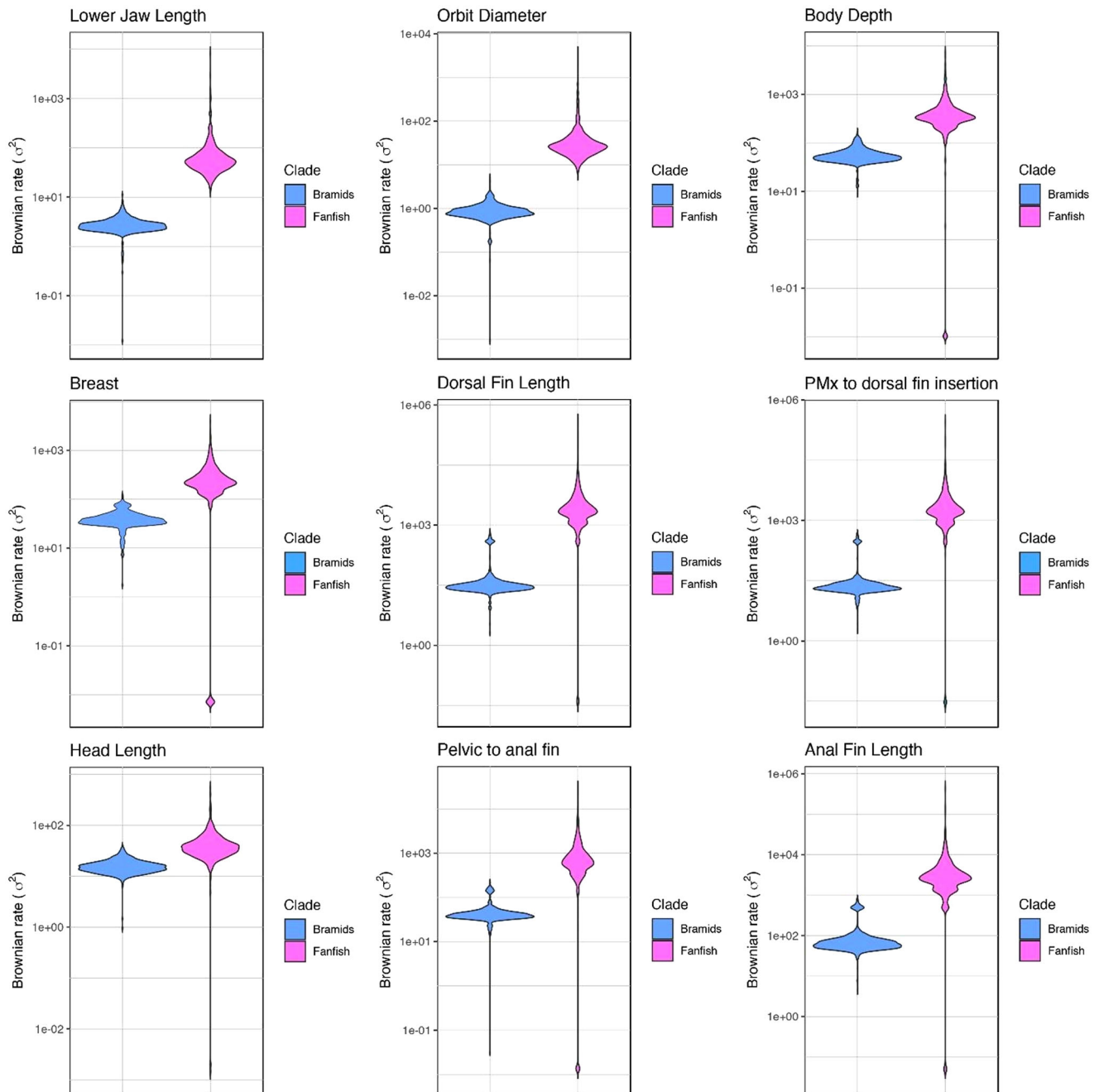
FIGURE 5 Violin plots depicting Brownian rate of morphological evolution of various traits in the Bramidae, comparing the morphologically distinct Ptericlinae to the remaining bramids.

Bramidae. When differences were noted, they were largely between the fanfishes and other members of the Bramidae (Figure 4; Supporting Information: Figures 2 and 3). However, some notable exceptions were also observed. For instance, *Pteraclis* and *Taractes* are the only two bramids that differed in ontogenetic trajectories for both head length and lower jaw length, with *Pteraclis* possessing the shortest jaws/head length and *Taractes* possessing the longest. In addition, the fanfishes occupied both extremes when concerning eye size, with *Pteraclis*

possessing the smallest relative eye size and *Pterycombus* possessing the largest. Differences in eye diameter could be attributed to differences in visual acuity and ecological pressures (Beston & Walsh, 2019; Caves et al., 2017, 2018; Jarvis & Wathes, 2012), and this pattern may hint at undescribed ecological differences between these sister taxa; however, without more formalized tests (Holladay, 1997; Landgren et al., 2014; Moseley & Jones, 1993), any conclusions along these lines would be premature.

Contrary to our predictions, the rate of craniofacial evolution was typically higher in the fanfishes. Lower jaw length and orbit diameter exhibited elevated rates in the fanfish, while head length was comparable across the Bramidae. This could be attributed to the clear differences in body and head morphology between *Pteraclis* and *Pterycombus*. Many ontogenetic trends throughout the Bramidae are similar, with little deviation across the bramid genera. However, the fanfishes have unique ontogenetic trajectories which tend to correlate with their higher rates of morphological evolution. Given that the other genera have overwhelmingly lower rates of morphological evolution across these ontogenetic trends, it is possible that the fanfishes have broken numerous constraints to further exaggerate their Baupläne, leaving the other bramids constrained.

4.2 | Breaking constraints to extend medial fins

Constraints have been shown to be one of the many ways development can influence evolution (Cheverud, 1984; Conith et al., 2019, 2021; Hallgrimsson et al., 2009; Hendrikse & Parsons, 2007; Waddington, 1942). Darwin (1859) noted that increased phenotypic variability during early developmental stages would increase the likelihood of maladaptive outcomes, suggesting that constraints exist to canalize the developmental phenotype during these critical early stages. While this has received increasing attention since the modern incarnation of evo-devo (Raff, 2000), it remains difficult to pinpoint when phenotypic constraints act during development (Cheverud, 1984). Regarding difficult to acquire taxa such as the Bramidae, this question becomes increasingly challenging to answer. While bramid embryos are absent from museum collections, juveniles have been collected across various life stages, providing an opportunity to evaluate differences in morphological traits over ontogeny and reveal stages where variability is more or less constrained.

Here, we report significant shape differences across juvenile bramids, ultimately seeing that morphospace is parsed into three regions, and while shape differences among taxa were relatively small, the pattern was largely similar as that in adults, especially for PC1. At both stages PC1 separates fanfishes from other bramids, with the sister taxon, *Caristius*, occupying an intermediate position. Thus, evolution within the bramid stem lineage may have involved the bending, or breaking, of some constraint, resulting in divergence between the two bramid lineages. We speculate that this involved conformational changes in several organ systems to accommodate greatly expanded insertions of both medial fins—dorsal and anal.

A general trend among bramids is that medial fins are symmetrically positioned along the dorsal–ventral axis, whether elaborated (as in fanfishes) or not (as in nonfanfishes). Notably, however, medial fin placement is asymmetric in *Caristius*, with the dorsal fin extending anteriorly relative to the anal fin. If this represents the ancestral condition, then the evolution of nonfanfishes involved a loss of dorsal fin elongation, whereas in fanfishes the anal fin was elongated to match the positioning of the dorsal fin. We note that the anterior extension of the dorsal fin in fanfishes is more extreme than that in *Caristius* and extends well into the anterior region of the neurocranium. We have described this unique morphology previously (Gilbert et al., 2021), and suggest that this marks one constraint that needed to be overcome in fanfishes—that is, the extension of postcranial skeletal structures onto the cranium.

The anterior position of the anal fin is likely to be under even greater constraint, as it is limited by the positioning of the vent. Extending the anal fin anteriorly requires not only an elaboration of the fin skeleton, but also a reconfiguration of the coelom, digestive, and reproductive organs. That fanfishes were able to circumvent this constraint is significant, and when combined with modifications to the skull to accommodate the extreme anterior extension of the dorsal fin (e.g., up to the naris in *Pteraclis*) speaks to the truly unique Bauplän of this lineage. A timeline of this hypothesis can be seen in Figure 6.

4.3 | The evolution of extreme fin morphology via modular fin development

The evolutionary success of teleosts has been credited to a flexible body plan, possibly facilitated by whole-genome duplication events that have provided the genetic raw material for greater complexity to evolve. Relevant to this study, it has been repeatedly suggested that modular fin architecture can result in a complex array of fin morphologies, as multiple fin "subunits" can evolve independently (Larouche et al., 2015, 2017, 2018; Mabee et al., 2002). Medial fins are hypothesized to have evolved before paired fins, roughly 400 million years ago (Coates, 1994), and have since evolved a variety of functions, including locomotion/maneuverability (Breder, 1926; Loofbourrow, 2006; Standen & Lauder, 2005), herding prey (Domenici et al., 2014), and advertising intentions (Allen & Nicoletto, 1997). Modularity can also be observed within medial fins, for example, between hard spines and soft fin-ray elements. The evolvability of medial fins is speculated to be the product of the duplication or deletion, as well as the coupling and decoupling, of various fin modules (Mabee et al., 2002), but
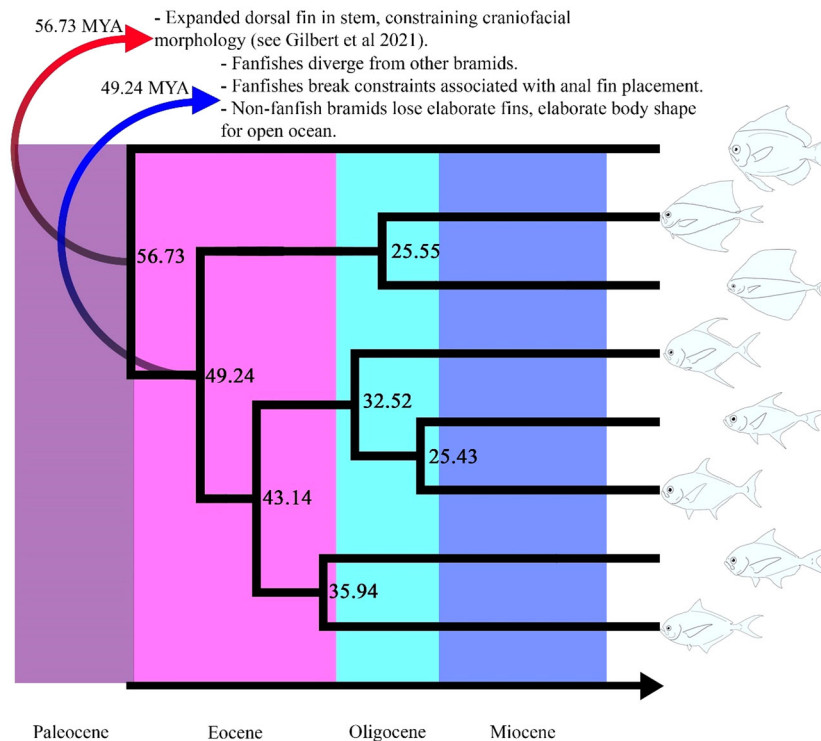
FIGURE 6 End of the Paleocene, 56.73MYA (red arrow): expanded dorsal fins are ancestral in the bramid stem with putative constraints on head/feeding morphology (Gilbert et al., 2021). Early Eocene, 49.24MYA (blue arrow); (1) nonfanfish bramids lose expanded dorsal fins, instead elaborating body shape for open water speed/ram-feeding, (2) fanfishes break constraints associated with anal fin placement and further extend the dorsal fin onto cranium, leading to rapid evolution of fin-insert size, but retain generally low rates of evolution in feeding morphology (e.g., jaw length, orbit size). Thus, all bramids retain largely open-water feeding morphologies (i.e., ram-feeding), possibly due an ancestral constraint. Nonfanfishes exhibit little anatomical diversification; however, fanfishes have broken one or more developmental constraints leading to the evolution of exaggerated medial fins, as well as a series of musculoskeletal changes to accommodate them (e.g., reduced neurocranial mineralization, Gilbert et al., 2021).

many questions remain open. For example, it has been hypothesized that the evolution of taxa possessing multiple dorsal fins, such as a typical scombriform representative (e.g., mackerel, tuna), is due to a duplication of a soft dorsal fin module (Mabee et al., 2002). Alternatively, it has been proposed that the origin of multiple dorsal fins stem from a more elongated fin becoming partitioned and divided (Sandon, 1956; Stewart et al., 2019). Further, it has been proposed, but not tested, that fishes characterized by continuous medial fins and an absence of spines, is due to the secondary loss of regional specification within fins (Mabee, 2002; Wagner, 1996).

What is unique about the bramid/caristiid clade is the apparent difference in medial fin placement between these two lineages, with bramids exhibiting symmetric placement of dorsal and anal fins relative to caristiids. This pattern is supported by ontogenetic data presented here (Supporting Information: Figure 4) that show disproportionately sized medial fins in Caristiidae, but relatively symmetrical fins in the Bramidae. The ancestral condition may be one where dorsal and anal fins are decoupled, which provided flexibility in the stem lineages

to evolve different fin patterns, increasing disparity in the family. Whether the coupling of medial fin growth in bramids is underlain by a coupling of developmental/genetic or ecological mechanisms remains an interesting yet open question. Further, comparing the patterns observed in Bramidae to other fish lineages that show similar patterns of extreme morphological evolution in medial fins (e.g., *Regalecus*, *Velifer*, and *Lampris*; Lampriformes) with clear phylogenies (Davesne et al., 2016; Olney, 1984) are needed. Previous hypotheses for such taxa have been proposed (Mabee et al., 2002), but have yet to be tested. Additional investigation into other taxa could help address questions regarding normal shifts in morphology and what aspects of morphology are regularly flexible enough to adapt.

5 | CONCLUSIONS

Evolutionary biology, for decades, has been largely dedicated to seeking out mechanisms of change. While the value of identifying a lack of change has sufficiently

increased in recent years (Gould, 1980; Holekamp et al., 2013; Schwenk & Wagner, 2004), our knowledge of these mechanisms is still limited. Over the past 40 years, the field of evolutionary biology has further recognized the value of identifying constraints associated with development and how these mechanisms ultimately shape evolution (Cheverud, 1984; Conith et al., 2021; Gould, 1980; Holekamp et al., 2013; Pigliucci & Preston, 2004). The exploration of extreme traits has shed light on the constraints that may be present in a system and has been done so in various systems (Emlen, 2000; Gilbert et al., 2021; Goyens et al., 2015; Moyers Arévalo et al., 2020; Nijhout & Emlen, 1998; Thiagavel et al., 2018). Here, we build on this by examining how the development, and evolution, of an extreme trait can influence a unique, enigmatic lineage— the Bramidae. To summarize our findings, the developmental paths of the bramid genera are similar, with exception to the fanfishes. Coupled with our results showing elevated rates of morphological evolution in the fanfishes, our data indicate that the Ptericlinae have broken various constraints that have allowed them to substantially differ from their bramid relatives (*Brama, Eugmegistus, Taractes, Tarachtichthys, Xenobrama*). The challenges that the fanfishes were required to overcome to extend their medial fins are substantial and speak to the unique Baupläne that is the result of these constraints being broken. How these challenges were overcome remains to be seen, but future investigative work into medial fin modularity is promising. Overall, we feel that this system offers opportunities to further explore the topic of constraints and, in the long term, into questions surrounding modularity.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.