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Original Article

Integration promotes morphological innovation in deep-sea anglerfishes (Eupercaria: Lophiiformes)

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Abstract

Anglerfishes (Lophiiformes) have evolved diverse morphological solutions for life in the deep sea (>200 m). Previous studies have shown that the bathypelagic lineage (Ceratioidei) exhibits high evolutionary rates; however, the intrinsic mechanisms underlying this accelerated evolution remained unclear. Here, we examine patterns of modularity and integration, rates of morphological evolution, and evolutionary rate matrices across the skulls of 100 anglerfish species spanning shallow and deep-sea habitats using geometric morphometrics and phylogenetic comparative methods. We find that both deep-benthic and bathypelagic anglerfishes exhibit stronger patterns of integration compared to their shallow-water relatives. The iconic bathypelagic anglerfishes (Ceratioidei) differ from other Lophiiformes by exhibiting an integrated upper–lower jaw system, likely driven by selection for feeding efficiency in resource-scarce environments. Jaw evolution in Ceratioidei, Chaunacoidei, and Ogcocephaloidei exhibits novel evolutionary trajectories that differ from the dominant pattern across Lophiiformes. Our findings suggest that extreme environments promoted morphological innovation in anglerfishes through evolution in novel phenotypic directions and strengthening of evolutionary integration.

Keywords: deep-sea, elaboration, innovation, integration, modularity

Introduction

Habitat transitions repeatedly drive evolutionary innovation across the Tree of Life (Brownstein et al., 2024; Rappaport & Oliverio, 2023; Storz et al., 2010). Island colonization in Darwin's finches (Grant, 2003) and Caribbean anoles (Losos et al., 1998), water-to-land shifts in tetrapods (Long & Gordon, 2004), and high-altitude adaptation in vertebrates (Storz et al., 2010) each demonstrate that the sustained selective pressures of a new habitat can accelerate phenotypic diversification (Wagner & Lynch, 2010). Across these systems, the ecological demands of novel environments shape morphological outcomes through the interplay of selection, genetic architecture, and evolutionary history (Dumont et al., 2012). Extreme environments, where key physical and chemical parameters such as temperature, pressure, and resource availability deviate substantially from those tolerable by most complex organisms (Merino et al., 2019), produce some of the most striking examples of phenotypic diversification and innovation (e.g., deep-sea fishes [Martinez et al., 2021], Antarctic notothenioid fishes [Colombo et al., 2015]). While habitat transitions more generally, including shifts between freshwater and marine environments, lowland and montane habitats, and benthic and pelagic lifestyles, are frequently associated with morphological diversification (Burress & Hart, 2024; Dumont et al., 2012), extreme environments intensify these dynamics by imposing multiple strong selective pressures. Yet, the macroevolutionary processes shaping trait evolution under harsh conditions still lack a clear mechanistic explanation.

One framework for understanding these macroevolutionary patterns lies in the networks of interacting traits. These trait relationships reflect adaptations to environmental pressures over evolutionary time and can be quantified through measures of evolutionary modularity (the semi-independent evolution of trait groups across species) and evolutionary integration (co-ordinated patterns of trait evolution across species). Evolutionary modularity is often associated with the evolution of innovation as it allows evolutionary changes in independent modules to meet specific ecological needs (Espinosa-Soto & Wagner, 2010; Lorenz et al., 2011; Wagner et al., 2007), especially in adaptive radiation (Chan et al., 2024; Sanger et al., 2012; Stefanini et al., 2025). Conversely, strong evolutionary integration was thought to offer structural stability while restricting innovation by limiting possible phenotypic space for exploration (Goswami & Polly, 2010; Goswami et al., 2014). Growing evidence has demonstrated that evolutionary integration can also facilitate rapid morphological evolution when multiple traits experience shared selective pressures (Armbruster et al., 2014; Evans et al., 2021; Goswami et al., 2014; Hu et al., 2016; Penna et al., 2017), particularly in lineages experiencing strong directional selection (Armbruster et al., 2014; Penna et al., 2017). The relationship between evolutionary integration and the evolution of morphological novelty may therefore depend on the selective regime and the specific modules involved.

The deep ocean (>200 m) represents one of Earth's most extreme environments for vertebrate life, imposing

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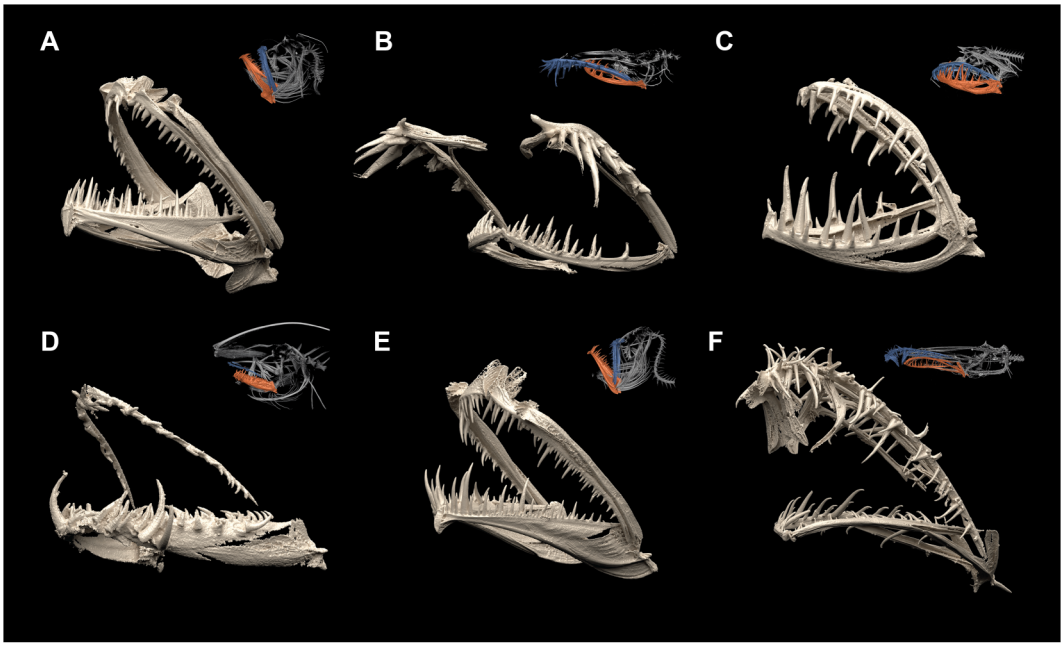

Figure 1. Oral jaw diversity across six ceratioid anglerfish genera. The upper jaw (premaxilla and maxilla) is colored blue, and the lower jaw (dentary and angular bone) is colored orange. (A) *Bufoceratias thele* (UW 156168), (B) *Thaumatichthys binghami* (UW 47537), (C) *Linophryne arborifera* (MCZ 49822), (D) *Gigantactis vanhoeffeni* (UW 157508), (E) *Melanocetus johnsonii* (UW 157527), and (F) *Lasiognathus beebei* (MCZ 167891). UW = University of Washington; MCZ = Harvard's Museum of Comparative Zoology.

high hydrostatic pressure, near-freezing temperatures, permanent darkness, and severe food limitation. Yet, it harbors surprisingly high morphological diversity (Martinez et al., 2021; Myers et al., 2021). Anglerfishes (Eupercaria: Lophiiformes) thrive in these extreme conditions, with lineages spanning from coral reefs to the bathypelagic zone. These fishes display phenotypic innovations, including enlarged jaws (Heiple et al., 2023; Miller et al., 2025), modified rostra (Maile & Davis, 2026; Maile et al., 2025), reduced immune systems, and sexual parasitism (Brownstein et al., 2024). Previous studies have established that anglerfishes and other deep-sea teleosts exhibit rapid rates of morphological evolution (Heiple et al., 2023; Maile et al., 2020; Martinez et al., 2021; Miller et al., 2025). While this rate acceleration may be driven by deep-sea environmental dynamics, including oceanographic heterogeneity (Boyd et al., 2019; Lappan et al., 2023) and vertical stratification (Eduardo et al., 2020, 2021), the intrinsic mechanisms translating these environmental challenges into morphological innovation remain poorly understood. Recent work suggests that habitat alters evolutionary constraints in anglerfishes (Miller et al., 2025). For example, deep-sea habitats have produced predominantly dorso-ventrally compressed body shapes in benthic specialists, a pattern broadly convergent among benthic teleosts (Friedman et al., 2020), and a much wider spectrum of body elongation in bathypelagic anglerfishes (Ceratioidei) along with divergent jaw and tooth morphology (Miller et al., 2025). However, how deep-sea habitats shape the evolution of trait covariation (modularity and integration) remains unclear.

Anglerfishes provide an ideal system for understanding environment-driven trait evolution. Phylogenetic evidence suggests that Lophiiformes ancestrally occupied shallow and deep-benthic habitats (Miller et al., 2025), with two independent transitions to shallow-only habitats in frogfishes (Antennarioidei) and the genus *Ogcocephalus*, and a single transition to the bathypelagic zone in ceratioid anglerfishes (Ceratioidei). This phylogenetic framework implies that the bathypelagic radiation of Ceratioidei represents a derived habitat transition. Each major anglerfish lineage exhibits habitat-specific specializations reflecting its distinct ecological challenges. Shallow-water frogfishes (Antennarioidei) evolved highly protrusible jaws enabling some of the fastest feeding strikes among vertebrates (Grobecker & Pietsch, 1979). Batfishes (Ogcocephaloidei) occupy both shallow and deep-benthic habitats, employing an esca capable of chemical and visual prey luring while actively using specialized pectoral fin positioning to modulate strike distance and speed (Christie et al., 2016). Deep-benthic specialists, such as sea toads (Chaunacidae) and monkfishes (Lophiidae), developed energy-efficient ventilation mechanisms that support extended ambush predation on the seafloor (Farina & Bemis, 2016; Long & Farina, 2019). Bathypelagic anglerfishes, the suborder Ceratioidei, colonized the deep-water column and underwent explosive phenotypic diversification. This single bathypelagic radiation presents extreme jaw morphologies (Miller et al., 2025) (Figure 1), including enlarged upper jaws and outward-pointing teeth that convergently evolved in genera such as *Lasiognathus* and *Thaumatichthys* to trap prey (Heiple et al., 2023; Pietsch, 2009). The well-established phenotypic diversity in anglerfishes suggests that differing selective regimes have altered evolutionary trajectories across shallow-water and deep-sea habitats (Santos et al., 2025), and assessing how these habitats reshape morphological evolution requires examining both the strength of trait covariation and the direction of evolutionary change.

To quantify evolutionary direction, we compare the major axis of evolutionary change within each suborder to the dominant axis across all Lophiiformes. These axes are defined as the first eigenvectors of suborder-specific and clade-

wide evolutionary rate matrices (R-matrices), capturing the direction of greatest evolutionary variance in trait space. Following Guillerme et al. (2023), we refer to evolution along this clade-wide axis as "elaboration" and to evolution orthogonal to it as "innovation." Both elaboration and innovation contribute to the occupation of morphospace. High elaboration indicates that a lineage's morphological divergence aligns with the major axis of variation observed across the clade, potentially reflecting shared selective pressures or ancestral patterns of trait covariation. High innovation indicates evolution in phenotypic directions that differ from this clade-wide pattern, potentially reflecting lineage-specific selective regimes or reorganized patterns of trait covariation.

Using geometric morphometrics from micro-CT scans of 100 species spanning all major lophiiform lineages, we test two alternative mechanisms by which deep-sea lineages may have achieved morphological innovation through shifts in trait covariation patterns in their skulls. First, increased modularity may allow cranial regions to evolve independently toward specialized functions, as suggested by the pattern of enlarged jaws (Heiple et al., 2023; Miller et al., 2025), modified rostra (Maile & Davis, 2026; Maile et al., 2025), and energy-saving respiratory systems (Farina & Bemis, 2016; Long & Farina, 2019). Alternatively, deep-sea lineages might exhibit increased integration, reflecting co-ordinated trait evolution in response to the multiple simultaneous challenges of deep-sea environments (extreme pressure, cold, darkness, and food scarcity; Gage & Tyler, 1991; Wilson & Hessler, 1987; Woolley et al., 2016). We evaluate these hypotheses by quantifying patterns of modularity and integration, evolutionary tempo (using variable-rate Brownian motion models), and innovation–elaboration decomposition of evolutionary rate matrices to test whether deep-sea habitats promote morphological innovation through shifts in trait covariation.

Materials and methods

Geometric morphometric analyses, phylogeny, and habitat

We utilized datasets from Miller et al. (2025) to analyze 100 anglerfish species representing all major lineages, covering 20 of the 21 anglerfish families (excluding only Lophichthyidae; Table S1). This study provided the high-resolution micro-CT scan dataset for raw shape co-ordinates (111 three-dimensional landmarks digitizing 7 key cranial bones: premaxilla, maxilla, dentary, angular, ceratohyal, hyomandibula, and neurocranium), a time-calibrated phylogeny based on genomic-scale data with 100 matching tips, and habitat classifications compiled through FishBase (Froese & Pauly, 2023), Fishes of Australia (Fishes of Australia, 2018), and previous literature (Friedman et al., 2020; Pietsch, 2009). The meshes were segmented in Amira 2020.3 and digitized using the Stratovan Checkpoint software.

This sampling captures the full phylogenetic breadth of the order while ensuring that each habitat category in our subsequent analyses ($n \geq 28$ species) retained sufficient sample size to detect meaningful patterns of integration and modularity. We retained the habitat classifications of Miller et al. (2025): shallow-benthic (0–200 m), deep-benthic (>200 m, seafloor-associated), and bathypelagic habitats (>200 m, open water column) based on the maximum depths. These categories distinguish environments that differ in light availability, hydrostatic pressure, and substrate association (the primary axes along which marine habitats are conventionally divided; Gage & Tyler, 1991; Marshall, 1971). Though we acknowledge these categories subsume within-group ecological variation, they capture the broadest selective contrasts relevant to cranial morphology in this radiation (Heiple et al., 2023; Maile et al., 2025; Miller et al., 2025).

For geometric morphometric analyses, we standardized each skull element using local Procrustes superimposition to remove the effects of rotational and translational biases (Rhoda et al., 2021). In this procedure, generalized Procrustes analysis was performed on each bone separately, and the resulting aligned landmark subsets were then concatenated into a common co-ordinate space using a mean shape configuration that preserves the relative orientation, position, and scale of each bone. Sliding semilandmarks were fitted using Procrustes distance rather than bending energy minimization to avoid inflating covariation among landmarks sharing the same curve (Zelditch & Swiderski, 2023). Subsequent analyses were performed using the geomorph R package (Baken et al., 2021), unless otherwise specified.

Patterns of evolutionary modularity

We evaluated six hypotheses of evolutionary modularity in lophiiform skulls based on the partitioning of functional and developmental modules established in previous literature (Larouche et al., 2023). Functional hypotheses identify modules based on feeding and respiratory activity (Camp & Brainerd, 2014; Camp et al., 2015; Hulsey et al., 2005; Liem, 1973; Westneat, 2004). The first functional hypothesis distinguished between the prey capture of the oral jaws and the buccal expansion system (neurocranium, ceratohyal, and hyomandibula) as two separate modules. The second functional model considered the hyomandibula, ceratohyal, and oral jaw as one co-ordinated suction feeding module. The third functional hypothesis separated the oral jaws (feeding module), the lateral buccal expansion units (neurocranium + hyomandibula), and the ventral buccal expansion component (ceratohyal). The fourth functional model further differentiated neurocranium from the lateral buccal expansion (hyomandibula).

Developmental hypotheses partitioned skull elements according to embryonic origins and ontogenetic differentiation patterns (Hulsey et al., 2005; Le Pabic et al., 2016). The first developmental model divided the skull into mandibular arch derivatives (oral jaws), hyoid arch derivatives (hyomandibula and ceratohyal), and the neurocranium. The second developmental hypothesis subdivided the oral jaw into dorsal and ventral elements based on neural crest cell migration and condensation patterns (Cerny et al., 2004).

We employed the "phylo.modularity" function in geomorph to calculate the covariance ratio (CR) of each proposed module partitioning by quantifying their modularity signals (Adams, 2016; Adams & Collyer, 2019; Adams & Felice, 2014). We then compared the effect size of each modularity signal using "compare.CR" to assess the strongest supported hypothesis (Adams & Collyer, 2019).

Patterns of phenotypic integration

Integration in the anglerfish skull was assessed within each bone and between bone pairs. We quantified integration within each cranial element (within-bone integration) with the relative eigenvalue index (Vrel). This metric quantifies covariation patterns while excluding zero-variance dimensions that arise from Procrustes superimposition (Conaway & Adams, 2022; Pavlicev et al., 2009). As Vrel values are not directly comparable, we used the "compare.ZVrel" function to compare effect sizes of Vrel across habitat groups (Conaway & Adams, 2022).

We then evaluated between-bone integration with two-block partial least squares (2B-PLS) analyses. This approach was applied to bone pairs to generate a matrix of observed PLS correlations (Adams & Felice, 2014; Collyer et al., 2015; Rohlf & Corti, 2000). As PLS scores are sensitive to sample size and distribution, we compared the effect size of between-bone integration using the "compare.pls" function to identify the variation in integration patterns between and within each habitat group (Adams & Collyer, 2016; Collyer et al., 2015). Effect sizes calculated from within-bone and between-bone analyses were then used to construct an adjacency matrix, which was visualized as a network plot.

Rates of shape evolution

To compare evolutionary rates (σ^2) across different cranial elements, we used the "compare.multi.evol.rates" function (Adams, 2014; Denton & Adams, 2015), setting "subset = FALSE" to account for differences in landmark number across bones (e.g., 21 for the premaxilla and 31 for the neurocranium). This function tests whether evolutionary rates differ among trait sets (bones) within a single model. To separately test whether rates differ across habitat groups for each individual bone and the overall skull, we used the "compare.evol.rates" function (Adams, 2014), which compares a single trait set across habitat groups.

The tempo of evolution was further investigated using a variable-rate Brownian motion model in BayesTraitsV4 at the individual bone level, building on the Miller et al. (2025) analyses of habitat-driven evolutionary patterns in lophiiform skull morphology overall. This Bayesian method incorporates uncertainty in topology and branch length estimates to detect clade- and species-specific rate shifts in trait data. To address known difficulties with evolutionary model-fitting using high-dimensional data (Adams & Collyer, 2018), we reduced the dimensionality of our data using principal component analysis (PCA; "gm.prcomp"), retaining axes that cumulatively explained 85% of the total shape variance for each bone and the full skull, following the variance-based retention approach of Felice & Goswami (2018) with a lower threshold to balance variance retention with computational tractability. This resulted in 28 axes for the whole skull, 6 axes for premaxilla, 6 axes for maxilla, 5 axes for dentary, 6 axes for angular, 11 axes for ceratohyal, 11 axes for hyomandibula, and 15 axes for neurocranium. To improve numerical stability, we multiplied PC scores by 1,000. Using uniform priors, we ran two independent chains each for 270,000,000 generations, discarding the first 70,000,000 generations as burn-in, with a thinning interval of 1,000. Model convergence was evaluated by assessing the trace plots in Tracer v1.7.1 (Rambaut et al., 2018), confirming effective sample sizes (ESS) > 200 for all parameters. Variable-rate output files were processed through the standalone PPPostProcess software. Variable-rate trees were visualized with branch colors mapped to relative evolutionary rates.

We also compared evolutionary modes across all cranial elements using four models in BayesTraits: Brownian motion with lambda transformation, variable-rate Brownian motion with lambda transformation, Ornstein–Uhlenbeck (OU), and OU with habitat-specific optima. Each model was run under identical computational conditions, with 50 stones at 1,000,000 generations each.

Innovation–elaboration analysis

We quantified evolutionary innovation and elaboration by examining the orientation of lineage-specific evolutionary trajectories relative to the overall phylogenetic axis. Four functionally linked linear jaw measurements were extracted from landmark configurations: premaxilla ascending process length, premaxilla dentigerous arm length, lower jaw out-lever (anterior teeth to jaw joint), and lower jaw in-lever (jaw joint to adductor insertion) (Figure S1). These mechanically interdependent traits capture key aspects of teleost feeding biomechanics (Muñoz et al., 2018): the premaxilla ascending and dentigerous processes determine the extent and configuration of upper jaw protrusion during prey capture, while the in-lever/out-lever ratio governs the force–velocity trade-off during jaw closing (Wainwright et al., 2004; Westneat, 2004). We used linear measurements rather than landmark-derived shape variables to avoid singular covariance matrices that arise with limited sample sizes in some suborders (Chaunacoidei: $n = 7$; Lophioidei: $n = 7$). All measurements were log-transformed and standardized by the log-centroid size computed from the whole skull landmark set. Specimens were grouped by suborder (Lophioidei, Antennarioidei, Chaunacoidei, Ogcocephaloidei, and Ceratioidei).

Evolutionary rate matrices (R-matrices) were estimated using Bayesian phylogenetic generalized linear mixed models (pGLMM) in MCMCglmm (Hadfield, 2010). We fit a single model with jaw traits as multivariate response variables and suborder-specific random effects to estimate separate rate matrices while accounting for overall phylogenetic covariance. We employed weakly informative inverse-Wishart priors ($\nu = 0.02$), which allow posterior estimates to be primarily data-driven. We ran three independent chains for 800,000 iterations each, with a 200,000-iteration burn-in and a thinning interval of 1,000. Convergence was confirmed via multivariate potential scale reduction factors (<1.1) and combined ESS > 200.

For each suborder, we extracted the major axis (first eigenvector) from its posterior distribution of evolutionary rate matrices and from the overall phylogenetic rate matrix using the dispRity package (Guillerme et al., 2023). Elaboration scores represent the absolute value of the projection of each suborder's major axis onto the overall phylogenetic major axis, quantifying the extent to which a lineage's evolutionary trajectory aligns with the dominant direction of morphological divergence across Lophiiformes. Innovation scores represent the perpendicular projection from this axis, quantifying evolution in directions that differ from this clade-wide pattern. To quantify evolutionary correlation across the overall phylogeny and within each suborder, we converted

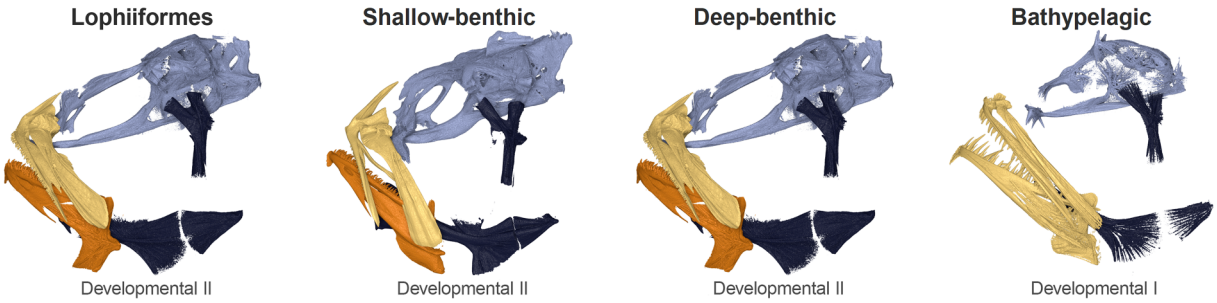

Figure 2. Best-fitting models of evolutionary modularity in Lophiiformes. Evolutionary modularity arrangements for all anglerfishes combined and each habitat separately. Each color represents a different module. The best-supported model by the covariance ratio test revealed shallow-benthic and deep-benthic as "developmental II" (upper jaw, lower jaw, neurocranium, and hyoid arch complex), and the bathypelagic group as "developmental I" (oral jaw, neurocranium, and hyoid arch complex). Skull illustrations in each panel represent CT-scanned specimens: *Chaunax pictus* (UW 158220; overall and deep-benthic), *Antennatus coccineus* (UW 20863; shallow-benthic), and *Bufoceratias thele* (UW 156168; bathypelagic). UW = University of Washington.

R-matrices to evolutionary correlation matrices by standardizing each covariance using the product of the respective trait standard deviations (Cheverud, 1996), and then summarized the results across the posterior distribution using posterior medians.

To evaluate whether observed innovation and elaboration scores could arise from phylogenetic divergence alone, we conducted a multivariate Brownian motion simulation analysis (1,000 replicates; see Supplementary Methods). In addition, we assessed the robustness of our results with a sensitivity analysis excluding the two clades with the smallest sample sizes (Chaunacoidei and Lophioidei) and reran the MCMCglmm analyses using the remaining three clades ($n = 86$ total species) with the same parameters.

Our innovation–elaboration and integration analyses quantify complementary aspects of anglerfish evolution. The former captures the direction of lineage-specific evolutionary trajectories, while the latter measures the strength of trait covariation regardless of direction. These analyses allow us to distinguish between innovation driven by coordinated trait evolution and independent divergence of loosely associated traits.

Results

Shift in patterns of modularity

Bathypelagic anglerfishes (Ceratioidei) displayed reduced modular organization compared to other anglerfishes (Figure 2). All habitat groups were best fit by partitioning models based on developmental hypotheses (Figure 2, Tables S2 and S3). While all modularity models were significant relative to the null distribution, alternative modularity hypotheses were not statistically distinguishable from each other. We therefore ranked models by effect size. The strongest modular signal was observed in shallow-benthic forms like frogfishes ($Z_{CR} = -7.43$, supporting the "developmental II" model), followed by deep-benthic ($Z_{CR} = -5.97$, supporting the "developmental II" model), and bathypelagic taxa ($Z_{CR} = -4.93$, supporting the "developmental I" model) (Table S3). The "developmental II" model divides the skull into four modules, comprising the neurocranium, the derivatives of the hyoid arch (hyomandibula and ceratohyal), the upper jaw, and the lower jaw. The "developmental I" model is configured similarly, but combines upper and lower jaw elements into a single mandibular arch unit.

Patterns of integration in anglerfishes

We compared overall skull integration within each habitat group to integration across all Lophiiformes using the effect size of relative eigenvalue index (Z_{rel}). Deep-sea lineages showed elevated skull integration relative to the Lophiiformes-wide pattern. Deep-benthic species in particular ($Z_{rel} = -0.99$) differed significantly from overall Lophiiformes ($Z_{rel} = -1.59$; $p = .007$), and bathypelagic species showed a similar trend ($Z_{rel} = -1.22$; $p = .086$). Shallow-benthic species ($Z_{rel} = -1.45$; $p = .467$) did not differ from the all-Lophiiformes value (Table S4). These results suggest that deep-sea habitats are associated with higher cranial integration compared to the broader phylogenetic pattern.

Examining covariation between individual cranial elements revealed that both deep-sea benthic and pelagic groups showed stronger between-bone integration than shallow-water forms. We examined the covariation between seven key cranial elements: the premaxilla, maxilla, dentary, angular, neurocranium, hyomandibula, and ceratohyal (Figure 3A; Table S5). Bathypelagic anglerfishes (Ceratioidei) demonstrated the most extensive integration network, with 20 of 21 possible cranial-pair interactions reaching significance and 10 pairs exhibiting the strongest integration across all habitat groups (Figure 3A; Table S5). This pattern was particularly pronounced in the oral jaw complex, where angular–maxilla (bathypelagic $Z_{PLS} = 3.28$; shallow-benthic $Z_{PLS} = 2.84$; and deep-benthic $Z_{PLS} = 2.34$), angular–premaxilla (bathypelagic $Z_{PLS} = 2.71$; shallow-benthic $Z_{PLS} = 1.42$; and deep-benthic $Z_{PLS} = 1.34$), angular–dentary (bathypelagic $Z_{PLS} = 2.65$; shallow-benthic $Z_{PLS} = 1.22$; and deep-benthic $Z_{PLS} = 1.00$), and maxilla–dentary (bathypelagic $Z_{PLS} = 1.82$; shallow-benthic $Z_{PLS} = 1.55$; and deep-benthic $Z_{PLS} = 1.17$) pairs showed elevated covariation (Table S5).

Integration within each cranial bone showed more conserved patterns than between-bone integration across Lophiiformes. Most cranial bones exhibited weaker internal integration than expected, except for the angular bone in deep-benthic species, which displayed the strongest within-bone integration ($Z_{rel} = 0.32$; shallow-benthic $Z_{rel} = -0.93$; and bathypelagic $Z_{rel} = -0.51$) (Table S5).

Rates of evolution in anglerfishes

Evolutionary rates varied substantially across cranial elements. We found consistently elevated evolutionary rates in

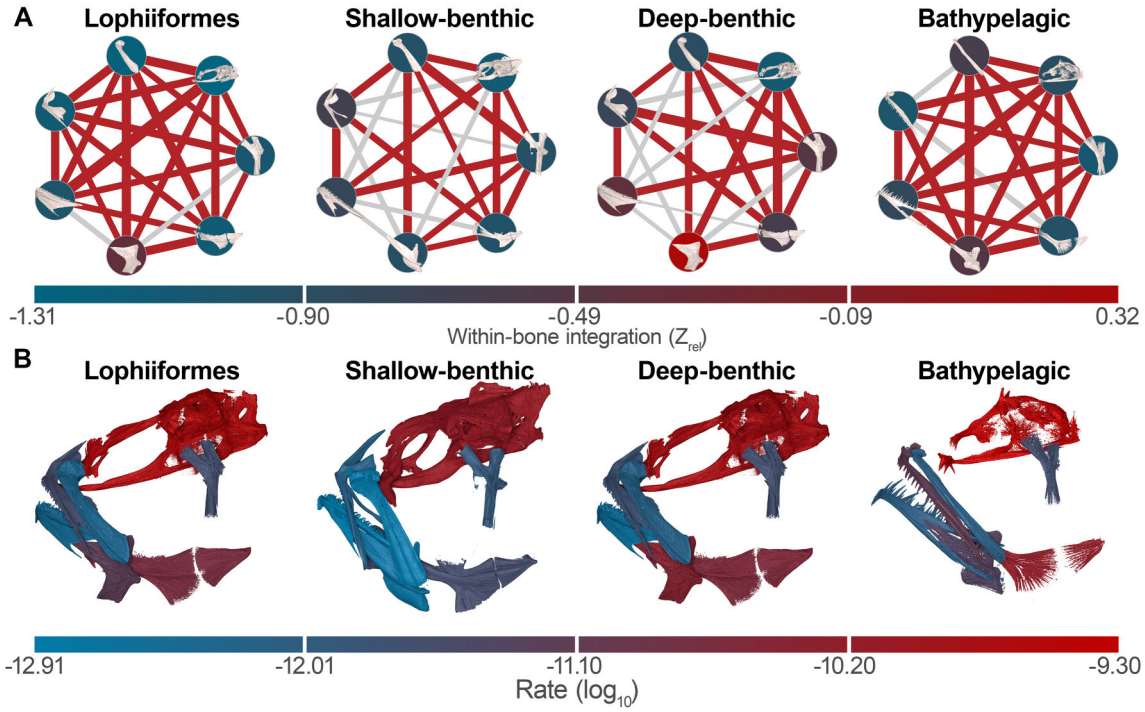

Figure 3. Integration networks and evolutionary rate estimates across seven cranial bones of the anglerfish skull. (A) Network plots of phylogenetic integration. Lines represent the effect size of between-bone integration (Z_{PLS}) using phylogenetic two-block partial least squares, and nodes indicate the effect size of within-bone integration (Z_{rel}) using the relative eigenvalue index. Line thickness corresponds to higher Z_{PLS} values, lines colored in red reflect significant covariation between bones, and node colors reflect the relative effect size. (B) Evolutionary Brownian rate estimates for each cranial bone across habitats. Skull illustrations in each panel represent CT-scanned specimens: *Chaunax pictus* (UW 158220; overall and deep-benthic), *Antennatus coccineus* (UW 20863; shallow-benthic), and *Bufoceratias thele* (UW 156168; bathypelagic). UW = University of Washington.

the neurocranium and ceratohyal, contrasting with slower evolution in the oral jaw complex (premaxilla, maxilla, and dentary) across all lineages (Figure 3B; Table S6). We compared four evolutionary models: variable-rate Brownian motion, Brownian motion with a lambda transformation, habitat-specific optima Ornstein–Uhlenbeck, and single-peak Ornstein–Uhlenbeck. All bone elements were best supported by the variable-rate model (Table S7).

Bathypelagic species showed dramatically accelerated evolutionary rates compared to shallow-benthic forms across all cranial elements, including premaxilla (2.68-fold), ceratohyal (3.85-fold), dentary (2.33-fold), maxilla (2.01-fold), and neurocranium (2.13-fold) (Table S8; e.g., premaxilla: bathypelagic $\sigma^2 = 2.39 \times 10^{-7}$, shallow-benthic $\sigma^2 = 8.92 \times 10^{-8}$). For the overall skull, both bathypelagic and deep-benthic species demonstrated significantly elevated evolutionary rates relative to shallow-benthic species, with the bathypelagic group exhibiting the fastest rates for most cranial elements, although deep-benthic taxa evolved fastest specifically for the angular bone.

While comparative rate analysis revealed general habitat-based differences in net evolutionary rates (Figure 3B), BayesTraits analysis identified rate shifts in specific lineages and divergence events (Figure 4). We detected rapid divergences in skull shape along the branches separating major lineages from monkfishes (Lophioidei) near the base of Lophiiformes. This pattern was consistent across neurocranium, hyomandibula, ceratohyal, and angular bones (Figure 4). Among different lineages, shallow-water frogfishes (Antennarioidei) exhibited slow, homogeneous rates across most cranial elements, including the premaxilla, dentary, maxilla, angular, hyomandibula, and ceratohyal. In contrast, deep-benthic groups (monkfishes Lophioidei and batfishes Ogcocephaloidei) showed rate acceleration concentrated at specific divergence nodes, with key accelerations occurring at the crown nodes of *Zalieutes* (hyomandibula), *Malthopsis* (neurocranium), and *Sladenia* (dentary and ceratohyal). Ceratioid families displayed the most dramatic rate fluctuations, with accelerated evolution particularly evident in taxa such as *Lasiognathus beebei* (premaxilla, maxilla, dentary, neurocranium, and hyomandibula), *Linophryne arborifera* (neurocranium, maxilla, hyomandibula, and ceratohyal), and *Lophodolos acanthognathus* (neurocranium and angular). These results were consistent with those of Miller et al. (2025), demonstrating that the evolution of phenotypic novelty in anglerfishes was not limited to the base of the radiation.

Within these lineage-specific patterns, a consistent ecological signal emerged in the evolution of the premaxilla, angular, and hyomandibula, where shallow-water Antennarioidei showed the lowest rates, and lineages with deep-water representatives (Lophioidei, Chaunacoidei, Ogcocephaloidei, and Ceratioidei) displayed faster rates (Figures 4A, D, and F). This co-ordinated pattern of lineage-specific rate variation across cranial elements is consistent with the between-bone integration patterns recovered above.

Deep-sea lineages achieved morphological innovation

Deep-sea anglerfishes achieved morphological diversity primarily through innovation rather than elaboration. Elabora-

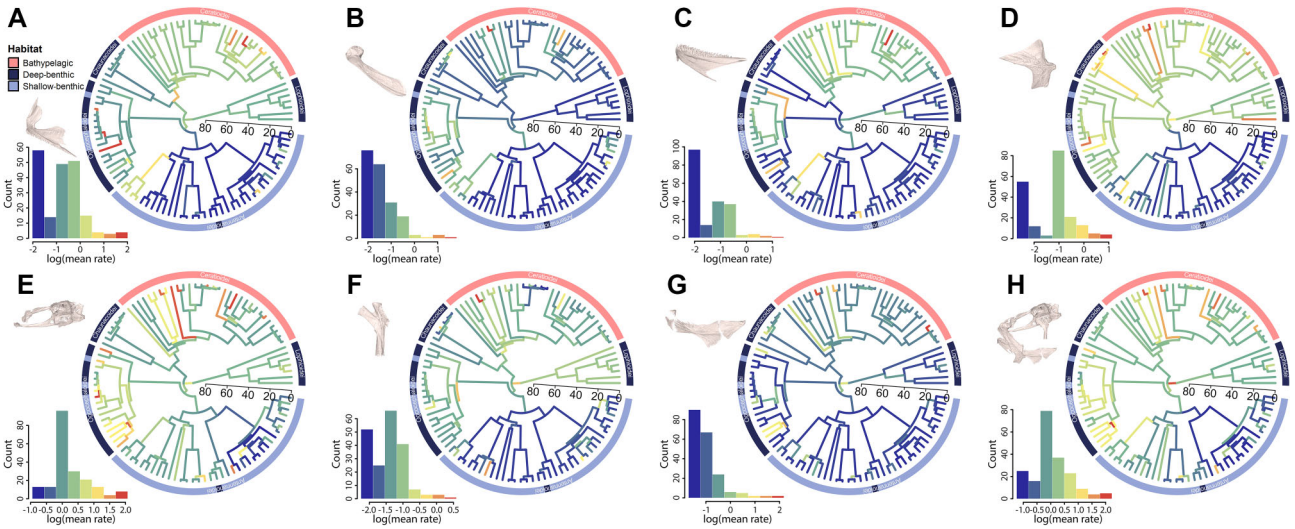

Figure 4. Evolutionary rates across cranial modules and the full skull. Fan phylogenies illustrating variable evolutionary rates for each cranial element: (A) premaxilla, (B) maxilla, (C) dentary, (D) angular, (E) neurocranium, (F) hyomandibula, (G) ceratohyal, and (H) full skull. Branch colors reflect evolutionary rate estimates, ranging from cool (blue; low rates) to warm (red; high rates) along a rainbow color scale. Tip colors indicate habitat group: shallow-benthic, deep-benthic, and bathypelagic. Rates were estimated using a variable-rate Brownian motion model with a lambda tree transformation. For each panel, the corresponding cranial element is illustrated from a CT segment of *Chaunax pictus* (UW 158220), with the focal bone isolated and shown alongside its respective rate tree. UW = University of Washington.

tion scores, representing evolution along the dominant phylogenetic axis, were not credibly different across suborders (Figure 5A; Table S9). In contrast, deep-sea lineages (Chaunacoidei, Ogcocephaloidei, and Ceratioidei) exhibited credibly higher innovation scores than shallow-water Antennarioidei (posterior median differences = 2.52, 1.43, and 3.69, respectively; probability of direction (pd) > 0.95 for all comparisons; Figure 5B; Table S9), indicating that jaw evolution in these lineages has diverged from the clade-wide trend.

Evolutionary correlation matrices revealed divergent correlation patterns in anglerfish jaw evolution (Figure 5C). Lophiiformes as a whole, as well as Antennarioidei specifically, showed moderate positive correlations among premaxilla dentigerous arm length, lower jaw out-lever, and lower jaw in-lever ($r = 0.31$–0.74), with a decoupled premaxilla ascending process length. Lophioidei and Chaunacoidei exhibited similar moderate integration ($r = 0.19$–0.57). Ceratioidei displayed unique evolutionary trade-offs, with strong negative correlations between the length of the premaxilla's ascending process and the lower jaw's out-lever ($r = -0.66$) and between the length of the premaxilla's dentigerous arm and the lower jaw's in-lever ($r = -0.72$). In contrast, Ogcocephaloidei showed the highest integration, with premaxilla dentigerous arm length and lower jaw out-lever exhibiting strong evolutionary coupling ($r = 0.90$). Sensitivity analyses excluding the two smallest clades confirmed consistent innovation and evolutionary correlation patterns (Table S10; Figure S2).

Simulation analyses confirmed that elevated innovation scores in deep-sea lineages are not explained by phylogenetic divergence time alone. Under a multivariate Brownian motion null model, observed innovation scores for Ceratioidei, Ogcocephaloidei, and Chaunacoidei significantly exceeded null expectations ($p = .001$, $p = .007$, and $p = .046$, respectively; Table S11). The observed innovation score for Ceratioidei (4.49) was nearly three times the 95th percentile of the null distribution (1.52). In contrast, Antennarioidei and Lophioidei did not differ from the null ($p = .303$ and $p = .644$, respectively), consistent with evolution along the shared phylogenetic axis. Ceratioidei and Ogcocephaloidei also showed significantly elevated elaboration scores relative to null expectations ($p = .016$ and $p = .048$), suggesting that deep-sea lineages have diverged more extensively overall.

Discussion

Integration facilitates innovation in anglerfishes

The deep sea repeatedly produces morphological extremes, and the anglerfish system provides insight into how deep-sea habitats shape phenotypic innovation. While exceptional diversity and evolutionary rates have been repeatedly demonstrated for anglerfishes (Heiple et al., 2023; Maile et al., 2025; Miller et al., 2025), the intrinsic mechanisms permitting this morphological diversification were unclear. Our results suggest that the evolution of novel deep-sea phenotypes was facilitated through restructured and heightened trait coordination, particularly between the upper and lower jaws (Figures 3A and 5). Since strong integration can bias evolutionary trajectories along axes of high covariation (Goswami & Polly, 2010; Goswami et al., 2014), how, then, can increased integration accompany morphological innovation in deep-sea habitats?

Habitat transitions can redirect evolutionary constraints and therefore open new pathways for morphological divergence, yet this constraint restructuring may require an evolvable developmental foundation. We propose that an ancestral modular framework of the anglerfish skull may have permitted the initial phenotypic exploration by releasing skull regions from shared constraints. Our results recover a four-module lophiiform skull (the upper jaw, the lower jaw, the hyoid arch derivatives, and the neurocranium) that may allow trait relationships to be reconfigured as lineages colonized different habitats. Next, deep-sea lineages evolved elevated integration that enabled rapid expansion into unex-

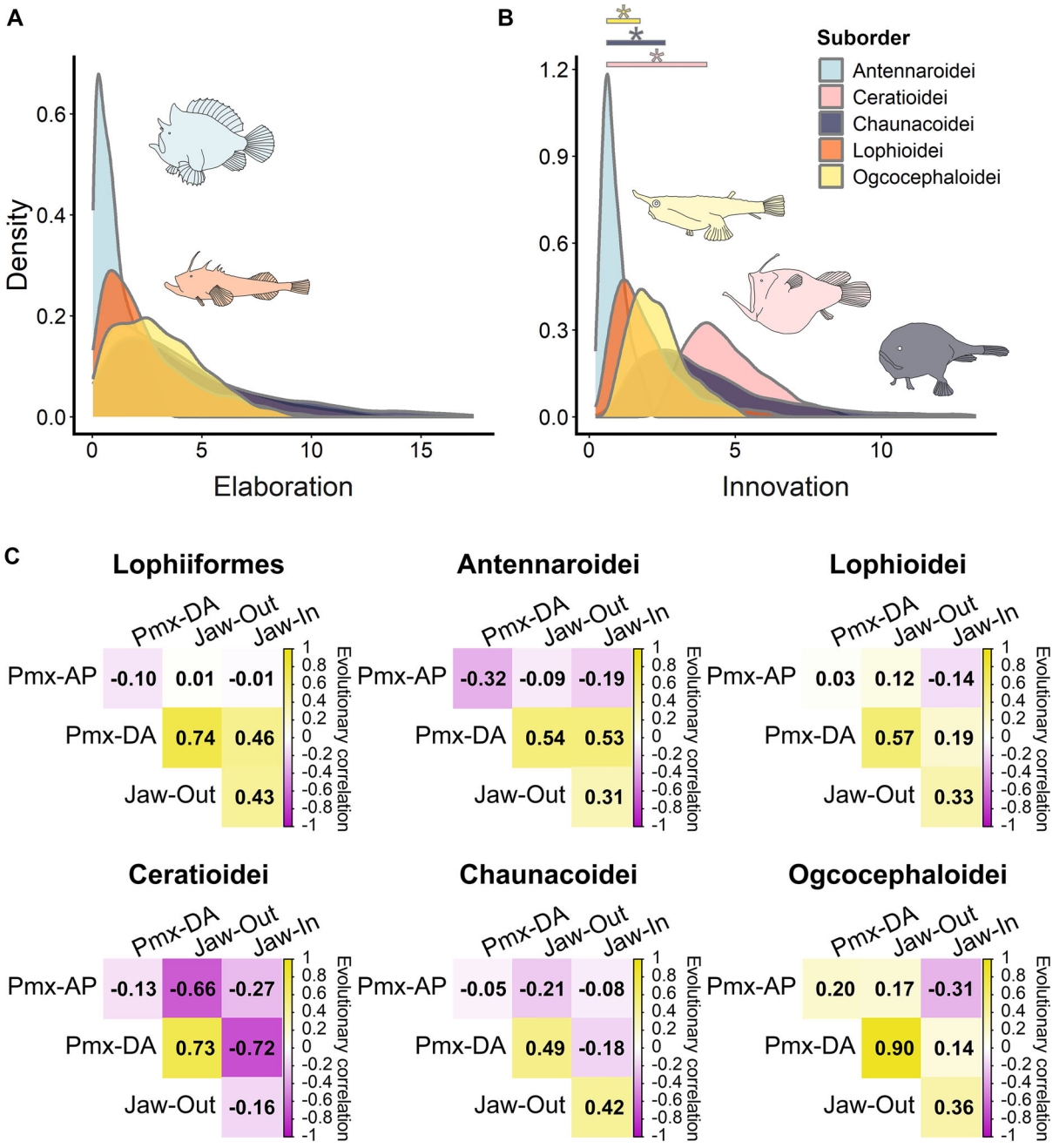

Figure 5. Evolutionary innovation and elaboration in jaw morphology across anglerfish lineages. (A) Elaboration scores and (B) innovation scores across five anglerfish suborders, quantifying the extent to which each lineage's evolutionary trajectory aligns with (elaboration) or diverges perpendicularly from (innovation) the major phylogenetic axis of morphological divergence. The *y*-axis indicates absolute projection scores (unitless). Asterisks indicate suborder pairs with a probability of direction (pd) > 0.95 (see Table S9). (C) Evolutionary correlation matrices for four jaw traits: Prem-AP (premaxilla ascending process length), Prem-DA (premaxilla dentigerous arm length), Jaw-Out (lower jaw out-lever), and Jaw-In (lower jaw in-lever). Colors indicate correlation strength from negative (−1; purple) to positive (+1; yellow).

plored regions of morphospace. The derived nature of bathypelagic colonization in Ceratioidei suggests these changes in integration and modularity represent evolutionary responses to deep-sea selective pressures, particularly the seafloor-to-midwater habitat transition.

A documented evolutionary transition preceding the crown of Lophiiformes supports this ancestral modularity. In most teleosts, the branchiostegal apparatus operates as part of an integrated suction-feeding and ventilatory system, coupling hyoid kinematics to oral jaw expansion (Camp & Brainerd, 2014). The evolution of restricted gill openings in anglerfishes and their sister group Tetraodontiformes (another radiation of morphological extremes including pufferfishes and ocean sunfishes) decoupled ventilation from rapid buccal expansion (Farina et al., 2015). This decoupling may have permitted the oral jaws and ventilatory apparatus to evolve along independent trajectories (Figure 2). The modular pattern in bathypelagic ceratioids appears to have subsequently reorganized by integrating the previously semi-independent upper and lower jaw modules

into a single oral-jaw complex, likely reflecting selection on whole-jaw prey capture in resource-scarce bathypelagic environments, while the hyoid arch complex remained a separate module. A complementary pattern is documented in Tetraodontiformes, where the evolution of the beak arose within a strongly integrated skull (Troyer et al., 2024). These sister radiations suggest that strong integration is compatible with and may facilitate morphological innovation.

Patterns of integration across deep-sea habitats

From this modular foundation, different anglerfish lineages evolved distinct integration patterns matched to the selective demands of their habitat. The evolutionary mechanism underlying this deep-sea morphological diversification is heightened integration, yet bathypelagic and deep-benthic lineages achieve this through fundamentally different frameworks. The former shows extensive between-bone coordination across the jaw complex, while the latter is centered on localized integration of the angular bone.

Bathypelagic specialists (Ceratioidei) have reorganized their cranial skeleton into a deeply integrated skull, with reduced modularity reflecting the merging of previously semi-independent jaw elements. Within this network, integration is particularly concentrated in the oral jaw complex, with the angular bone serving as the hub of covariation across upper and lower jaw elements. This jaw-wide integration is further characterized by strong negative evolutionary correlations between upper and lower jaw elements. This covariation structure enables bathypelagic anglerfishes to evolve diverse jaw configurations, ranging from *Thaumatichthys* with its trap-like mouth featuring an enlarged upper jaw with long hooked teeth (Bertelsen et al., 1981) (Figure 1B) to *Gigantactis* with robust dentition on the lower jaw paired with a reduced upper jaw (Bertelsen et al., 1981) (Figure 1D). This tight jaw integration may enable co-ordinated biomechanical solutions for capturing large, scarce prey, paralleling the enlarged gape and jaw flexibility documented across deep-sea predators including stomiid dragonfishes as adaptations for higher capture-per-encounter rates in food-limited environments (Drazen & Sutton, 2017; Kenaley, 2012). However, given that Ceratioidei represents a single transition to the bathypelagic zone, we cannot determine whether their distinct integration patterns reflect lineage-specific characteristics, such as the evolution of the bioluminescent lure (Maile & Davis, 2026), rather than the bathypelagic habitat alone. We note that our comparisons between shallow-benthic and deep-benthic lineages, which involve multiple independent transitions across the phylogeny, provide partial corroboration that depth-related selective pressures shape cranial integration independently of any single clade's history. Nonetheless, disentangling the effects of habitat from lineage-specific innovation for the bathypelagic result specifically would require examination of other independent teleost deep-sea radiations.

Deep-benthic anglerfishes (Chaunacoidei and Ogcocephaloidei) achieve comparable morphological innovation to bathypelagic ceratioids through a contrasting framework. Although within-bone integration is generally weak across all anglerfishes, deep-benthic lineages exhibit the strongest such integration among the habitat groups, concentrated in the angular bone (a key component of the lower jaw lever system; Westneat, 2004) (Figure 3A). This localized integration may provide a mechanical advantage for capturing benthic prey through sit-and-wait predation (Long & Farina, 2019; Nagareda & Shenker, 2008; Westneat, 2005). In teleost fishes, the angular is a critical component of the jaw-closing lever system, transmitting adductor muscle force around the quadrate-articular joint (Westneat, 2004). The geometry of the lower jaw lever system, including angular proportions, directly determines the trade-off between force and velocity transmission during jaw closing, and variation in these lever ratios is broadly associated with dietary ecology across fish communities (Wainwright & Bellwood, 2002; Wainwright et al., 2004). While direct biomechanical modeling of deep-benthic anglerfishes would be needed to confirm performance advantages, the coevolution of jaw lever system bones as tightly integrated functional units documented in labrid fishes (Gartner et al., 2023) supports the functional significance of angular integration in shaping deep-benthic jaw evolution. Alternatively, the strong trait covariation observed in deep-benthic specialists may partly reflect reduced morphological dimensionality imposed by dorsoventral compression itself, which constrains the axes along which jaw elements can independently vary. Analogous patterns of integration have been documented in batoids, where dorsoventral flattening coincides with strong covariation among pectoral fin elements (López-Romero et al., 2025). Whether driven by functional demands of benthic predation, morphological constraint imposed by body plan compression, or both, the localized integration in deep-benthic anglerfishes represents a distinct pathway to morphological innovation compared to the whole-jaw integration network of bathypelagic ceratioids.

Mosaic evolution and functional demands

Beyond these habitat-specific integration patterns, the mosaic evolution across the anglerfish skull reveals how functional demands shape cranial evolution across the radiation. The neurocranium and ceratohyal exhibit consistently elevated evolutionary rates across all lineages, contrasting with slower evolution in the oral jaw complex (Figure 3B). Rapid neurocranial evolution likely reflects its structural roles in accommodating diverse body plans ranging from dorsoventrally compressed monkfishes to globose ceratioids and housing divergent orbital morphologies associated with sensory strategies. Deep-benthic species exhibit enlarged orbits for visually detecting prey just above the seafloor (Colmenero et al., 2010; Miller et al., 2025), whereas bathypelagic ceratioids show reduced orbital size, relying instead on bioluminescent lures to draw prey within striking range (Kitchell, 1979; Miller et al., 2025; Pietsch, 2009). Meanwhile, the accelerated evolution of the ceratohyal likely reflects ventilatory specialization, as deep-sea lineages possess an enlarged branchiostegal apparatus supporting gill chamber inflation required for extended ambush predation (Long & Farina, 2019). The neurocranium and ceratohyal appear to be cranial modules under strong and divergent functional pressures across anglerfishes. The oral jaw complex, by contrast, shows the most pronounced integration reorganization in deep-sea lineages despite comparatively modest rate acceleration, suggesting that rate acceleration and integration restructuring need not coincide across the skull.

Conclusion

Our analyses reveal three key features of cranial evolution in anglerfishes. First, deep-sea anglerfishes consistently evolve stronger cranial integration than their shallow-water relatives, consistent with that integration is associated with morphological evolution in this radiation. Second, deep-sea lineages achieved morphological diversity primarily through innovation, evolving in phenotypic directions that depart from the dominant axis across Lophiiformes. Third, mosaic evolutionary rates reveal the neurocranium and ceratohyal as the most dynamic cranial modules across the anglerfish radiation. These results illustrate how evolutionary integration may drive morphological innovation in extreme environments.

These findings situate anglerfishes within a broader pattern of morphological evolution in which the deep sea repeatedly functions as a catalyst for phenotypic innovation across distantly related fish lineages (Martinez et al., 2021; Myers et al., 2021), adding to a growing body of evidence that evolutionary integration can accompany and even promote morphological innovation. Our results support a shift in perspective, from modularity as the primary facilitator of innovation toward integration as an equally potent mechanism under strong directional selection. Alongside radiations where modularity has been implicated in morphological diversification, such as Antarctic icefishes (Neves et al., 2025), our findings suggest that the direction of covariation reorganization (toward integration or modularity) may reflect the nature of selective pressures imposed. Environments demanding co-ordinated multitrait responses toward a shared optimum may favor integration, while those opening multiple divergent optima across an ecospace may favor modularity. This perspective extends beyond the deep sea. Habitat transitions that impose strong correlated selection toward a shared functional optimum may promote innovation through the strengthening of evolutionary integration. Testing this hypothesis across additional radiations (e.g., Liparidae and *Sebastes*, which have radiated across depth gradients) spanning diverse selective regimes remains an important goal for understanding the macroevolutionary consequences of trait covariation across the Tree of Life.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

All data and R code supporting the results are archived on Figshare and publicly available at https://doi.org/10.6084/m9.figshare.33110411 (Chan et al. 2026). CT scans were previously published by Miller et al. (2025) and are publicly available on MorphoSource (https://www.morphosource.org/).

Author contributions

H.C., E.C.S., and K.M.E. designed research; H.C. analyzed data; and H.C., E.C.S., and K.M.E. wrote the paper. All authors contributed to the final paper.

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Conflict of interest

The authors declare that they have no competing interests.

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