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A phylogenomic framework for pelagiarian fishes (Acanthomorpha: Percomorpha) highlights mosaic radiation in the open ocean

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The fish clade Pelagiaria, which includes tunas as its most famous members, evolved remarkable morphological and ecological variety in a setting not generally considered conducive to diversification: the open ocean. Relationships within Pelagiaria have proven elusive due to short internodes subtending major lineages suggestive of rapid early divergences. Using a novel sequence dataset of over 1000 ultraconserved DNA elements (UCEs) for 94 of the 286 species of Pelagiaria (more than 70% of genera), we provide a time-calibrated phylogeny for this widely distributed clade. Some inferred relationships have clear precedents (e.g. the monophyly of ‘core’ Stromateoidei, and a clade comprising ‘Gempylidae’ and Trichiuridae), but others are unexpected despite strong support (e.g. Chiasmodontidae + *Tetragonurus*). Relaxed molecular clock analysis using node-based fossil calibrations estimates a latest Cretaceous origin for Pelagiaria, with crown-group families restricted to the Cenozoic. Estimated mean speciation rates decline from the origin of the group in the latest Cretaceous, although credible intervals for root and tip rates are broad and overlap in most cases, and there is higher-than-expected partitioning of body shape diversity (measured as fineness ratio) between clades concentrated during the Palaeocene–Eocene. By contrast, more direct measures of ecology show either no substantial deviation from a null model of diversification (diet) or patterns consistent with evolutionary constraint or high rates of recent change (depth habitat). Collectively, these results indicate a mosaic model of diversification. Pelagiarians show high morphological disparity and modest species richness compared to better-studied fish radiations in contrasting environments. However, this pattern is also apparent in other clades in open-ocean or deep-sea habitats, and suggests that comparative study of such groups might provide a more inclusive model of the evolution of diversity in fishes.

1. Introduction

The open ocean represents one of the largest habitats on Earth. Highly connected and seemingly homogeneous in comparison to environments that are structurally complicated, patchy or readily subdivided, the global pelagic realm appears an unpromising setting for reproductive isolation and subsequent speciation [1–3]. Despite broad ranges and high mobility of larvae and adults [4], there are

conspicuous examples of diversification among open-ocean fishes [5]. Perhaps the most striking is Pelagiaria, a group comprising nearly 300 species placed in 15 taxonomic families [6]. Pelagiaria includes tunas, which are among the most commercially significant, anatomically well-understood and physiologically remarkable of all fishes [7]. Tunas represent only about 5% of pelagiarian species, and are joined by a diversity of less prominent but no less spectacular lineages, including: swallows (Chiasmodontidae), which contain bioluminescent species as well as those that engulf prey larger than themselves [8]; butterfishes and kin (Stromateoidei), which possess remarkable pharyngeal feeding structures and often develop commensal relationships with pelagic invertebrates [9]; scabbardfishes (Trichiuridae), with long, eel-like bodies [10]; the butterfly kingfish (*Gasterochisma*), which evolved endothermy independently of the closely related tunas [11]; and the mysterious ragfish (*Icosteus*), which possesses a weakly mineralized, largely cartilaginous skeleton, and displays contrasting juvenile and adult forms once assigned to separate species [12].

How Pelagiaria diversified in the open ocean remains an outstanding question. Previous studies hypothesized that the group represents an ancient adaptive radiation, catalysed by ecological release arising from the Cretaceous/Palaeogene (K/Pg) extinction [6,13,14]. This interpretation rests on circumstantial evidence: palaeontological and molecular estimates of an early Palaeogene origin; inconsistent support for deep divergences suggestive of rapid diversification among anatomically disparate lineages; and selective extinction of some pelagic fish groups at the K/Pg that could have opened ecological opportunities in open-ocean settings. The dominant model of adaptive radiation posits rapid taxonomic and ecological divergence early in clade history [15], but several obstacles have prevented a direct test of this macroevolutionary hypothesis for Pelagiaria. First, pelagiarian interrelationships are wildly inconsistent between studies (electronic supplementary material, figure S1). Second, the time scale for pelagiarian diversification is unclear, with molecular clock estimates ranging from late Eocene (*ca* 35 Ma) for the clade as a whole [16,17] to Late Cretaceous (*ca* 70 Ma) for more nested radiations [18]. Third, patterns of phenotypic, ecological, and lineage diversification remain unquantified for this group.

We assembled a dataset of ultraconserved DNA elements (UCEs) and their flanking sequences representing over 1000 loci sampled from nearly three quarters of known genera and all families of Pelagiaria except the monotypic Amarsipidae. We married these new genetic resources with other data from modern pelagiarians in order to: (i) infer phylogenetic relationships; (ii) test the hypothesis of early Cenozoic divergence; (iii) quantify patterns of phenotypic, ecological, and lineage diversification to test the previous hypothesis of adaptive radiation [19,20]. More broadly, we seek to establish a mature systematic and evolutionary framework for Pelagiaria that can inform our understanding of diversification in the open ocean and other expansive, spatially continuous habitats, thereby providing a contrast to extensively studied fish systems associated with settings like reefs [21–23].

2. Material and methods

(a) Sequencing protocols

We generated new sequence data for 108 samples, spanning 94 of the 286 species of Pelagiaria (71% of genera) and 14 outgroup

species. We followed laboratory protocols for DNA extraction, genomic library preparation, hybrid-enrichment and sequencing from [24], targeting a set of approximately 1200 UCE loci useful for phylogenetic studies of acanthomorphs [25]. We generated data matrices of 75% (alignment of each locus contains 84 of 112 taxa) and 95% (106 of 112 taxa) completeness for primary phylogenetic analyses. The electronic supplementary material contains additional details of this and other analyses.

(b) Phylogenetic analyses

We adopted three phylogenetic approaches. First, we performed maximum likelihood (ML) and Bayesian phylogenetic inference on partitioned, concatenated alignments for both 95% and 75% complete matrices. Second, we conducted Bayesian concordance analysis (BCA) using BUCKy version 1.4.4 [26,27] in order to evaluate the agreement in phylogenetic signal among individual loci in our dataset. Third, we performed coalescent-based analyses in the program ASTRAL v. 4.4.4 [28] using datasets of loci containing sequences for at least 75% and 95% of our sampled species.

(c) Divergence-time estimation

We incorporated fossil-based age priors for 20 nodes, 14 within Pelagiaria and 6 among outgroups. Prior distributions were empirically informed by the age distribution of additional fossil outgroups as in [24,25]. We used two strategies to estimate divergence times for a fixed topology obtained from the Bayesian and ML analyses of the 75% complete matrix, which both recovered topologically identical trees. First, we performed dating analyses on 10 independent subsets of 25 UCE loci in BEAST v. 1.8 [29]. Second, we used MCMCTree from the PAML package [30] to incorporate larger amounts of sequence data (by-site partitioning: 61 947 bp; locus-partitioning: 76 956 bp or 93 loci) into our divergence-time estimates than is feasible in BEAST. We used lognormal calibration densities for BEAST analyses and uniform densities (with 5% probability mass beyond the soft maximum bound) for MCMCTree analyses (further details in electronic supplementary material). In order to incorporate temporal and topological uncertainty into subsequent comparative analyses, we generated two sets of 100 trees from the posterior distribution of BEAST analyses. Our first set of trees for comparative analyses addresses temporal uncertainty, and was drawn from the post-burnin runs of the fixed-topology BEAST analyses described above. To incorporate uncertainty in timing and relationships, we drew trees from the posterior distribution of a different BEAST analysis that estimated divergence times using 25 randomly selected UCE loci but which did not impose a topological constraint.

(d) Quantifying patterns of lineage diversification

We assessed patterns of diversification dynamics within Pelagiaria using BAMM 2.5.0 [31,32] on each of 100 individual trees from the posterior sample of the topologically unconstrained and constrained BEAST divergence dating analyses described above, with adjustments for incomplete taxonomic coverage using family-specific sampling fractions. For comparison, we also estimated speciation rates for Pelagiaria and additional marine fish clades by using the R package fishtree [33] and by parsing BAMM outputs given in the supplement of Rabosky *et al.* [34]. We report estimates that allow time-varying rate regimes for consistency with our results (λ_{BAMM} of [34]), with the caveat that phylogenies differ (in terms of topology, time scale and sampling fraction) between our study and [34].

(e) Quantifying patterns of morphological and ecological diversification

We examined three sets of morphological and ecological traits: fineness ratio (relative body depth; fork length divided by maximum body depth as measured from published images; $n = 80$), an index of body elongation reflecting the principal axis of body shape variation in many surveys of fish diversity [21] and relevant to locomotor mode and drag reduction [35]; depth ecology compiled from rfishbase [36], measured as \log_{10} of mean (average of reported maxima and minima; $n = 70$) depths; and diet data binned categorically as large, evasive prey (e.g. fishes and squids), gelatinous zooplankton (e.g. jellyfishes, salps), and smaller zooplankton, based on the food item that had the highest score for the metric reported for each species (i.e. per cent frequency occurrence or total wet weight of food item) in the literature ($n = 66$). Fineness ratio and depth were subjected to subclade disparity through time (DTT) analyses [37] using the R package GEIGER [38]. Deviations from the Brownian null were assessed using the rank-envelope test [39], which indicates both the presence of significant deviations and their timing. Positive deviations signal greater within-subclade variation than expected, while negative deviations reflect higher than expected partitioning of variation between subclades [37]. The latter is often interpreted as consistent with models of adaptive radiation [39]. Diet data were examined using the comparative approach applied by Ribeiro *et al.* [40], which detects time intervals characterized by more or fewer shifts in a multistate, discrete trait than expected under a simulated null. We modified this procedure by extending it across multiple trees, recording significant deviations within 1 Myr intervals for each tree.

3. Results

(a) Phylogenetic relationships

Monophyly of Pelagiaria is well supported in both concatenated and coalescent-based analyses (figure 1; electronic supplementary material, figures S1–S4), as is that of all traditional families with the exception of ‘Gempylidae’. Likewise, relationships within families are resolved and strongly supported, and show broad correspondence to past morphological analyses [42–46].

Several lineages classified in monotypic or monogeneric families (*Arripis*, *Icosteus aenigmaticus* and *Pomatomus saltatrix*) behave as rogue taxa (electronic supplementary material, figure S5), showing inconsistent relationships between phylogenies inferred under different approaches. We invariably resolve three large suprafamilial clades: (i) Caristiidae, Bramidae, *Scombrobrax heterolepis* (Scombrobracidae), ‘Gempylidae’ and Trichiuridae; (ii) Scombridae as the sister lineage of a group containing Chiasmodontidae and the species of *Tetragonurus*; and (iii) Stromateidae as sister to a lineage containing species of *Ariomma* and Nomeidae, representing a ‘core’ stromateoid radiation. The relationships of these three major suprafamilial clades to one another, and to Centrolophidae, are inconsistent between analyses.

Some relationships in each of the suprafamilial clades are found in a larger proportion of gene trees than alternative topologies, resulting in relatively high genome-wide concordance factor (CF) estimates (electronic supplementary material, figure S6). The highest sister-lineage CF estimates are for Chiasmodontidae + *Tetragonurus* (CF = 0.495 [95% CI: 0.469–0.521]), ‘Gempylidae’ + Trichiuridae (CF = 0.482 [95% CI: 0.458–0.506]) and *Ariomma* + Nomeidae (CF = 0.445

[95% CI: 0.420–0.472]). *Scombrobrax heterolepis* and Stromateidae each scored high CF estimates for bipartitions with their sister clades (‘Gempylidae’ + Trichiuridae and *Ariomma* + Nomeidae, respectively). The rogue taxa *Arripis*, *Icosteus aenigmaticus*, and *Pomatomus saltatrix* show equivocal results when examined through individual UCE gene trees, and are resolved with numerous candidate sister lineages in nearly equal numbers of gene trees. *Pomatomus saltatrix* exemplifies this pattern, with an equal proportion of loci resolving it in a bipartition with either Scombridae or *Arripis*, while the 95% confidence interval for genome-wide concordance factors for either of these taxa overlap with those of eight other families. Scombridae does not behave like a rogue taxon, but six families, including the three rogue taxa, appear in bipartitions with Scombridae at higher frequencies than either Chiasmodontidae or *Tetragonurus* alone. However, the combined number of loci that support bipartitions of Scombridae with Chiasmodontidae and *Tetragonurus* is higher than the number supporting alternative topologies.

(b) Divergence-time estimates

Divergence time estimates were congruent between topologically constrained analyses, with broadly overlapping 95% credible intervals for most nodes. We refer to dates inferred from an analysis of 25 UCE loci in BEAST unless otherwise noted (figure 1; electronic supplementary material, figure S7), with age estimates from this and MCMCTree analyses provided in electronic supplementary material (electronic supplementary material, table S1 and figure S8). We estimate the age of crown Pelagiaria as 72.76 Ma, or latest Campanian, and plausible times of origin span nearly the entire Campanian–Maastrichtian interval of the Late Cretaceous (95% HPD: 66.39–81.65 Ma). MCMCTree analyses yield younger age estimates for the pelagiarian root (67.72–66.44 Ma) and narrower credible intervals for this and other nodes; the analysis with by-site partitioning cannot exclude the possibility that the crown originated after the K/Pg. Short internodes characterize the deepest divergences within Pelagiaria, and well-supported sub-clades originate around or shortly after the K/Pg boundary: Stromateidae + *Ariomma* + Nomeidae (‘core’ stromateoids), *Tetragonurus* + Chiasmodontidae, Scombridae, Bramidae + Caristiidae, *Scombrobrax heterolepis* + ‘Gempylidae’ + Trichiuridae. Origins for crown Stromateidae, Chiasmodontidae, Bramidae, ‘Gempylidae’ and Trichiuridae fall within the Eocene. Crown groups for all other adequately sampled, non-monotypic families are Miocene in age. The rogue taxa *Pomatomus saltatrix*, *Icosteus aenigmaticus*, and *Arripis* branch deeply within pelagiarian phylogeny, implying tens of millions of years of independent evolutionary history for each.

(c) Patterns of lineage diversification

BAMM analyses find little support for diversification dynamics of subclades that differ significantly from that of the entire radiation, with the credible set inferred for a majority of topologically unconstrained and constrained trees comprising a single rate regime (88 and 100%, respectively; electronic supplementary material, figure S9). Estimated mean rates at the roots of individual trees are higher than those for their tips, but there is substantial variation in mean rates and the degree of decrease across trees (figure 2a; electronic supplementary material, figures S9–S11). The mean of mean rates for the

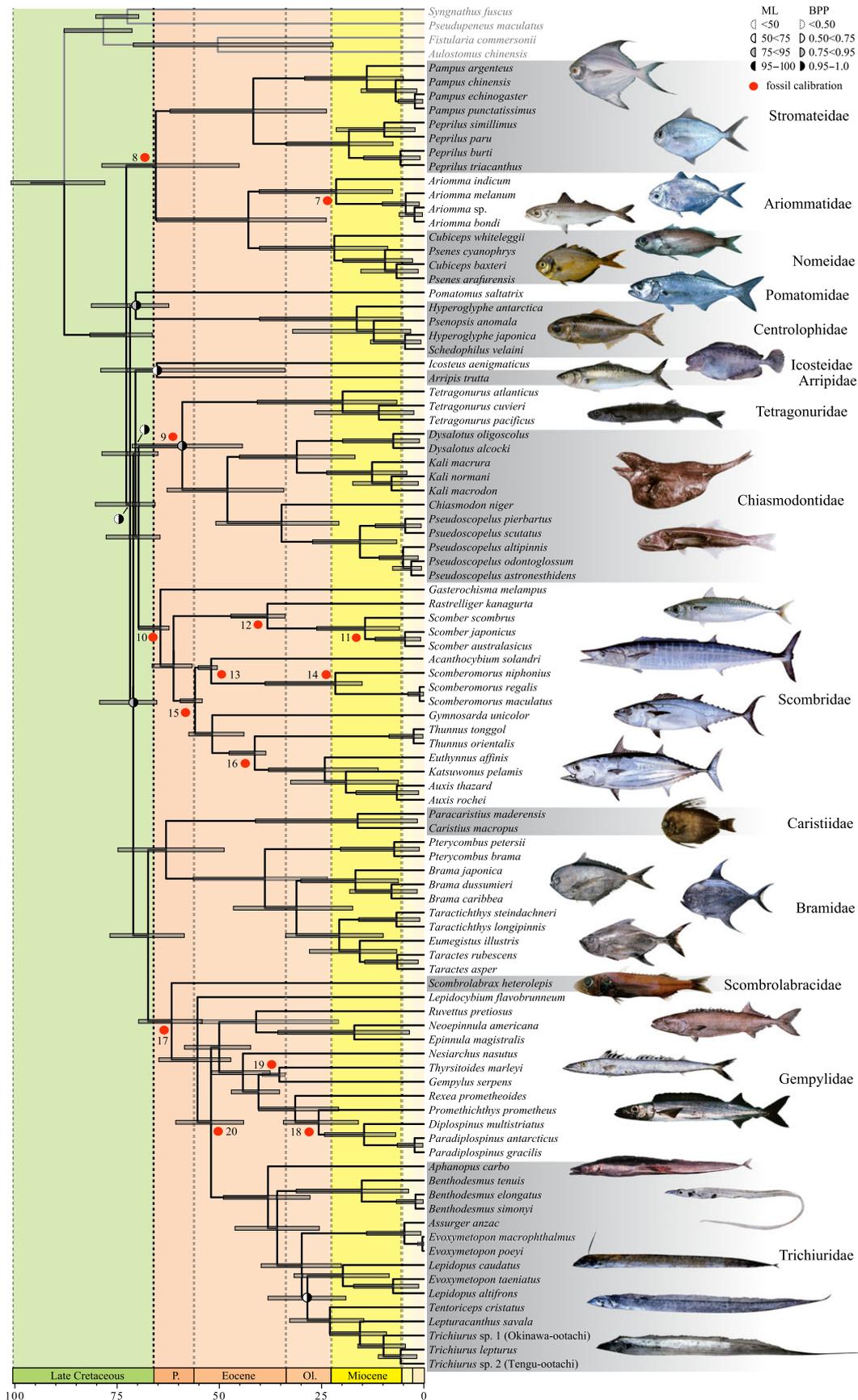


Figure 1. Time-calibrated phylogeny of Pelagia based on topology inferred from 75% complete data matrix (1007 UCE loci). Statistical support values for nodes are indicated by monochrome shaded discs. Maximum likelihood bootstrap (ML) and Bayesian posterior probability (BPP) support are indicated by the left and right halves of the discs, respectively. Nodes without discs received support of 100% ML and 1.0 BPP. Red discs indicate the placement of fossil calibrations, with numerals corresponding to calibration numbers given in electronic supplementary material. *Pampus argenteus*, *Ariomma indicum*, *Ruvettus pretiosus*, *Promethichthys prometheus*: J. E. Randall (CC BY-NC); *Peprilus burti*: © R. Robertson (with permission); *Ariomma bondi*: © J. Kolding (with permission); *Cubiceps whiteleggii*: H. B. Osmany (CC BY-NC); *Pomatomus saltatrix*: NOAA; *Icosteus aenigmaticus*: J. P. Williams (CC BY-NC); *Arripis trutta*: Australian National Fish Collection/CISRO (CC BY-NC); *Aphanopus carbo*: © Pedro Niny Duarte/Universitário dos Açores (with permission). All other images from [41] (pls 144 B,G,E; 145 B; 217 D-E; 219 D-E; 220 F-G; 221 E; 223 E; 224 B,D,F-G; 233 A, G-E), © Tokai University Press, used with permission. See electronic supplementary material table S2 for further details.

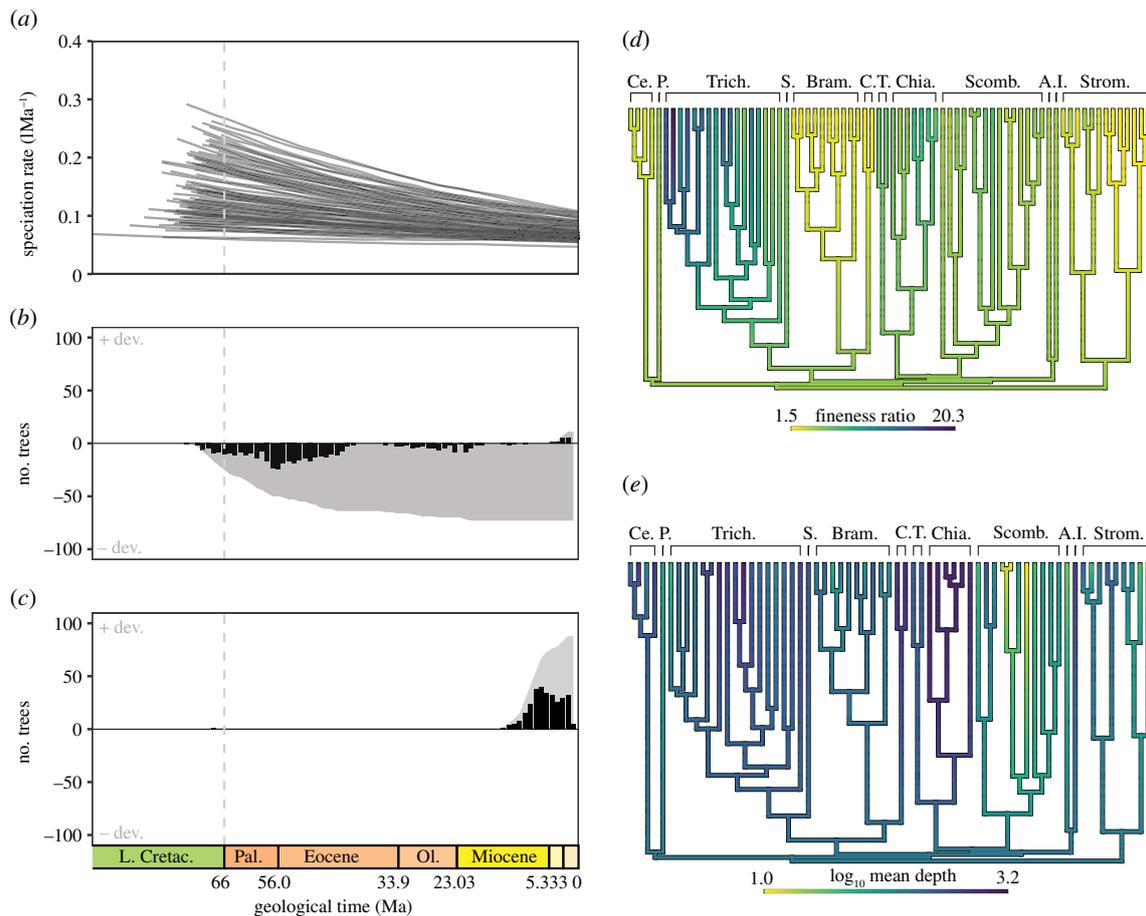


Figure 2. Patterns of evolutionary diversification in Pelagiaria. (a) BMM-estimated mean speciation rates for 100 time-scaled phylogenies drawn from the posterior distribution of a topologically constrained BEAST divergence dating analysis ($n = 100$). Dashed vertical line indicates the K/Pg boundary. (b) Proportion of trees showing significant deviations from a subclade disparity through time (DTT) trajectory based on a constant rate Brownian motion null model for fitness ratio. Bar height at a given timestep indicates number of trees showing significant positive (above horizontal line) or negative (below horizontal line) deviations from the null. Grey envelope represents an accumulation curve, indicating the total number of trees showing at least one interval of significant deviation before that time. (c) Proportion of trees showing significant deviations from a subclade disparity through time (DTT) trajectory based on a constant rate Brownian motion null model for \log_{10} (mean depth). (d) Contour mapped [47] consensus of trees used in (a–c) showing evolution of fitness ratio. (e) Contour mapped consensus of trees used in (a–c) showing evolution of depth ecology. Differences between trees in (d) and (e) reflect differing availability of data for fitness ratio and depth ecology. Abbreviations: A., Arripidae; Bram., Bramidae; C., Caristiidae; Ce., Centrolophidae; Chia., Chiasmodontidae; L., Icosteidae; P., Pomatomidae; S., Scombrobracidae; Scomb., Scombridae; Strom., ‘core’ Stromateoidei (Ariommatidae + Nomeidae + Stromateidae); T., Tetragonuridae; Trich.: Trichiuroidei (‘Gempylidae’ + Trichiuridae).

constrained and unconstrained tree sets, respectively, are 0.149 IMyr^{-1} (range of means = $0.0634\text{--}0.292 \text{ IMyr}^{-1}$) and 0.184 IMyr^{-1} ($0.0769\text{--}0.351 \text{ IMyr}^{-1}$) at the base of the tree, 0.0732 IMyr^{-1} ($0.0469\text{--}0.108 \text{ IMyr}^{-1}$) and 0.0942 IMyr^{-1} ($0.0568\text{--}0.147 \text{ IMyr}^{-1}$) at the tips, and 0.0963 ($0.0537\text{--}0.155 \text{ IMyr}^{-1}$) and 0.122 IMyr^{-1} ($0.0668\text{--}0.203 \text{ IMyr}^{-1}$) overall. Credible intervals about the mean values of root and tip rates are broad, and these overlap for nearly all trees (unconstrained: 98/100; constrained: 97/100; electronic supplementary material, figure S11).

(d) Patterns of morphological and ecological diversification

We reject constant-rate, diffusive change in fitness ratio in Pelagiaria. Rank-envelope tests show significant negative excursions overwhelmingly placed in the early phases of pelagiarian diversification for the samples of topologically unconstrained and constrained trees (figure 2b; electronic supplementary material, figure S10b). Half of all trees show at least one negative deviation at or before the earliest Eocene (i.e.

where the height of the accumulation curve is 50 trees; constrained: 56 Ma; unconstrained: 59 Ma), and a majority of trees show negative deviations before the end of the epoch (constrained: 66%; unconstrained: 95%). This implies the concentration of differentiation in gross body form early in pelagiarian phylogeny, but mostly occurring after the K/Pg. Positive deviations are recorded for a minority of trees near the Recent for both tree samples (figure 2b; electronic supplementary material, figure S10b). By contrast, depth ecology does not show negative excursions from a Brownian null early in pelagiarian history, but a majority of trees (constrained: 88%; unconstrained: 92%) show significant positive excursions from Brownian expectations in the Neogene (figure 2c; electronic supplementary material, figure S10c). Unlike body shape and depth ecology, there is no strong indication that evolution of diet deviates significantly from null expectations; only a few trees show more changes than expected during the Neogene (electronic supplementary material, figure S12a,c). We infer a probable diet of evasive prey for the last common ancestor of pelagiarians (electronic supplementary material, figure S12b,d).

4. Discussion and conclusion

(a) Agreement and disagreement with past phylogenetic hypotheses

Our analysis supports many patterns of relationships inferred from morphology, including the monophyly of all pelagiarian families excluding ‘Gempylidae’ (see also [48]), and details of intrafamilial relationships. The latter is apparent for Trichiuridae [44], Chiasmodontidae [46] and especially Scombridae, where UCE data agree with the established tribal classification [45,49] more closely than previous molecular studies [6,16,18,50]. Our results confirm nesting of Trichiuridae within ‘gempylids’ [43,44,48,51,52], and the sister-group relationship between Caristiidae and Bramidae mirrors anecdotal associations [53,54].

Our results do not support two motifs of morphological classifications: Scombroidei, a clade comprising Scombridae and Trichiuroidei to the exclusion of other groups [55]; and Stromateoidei, encompassing Centrolphidae, Nomeidae, Stromateidae, and the species of *Ariomma* and *Tetragonurus* [9]. *Scombrobrax heterolepis* is the sister lineage of trichiuroids to the exclusion of scombrids, consistent with pre-cladistic interpretations [56,57]. This, along with resolution of *Gasterochisma melampus* as the earliest diverging scombrid, indicates characters used to unite Scombridae and Trichiuroidei [48] are homoplastic. As in previous molecular analyses [6,16,50,58], our phylogeny does not resolve Stromateoidei as a clade. Particularly striking is the well-supported sister-group relationship between the putative stromateoid *Tetragonurus* and chiasmodontids. Although they share superficial similarities like dark coloration and mesopelagic ecology, these lineages display marked differences, particularly with respect to feeding. *Tetragonurus* possesses greatly enlarged posterior pharyngeal bones (comprising fused third and fourth pharyngobranchials) that extend into papillae-lined pharyngeal sacs classically regarded as a stromateoid synapomorphy, coupled with short, box-like jaws bearing slicing dentary teeth [9]. These features appear to relate to a near-exclusive diet of gelatinous zooplankton [9]. By contrast, chiasmodontids have large jaws bearing long teeth combined with a distensible stomach and body walls, permitting ingestion of large fishes whole and inspiring the group’s common name of swallowers.

(b) The time scale of pelagiarian evolution

Our time-calibrated phylogeny indicates the emergence of several distinctive crown pelagiarian lineages near the K/Pg boundary, with these groups first known from body fossils around or just before the Palaeocene–Eocene boundary [59,60]. Quantitative biostratigraphic models reject or cast considerable doubt on Cretaceous origins for some pelagiarian sub-clades [6], although we estimate a latest Cretaceous age for the clade as a whole (cf. [25,34]). This consilience stands in contrast to previous studies delivering much younger [16,61] or older [18] estimates that might reflect inadequate or inaccurate calibration schemes. Short stem lineages associated with the crown radiations of scombrids, trichiuroids, and core stromateoids suggest that their distinctive morphologies arose in as little as 5–7 Myr. Similar circumstances surround the origin of other distinctive percomorph morphologies [24,40] in terms of the duration over which these new body shapes evolved as well as their absolute timing.

The appearance of scombrids, trichiuroids and other distantly related predatory percomorphs in the early Palaeogene has been interpreted as a response to the extinction of major Mesozoic groups of predatory marine teleosts [13,14,62]. The parallel origin of these lineages is one of the more promising possible examples of ecological release associated with the radiation of percomorphs at this time [25]. By contrast, potential drivers of diversification of other pelagiarian groups are less obvious, although open-ocean ecosystems underwent apparent collapse [63] and subsequent restructuring [64–66] associated with the K/Pg. These suggest a broad range of ecological opportunities of the kind thought to be critical in triggering divergence [15]. For example, a hypothesized proliferation of jellyfishes in the early Palaeogene [63] could have provided the substrate for diversification of pelagiarian clades that directly feed upon [9] or are otherwise associated with gelatinous zooplankton [67].

(c) Mosaic diversification in Pelagiaria

Our comparative analyses provide insights on two critical questions. First, they indicate the degree to which Pelagiaria follows patterns predicted for adaptive radiations [15], as well as the more specific hypothesis of diversification triggered by extinction-mediated ecological release [6]. Second, and more generally, they provide insight into the origin of diversity in expansive habitats that seem unlikely settings for evolutionary radiations [1].

The range of mean tip rates for Pelagiaria (0.0469–0.147 IMyr^{-1}) spans that recovered by Rabosky *et al.* [34] (0.0761 IMyr^{-1}), but is lower than tip rates across actinopterygians as a whole (0.164 IMyr^{-1} [34]). The range of mean overall pelagiarian speciation rates (0.0537–0.203 IMyr^{-1}) encompasses both past estimates for the clade (0.0577 [34]) as well as those over the history of actinopterygians (0.141 IMyr^{-1} [68]; 0.0904 IMyr^{-1} [34]). Faster speciation rates at the root of pelagiarian phylogeny than at the tips could be interpreted as a consequence of a diversity-dependent slowdown under a niche-filling model of adaptive radiation [69], but this peak in speciation predates hypothesized ecological opportunity in the early Palaeocene and the major divergences in overall body form centred in the Palaeocene–Eocene (figure 2b; electronic supplementary material, figure S10b). Planktonic foraminifera do show a pronounced rise in richness during the Maastrichtian [70] thought to stem from ocean stratification conducive to diversification [71]. No corresponding increase in origination of pelagic fish tooth morphotypes occurs at this time [66], implying that if diversification did occur during this interval, it might have been morphologically cryptic. However, broadly overlapping credible intervals for tip and root rates, along with past estimates of more constant speciation rates in the group over much of the Cenozoic [34], suggest a cautious approach to interpreting temporal variation in pelagiarian speciation.

Patterns of phenotypic and ecological evolution only partially conform to theoretical expectations for adaptive radiations [15]. The early history of Pelagiaria is characterized by substantial partitioning of body-form diversity between rather than within lineages, manifest in the establishment of morphologically distinctive clades. These deviations are overwhelmingly placed in the early Palaeogene, making them consistent with morphological diversification mediated by the K/Pg and observations from the fossil record [14,66].

Patterns recovered for ecological attributes differ. In the case of depth, significant deviations from the null are positive and concentrated in the Neogene, long after either the origin of the clade or the K/Pg. This could reflect either an Ornstein–Uhlenbeck or accelerating model of evolution for depth ecology for this recent interval [39]. The timing of changes in dietary preference lack consistent deviations from a null model, indicating constant transitions over clade history.

The absence of unanimous support for an ‘early burst’ model of evolution across these attributes reflects a more general pattern in comparative studies, which yield similarly ambiguous evidence even for clades considered textbook examples of adaptive radiation [72]. In response, some have advocated a return to a more classic model of adaptive radiation [73] that focuses on the origin of major dietary or locomotor adaptations associated with higher taxa rather than species [19]. Others have argued that an emphasis on ‘early burst’ dynamics obscures understanding of the more nuanced nature of evolutionary diversification [23]. We find evidence of mosaic radiation in Pelagiaria: potentially declining rates of speciation from the time of the clade’s origin followed later by establishment and subsequent stasis of gross body forms and presumed locomotor mode [35], but substantial lability in aspects of depth ecology and diet throughout the history of the group. Pelagiaria therefore combines some features of ‘early burst’-style radiation in terms of gross phenotype [40] with more sustained change in ecological traits [23]. Both our time-calibrated tree and the fossil record suggest that many distinctive morphological features associated with feeding in specific lineages (e.g. non-protrusible jaws in trichiurids and scombrids; enlarged fangs in trichiurids and scombrilabrids; pharyngeal sacs and papillae in ‘stromateoids’ [9,48]) appeared early in pelagiarian history [60,74], with little subsequent modification even as diets within clades have varied. This finds a parallel in labrids, which show declining rates for the origin of major anatomical feeding innovations, but constant—or potentially accelerating—rates of dietary transition over time [23]. These shared patterns of trophic flexibility in the face of anatomical specialization are evocative of Liem’s paradox [75] on a macroevolutionary scale.

(d) Radiation in the open ocean

Diversification of Pelagiaria in what at first might appear to be the homogeneous environment of the open ocean evokes classic debates on how diversity can arise and persist in uniform settings [3]. But as in well-studied radiations, pelagiarians have clearly diverged along a combination of trophic and spatial axes. Dietary specializations of the group range from plankton [76] to gelatinous zooplankton [9] to pelagic arthropods, cephalopods, and fishes [9,76,77]. Pelagiarians have also partitioned the open ocean along a series of spatial or habitat axes, including depth gradients and intimate associations with pelagic invertebrates including salps, medusae and siphonophores [67,78–80].

Pelagiarians show potentially informative differences with well-studied fish radiations in terms of relative levels of morphological diversity and species richness. Labrids [23], South American cichlids [81] and cichlid radiations in both Lake Victoria and Lake Malawi [82] all outnumber pelagiarian species richness by more than a factor of two, but these other radiations are arguably more conservative in terms of body-shape diversity than pelagiarians. As a crude comparison,

each of these species-rich examples comprises only a single family or subfamily in contrast to the at least 15 anatomically disparate families of Pelagiaria. Of these other groups, labrids make the most useful comparison with pelagiarians: both are marine, broadly distributed, and originate during the interval surrounding the K/Pg [23]. However, labrids principally diversified in association with reefs [22], which would seem to represent a first-order factor underlying macroevolutionary contrasts with pelagiarians. Both groups have pelagic larvae, but most pelagiarians have extensive dispersal capabilities at all stages of life history that should further oppose evolutionary differentiation by maintaining gene flow over broad spatial scales [2]. Indeed, many pelagiarian species have wide geographical distributions [4], with some consisting of a single, global population with no obvious geographical structure [83]. High variation in estimated speciation rate across individual trees in our analyses complicates comparison with other lineages, and is compounded by potentially misleading comparisons of mean rates from analyses restricted to focal clades (as of Pelagiaria here) to those where rate estimates for the focal clade are informed by data for other lineages [84]. A recent analysis of diversification dynamics across fishes [34] considers these contrasting groups within a common phylogenetic and analytical framework, and finds mean overall speciation rates for pelagiarians (0.0569 Myr^{-1}) are lower than those of labrids (0.0789 Myr^{-1}) and other iconic reef fish lineages (e.g. Acanthuridae: 0.0900 Myr^{-1} ; Chaetodontidae: 0.116 Myr^{-1} ; Pomacentridae: 0.102 Myr^{-1}). None of these reef fish groups shows an early peak in speciation rate, but instead show an increase in rate commencing in the Neogene and continuing to the present day [34].

Pelagiarians display a remarkable range of morphologies given their modest species richness; scombrids alone nearly equal the body-shape disparity of labrids, which comprise an order of magnitude more species [22]. This pattern is not unique to pelagiarians, and many radiations associated with pelagic or deep-sea settings show a combination of high morphological disparity and low taxonomic richness (Lampridiformes [85] and Stephanobercyiformes [86] represent extreme examples). Some high-richness, low-disparity fish clades in the deep sea (e.g. Myctophidae) have species-specific bioluminescence hypothesized to facilitate speciation [87], and might therefore represent exceptions to a general rule. These patterns, and the contrasts they might make with the better-documented macroevolutionary histories of fishes in other environmental settings like reefs [22,23,88], are little studied but could help provide a more inclusive comparative perspective on the evolution of diversity in fishes.

Data accessibility. UCE raw read data are archived in the NCBI Sequence Read Archive (SRA) under BioProject number PRJNA561597. Data and scripts for 75% complete BEAST analyses, MCMCTree analyses and all comparative analyses are archived in Dryad Digital Repository (doi:10.5061/dryad.sq067ng).

Authors’ contributions. M.F. and R.C.H. designed the project. R.C.H. and B.C.F. generated UCE sequences and R.C.H. conducted phylogenetic analyses, with contributions from D.Č. Molecular laboratory work and sequencing was conducted in laboratory facilities overseen by B.C.F. and T.J.N. K.L.F., H.T.B., R.C.H. and M.F. gathered trait data and conducted comparative analyses. M.M. contributed tissue samples. M.F. and R.C.H. designed and wrote the manuscript. All authors read, made suggestions about and approved the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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