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Phylogenomic resolution of the monotypic and enigmatic *Amarsipus*, the Bagless Glassfish (Teleostei, Amarsipidae)

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Abstract

Amarsipus carlsbergi is a rare mesopelagic fish distributed in the Indian and Pacific Oceans and is the only species classified in the family Amarsipidae. Since its description in 1969, phylogenetic hypotheses have varied regarding its relationship with other percomorph lineages, but most have indicated a close relationship with the traditional suborder Stromateoidei. Molecular phylogenies place families previously classified in Stromateoidei within a diverse clade—Pelagiaria—that includes fishes such as tunas, cutlassfishes and pomfrets. A recent analysis of a small number of loci resolved a clade containing *Amarsipus* and the stromateoid lineage *Tetragonurus*. A subsequent high-throughput sequence phylogeny based on ultraconserved elements (UCEs) of Pelagiaria lacked *Amarsipus*, but revealed both strong support for stromateoid paraphyly and high levels of gene tree incongruence. We gathered UCE sequence data for 610 UCE loci from *Amarsipus* and integrate these with samples from all remaining pelagiarian families. This provides a taxonomically comprehensive phylogenomic framework to test the evolutionary relationships of *Amarsipus*, and evaluate the support for stromateoid monophyly. As in previous studies, our analyses find high levels of gene tree topological discordance with regard to some deeper pelagiarian inter-relationships. However, we resolve *Amarsipus* as the sister lineage of a clade containing *Tetragonurus* and a family not considered a stromateoid lineage, Chiasmodontidae. This relationship is supported by both high gene tree concordance and node support. Our analyses also provide strong support for the paraphyly of Stromateoidei, casting uncertainty on previous hypotheses of the evolution of morphological traits across members of Pelagiaria.

KEYWORDS
concordance factors, Pelagiaria, Stromateoidei, ultraconserved elements

1 | INTRODUCTION

Acanthomorph (spiny rayed) fishes represent an exceptionally diverse clade that comprise more than 19,000 species and 320 families (Fricke et al., 2020), and pose many challenges for ichthyologists interested in their phylogenetic relationships. While acanthomorph phylogenetic uncertainty spans both ancient and more recent divergences, some of the most pernicious challenges involve the resolution of deep inter-relationships where identification of shared derived morphological features among lineages with long, independent evolutionary histories can be difficult (Girard et al., 2020; Johnson, 1993; Nelson et al., 2016). The application of molecular phylogenetics has advanced many aspects of our understanding of acanthomorph relationships (e.g. Alfaro et al., 2018; Betancur-R et al., 2013; Hughes et al., 2018; Near et al., 2013; Thacker et al., 2015), but it has also highlighted challenging areas where evolutionary phenomena such as incomplete lineage sorting (ILS) or limited phylogenetic informativeness pose barriers to phylogenetic analysis with relatively small numbers of loci (Harrington et al., 2016). This challenge is conspicuous for Pelagiaria, an acanthomorph subclade of mostly pelagic, open-ocean fishes that includes some of the most extensively studied species from a morphological standpoint (e.g. Scombridae, the tunas and mackerels) as well as less familiar and deep-sea lineages (e.g. the Ragfish, *Icosteus aenigmaticus* and swallowers of the family Chiasmodontidae). Our understanding of the interrelationships among pelagiarian families remains clouded by numerous opposing systematic hypotheses informed by either morphological or molecular data.

Hints that the morphologically disparate lineages comprising Pelagiaria share common ancestry appeared in several early molecular phylogenetic studies that lacked consistent taxonomic coverage of pelagiarian lineages (e.g. Chen et al., 2003; Smith et al., 2007; Yagashita et al., 2009). A mitogenomic study by Miya et al. (2013) provided the first comprehensive synthesis that included nearly all relevant families and defined Pelagiaria as a clade, uniting sixteen families previously classified among six different percomorph suborders. Christened Pelagia by Miya et al. (2013), the clade included members of two fixtures of 20th century acanthomorph classifications: the Scombroidei (Scombridae, Scombrolabracidae, Gempylidae and Trichiuridae) and the Stromateoidei (Amarsipidae, Ariommatidae, Centrolophidae, Nomeidae, Stromateidae and Tetragonuridae) (Greenwood, 1966). The billfishes, Xiphiidae and Istiophoridae, long classified in Scombroidei, are resolved as distantly related to all other pelagarians in molecular phylogenies (e.g. Alfaro et al., 2018; Harrington et al., 2016; Hughes et al., 2018; Little et al., 2010; Orell et al., 2006). Despite strong support for monophyly of Pelagiaria across diverse molecular phylogenetic studies, the monophyly of either the traditional Scrombroidei or Stromateoidei as subgroups within Pelagiaria is not supported (Alfaro et al., 2018; Betancur-R et al., 2013; Friedman et al., 2019; Hughes et al., 2018; Miya et al., 2013; Near et al., 2013; Orrell et al., 2006). The lack of support for stromateoid monophyly was an unanticipated result of molecular analyses due to the presence of a compelling morphological character shared among these fishes: the pharyngeal sac, a variously toothed sac-like structure located behind the gill arches, and hypothesized to facilitate the processing of gelatinous zooplankton such as jellyfish or salps that comprise the diet of many stromateoid species (Janssen & Harbison, 1981; Mansueti, 1963).

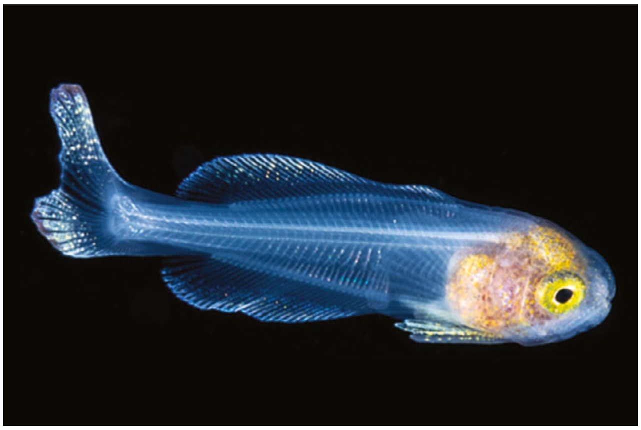

FIGURE 1 *Amarsipus carlsbergi*, photographed on 7 February 2019, Romblon, Phillipines. Photograph provided by courtesy of Linda Ianniello [Colour figure can be viewed at wileyonlinelibrary.com]

Amarsipus carlsbergi (Figure 1) is the only species in the family Amarsipidae and has been classified in Stromateoidei since its discovery and description (Haedrich, 1969). Although *Amarsipus* lacks the pharyngeal sac that is typical of other stromateoids, this rare species from the Indo-Pacific was allied with the stromateoids on the basis of several morphological features thought to be typical for the group, but of questionable systematic value: uniserial teeth in the jaws, an expanded lacrimal bone and an extensively developed subdermal canal system (Haedrich, 1969). Subsequent phylogenetic hypotheses based on morphology resolved *Amarsipus* as either sister to all stromateoids (Horn, 1984), nested within stromateoids (Doiuchi et al., 2004) or proposed that it may not even a member of the clade (Springer & Johnson, 2004; Figure 2). DNA samples for *Amarsipus* did not become available for molecular analyses until 2018, and phylogenetic analysis of several nuclear protein-coding loci and mitochondrial 16S RNA resolved *Amarsipus* and the stromateoid *Tetragonurus* as sister lineages (Campbell et al., 2018; Figure 2). As in previous molecular analyses (Betancur-R et al., 2013; Miya et al., 2013; Near et al., 2013), deeper nodes in Pelagiaria were poorly supported, and this molecular analysis did not resolve Stromateoidei as a monophyletic group.

A phylogenomic analysis of nearly 1,000 ultraconserved elements (UCEs) that included 15 of the 16 families of Pelagaria, lacking only *Amarsipus*, revealed substantial gene tree discordance that hampered resolution of deeper nodes in the phylogeny (Friedman et al., 2019). This was reflected by incongruent phylogenetic trees resulting from different methods of phylogenetic inference. While the phylogenomic analyses resolved a majority of stromateoid species in a strongly supported 'core' clade that contains Ariommatidae, Nomeidae and Stromateidae; the resolution of Centrolophidae and *Tetragonurus* in Pelagaria rendered Stromateoidei polyphyletic with varying degrees of node support. The placement of Centrolophidae was variable and

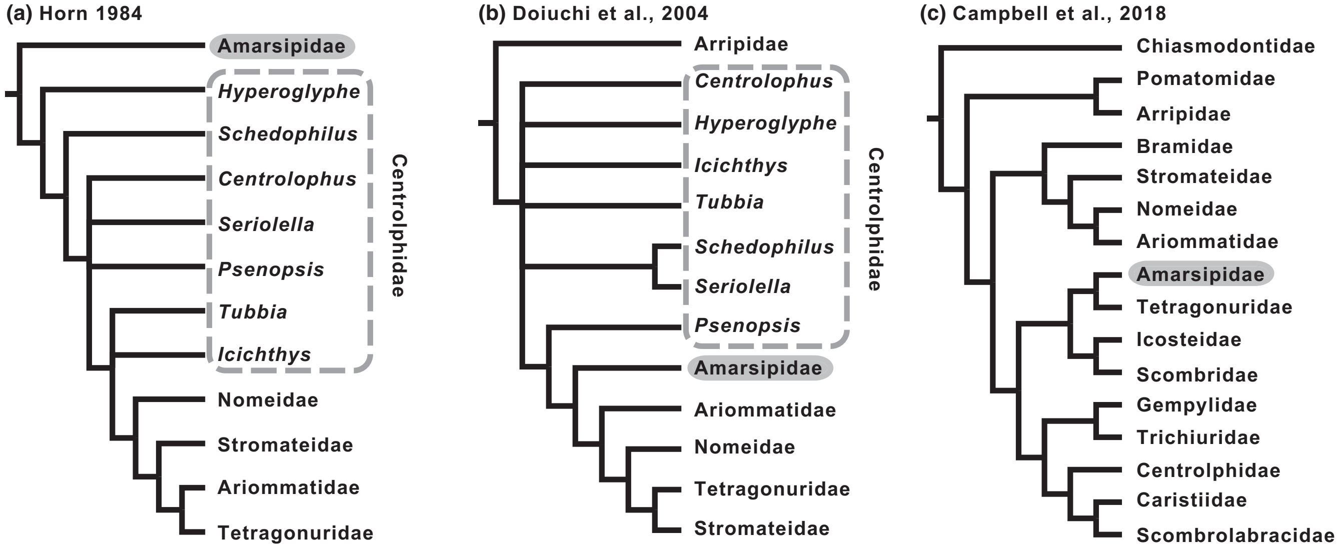

FIGURE 2 Previous phylogenetic hypotheses of *Amarsipus carlsbergi*. (a) Horn (1984), topology inferred from cladistic analysis of 27 morphological traits; (b) Doiuchi et al. (2004), topology inferred from 36 morphological traits; (c) Campbell et al. (2018), topology inferred from analysis of 10 genetic loci

had low node support across species tree- and concatenation-based analyses. However, the UCE phylogenies consistently resolved with strong support a sister relationship between *Tetragonurus* and Chiasmodontidae, a family that lacks a pharyngeal sac and previously had not been hypothesized to belong to the stromateoid group.

The evolutionary history of *Amarsipus carlsbergi* is important in evaluating the phylogenetic relationships of Stromateoidei and is critical to the assessment of the evolution of the pharyngeal sac among lineages of Pelagiaria. With *Amarsipus* lacking in the analyses of Friedman et al. (2019), it remained unknown whether genomic-scale data would corroborate the relationship between *Amarsipus* and *Tetragonurus* as inferred with a smaller number of loci (Campbell et al., 2018), or if this putative stromateoid lineage would resolve in a group with core stromateoids or with other pelagiarian lineages. In this study, we assess the phylogenetic relationships of *Amarsipus carlsbergi* using an expanded UCE data set that includes all families of Pelagiaria (Friedman et al., 2019).

2 | METHODS

2.1 | Generation of UCE loci from whole genome sequencing data

We extracted UCE sequences from paired-end Illumina sequence data obtained from a single individual of *Amarsipus carlsbergi* (CBM-ZF 17750; NCBI SRA SRX4707127) that was previously analysed in Campbell et al. (2018). Details on quality control protocols for the removal of low-quality bases, adapter contamination and combination of overlapping paired-end reads can be found in Campbell et al. (2018). Post-quality control reads were mapped to reference assemblies resulting from target capture of UCEs from Friedman et al. (2019). Museum voucher accession information as well as NCBI Sequence Read Archive (SRA) BioProject and BioSample accession numbers for each specimen are provided in Table S1. We performed three mappings to different pelagiarian species in order to confirm the fidelity of *Amarsipus* UCE data. These replicates were mapped against *Icosteus aenigmaticus*, *Kali normani* and *Thunnus orientalis*, the three samples that had the highest overall completeness in the 95% complete data set of Friedman et al. (2019). Mapping was conducted with Burrows–Wheeler Aligner (BWA) version 0.7.7-r441 using the MEM algorithm for both paired sequences and unpaired reads (Li & Durbin, 2009). The resulting Binary Alignment Map (BAM) files were processed with SAMTools version 1.3 (Li et al., 2009) to combine separate paired and unpaired BAM files and to filter for a minimum alignment score (MAPQ) of 30 (99.90% accuracy, -q 30). Consensus sequences for each UCE locus in the reference assembly were generated from the filtered BAM file with the proovread version 2.14 bam2cns subprogram (Hackl et al., 2014). The resulting consensus sequences were refined by removing bases with quality scores of less than 30 with seqtk version 1.3-r106 (https://github.com/lh3/seqtk). Resulting consensus sequences were aligned to the 95% complete UCE matrix from Friedman et al. (2019) with MAFFT version 7.130B (Katoh et al., 2002; Katoh & Standley, 2013). Although the *T. orientalis* reference assembly had the third most UCEs (610), it presented the most assembled bases (346,792) and largest mean contig length (568.51). The *T. orientalis* assembly was selected for use in all downstream phylogenetic analyses, although preliminary phylogenies were inferred with all three assemblies in order to verify the equivalent phylogenetic position of the mapping.

2.2 | Phylogenetic analyses

We used both concatenated supermatrix and species tree approaches. All phylogenies were inferred with a set of UCE loci that have 95% taxonomic completeness, and all of which contain sequence data for *Amarsipus*. Although previous studies demonstrated sensitivity of the deepest pelagiarian relationships to both the loci used and data matrix completeness (e.g. Campbell et al., 2018; Friedman et al., 2019; Miya et al., 2013), we restricted our analyses to this data matrix in order to reduce uncertainty in the resolution of *Amarsipus* by the inclusion of loci that lack coverage for this species. For analyses of concatenated data, we first determined partitioning schemes using PartitionFinder2 v2.1.1 (Lanfear et al., 2016) using the relaxed hierarchical clustering search algorithm (Lanfear et al., 2014) and Bayesian Information Criterion for partitioning scheme selection, and a GTR-Gamma model of molecular evolution. We conducted partitioned Bayesian tree inference using ExaBayes v1.5 (Aberer et al., 2014), with an analysis consisting of 4 Markov chain Monte Carlo (MCMC) runs for 10 million generations and trees and parameters sampled every 1,000 generations. We discarded the first 50% of sampled trees as burn-in and summarized the consensus tree using the Exabayes consens program. Topological convergence was assessed by ensuring that average standard deviation of split frequencies was below 5%. To confirm convergence in other parameter estimates, we used Tracer v1.7.1 (Rambaut et al., 2018), ensuring effective sample sizes above 200 and no postburnin directional trends in parameter traces. We also performed a partitioned maximum likelihood tree search on the concatenated data matrix using IQTree v 1.6.12 (Nguyen et al., 2015). This was conducted with the ultrafast bootstrap approximation and nearest-neighbour interchange optimization (Hoang et al., 2018) with 1,000 bootstrap replicates.

We implemented a summary species tree inference with ASTRAL-III v5.6.3 (Zhang et al., 2018), based on individual gene trees estimated for each UCE locus using IQTree v 1.6.12. For each locus, we determined the optimal model of molecular evolution using the ModelFinder Plus (Kalyaanamoorthy et al., 2017) option within IQTree. Individual-locus tree searches were conducted using Shimodaira–Hasegawa approximate likelihood ratio test (SH-aLRT) with 1,000 bootstrap replicates. Summary species tree analyses may be susceptible to influence from nodes that have marginal support within individual gene trees, and contracting branches that subtend weakly supported partitions has been shown to improve accuracy of species tree inference (Zhang et al., 2018). The relatively short UCE loci in our analysis (average length of 672 base pairs, and 259 parsimony informative sites per locus) may result in gene trees that contain low-support nodes among some taxa. In order to assess the influence of low-support gene tree nodes on our species tree topology, particularly with regard to the placement of *Amarsipus* and the status of stromateoid monophyly, we generated a series of species trees using gene trees for which branches were collapsed across a range of thresholds, corresponding to 15%, 30% and 45% bootstrap support.

2.3 | Hypothesis testing

We examined evidence for three hypotheses present in the postburnin tree sample generated by ExaBayes as described in the previous section. The three hypotheses evaluated were as follows: (a) monophyly of Stromateoidei as classically recognized (e.g. Haedrich, 1969), (b) the presence of a clade comprising Amarsipidae, Tetragonuridae and Chiasmodontidae and (c) monophyly of pelagiarians with a pharyngeal sac (i.e. classical Stromateoidei excluding Amarsipidae). Trees from ExaBayes were imported into R version 3.6.1 with the read.nexus function of *ape* version 5.3. The number of times each hypothesis was present in the postburnin tree sample was calculated with the is.monophyletic function of *ape* and the corresponding posterior probability generated by dividing this number by the number of trees examined. We then calculated Bayes factors by dividing the posterior probabilities of Stromateoidei monophyly and the monophyly of fishes with a pharyngeal sac by the posterior probability of a clade composed of Amarsipidae, Tetragonuridae and Chiasmodontidae.

2.4 | Analysis of concordance

We used BUCKy (Ané et al., 2007) to analyse the topological concordance across the set of gene trees inferred for each individual UCE locus. BUCKy summarizes the occurrence of topological partitions in the posterior distribution of gene trees from each loci's Bayesian gene tree search and provides concordance factors, which are estimates of the probability that any particular bipartition among taxa reflects the true topology of loci in the data set. For this analysis, we generated gene tree distributions using MrBayes v. 3.2.7 (Ronquist et al., 2012). In each MrBayes analysis, we ran four MCMC chains of 2 million generations in length, with a sampling frequency of 2000 generations, and a GTR-Gamma model of molecular evolution. Using the BUCKy program mbsum, branching patterns within each loci's posterior tree distribution were summarized, excluding the first 75% of the distribution as burn-in. Increases in the number of species in a phylogeny result in non-linear increases in possible topologies, which can be computationally intractable for BUCKy when dealing with large taxonomic data sets. To reduce the computational burden of summarizing partition patterns across our data set, we conducted our BUCKy concordance factors analysis using a single representative of each of the 16 pelagiarian families, selecting individuals from each family with the highest representation in the UCE gene trees (Table S2). We estimated concordance factors in BUCKy using an alpha level (prior parameter for expectation of locus linkage across the data set) of 1.0, but also compared concordance values when alpha was set to 0.75 and 0.5.

While BUCKy concordance factors provide a convenient method to assess the topological agreement across a multilocus data set, they do not explicitly reveal the node support from individual loci in the data set. We used the program Phyparts (Smith et al., 2015) to summarize the statistical node support from individual UCE gene trees in our data set. Given a reference tree topology for a set of taxa (e.g. our ASTRAL-III species tree or ExaBayes concatenated tree) and a set of gene trees, Phyparts summarizes the number of loci for which a node in the reference tree receives strong support, as well as the number of loci that strongly support alternative topologies or are uninformative to a particular relationship. For the Phyparts summary analysis, we used the IQTree-inferred gene trees generated for our species tree analyses (described above). As in BUCKy concordance factors analyses, we reduced computational burden of examining partition variation across many taxa by pruning our reference trees and individual UCE locus trees to a set of 42 taxa, with two representatives per family (unless the family is monotypic or for which we had only a single representative) (Table S3). This allowed us to summarize support for relationships among major pelagiarian lineages without attempting to summarize support for intrafamilial variation. We estimated support for partitions that occurred in our ASTRAL-III and concatenated IQTree analyses, with bootstrap support observed in individual UCE gene trees of 50 or 80 as the 'significant' threshold. While bootstrap values of 50 or 80 are not traditionally considered especially strong support in molecular gene trees, we were interested in the relative number of loci that exceed these thresholds for competing alternative relationships.

3 | RESULTS

3.1 | Alignment of reads and UCE sequence generation

After filtering for a minimum alignment quality score (MAPQ $\geq$ 30), 123,054 of the 258,232,994 paired reads and 80,050 of the 181,354,946 unpaired reads present after initial quality control processing aligned to the *Thunnus orientalis* reference UCEs. The resulting average per-site coverage across reference *Thunnus orientalis* UCEs is 30.13. After removing bases with a quality score of <30, the consensus sequences contained 337,705 bases with an average length of 553.61 across 610 UCE loci. After alignment with all samples, total length of the concatenated 610 UCE locus data set is 410,063 base pairs, with a mean of 672 base pairs per individual locus.

3.2 | UCE placement of Amarsipus and relationship of stromateoid families

The topology inferred from the concatenated, partitioned 610 UCE locus data set is identical between the Exabayes and IQTree analyses, and patterns of Bayesian posterior probability (BPP) and maximum likelihood bootstrap (BS) node support are also highly similar between analyses (Figure 3). *Amarsipus* was inferred as sister to a clade containing *Tetragonurus* and Chiasmodontidae with maximum node support (BPP of 1.0; BS of 100), as was the sister relationship between *Tetragonurus* and Chiasmodontidae. This clade containing *Amarsipus, Tetragonurus* and Chiasmodontidae is resolved as sister to Scombridae with strong support (BPP 1.0; BS 96). Other aspects of this topology that are strongly supported and are similar to what was reported in Friedman et al. (2019), and include a sister-group relationship between Bramidae and Caristiidae; a clade containing *Scombrolabrax*, Gempylidae and Trichiuridae; and a 'core stromateoid' clade that contains Ariommatidae, Nomeidae and Stromateidae. As in Friedman et al. (2019), Gempylidae was rendered paraphyletic due to the placement of *Lepidocybium*, which is sister to a lineage containing the remainder of Gempylidae and Trichiuridae. The primary differences between our topology and that of Friedman et al. (2019) involve the families identified by those authors as 'rogue' taxa: Arripidae, *Icosteus*, Centrolophidae and *Pomatomus*. These were shown to be highly sensitive to analytical framework or data filtering approach. While our concatenated analyses find strong support for a clade uniting *Pomatomus* and Centrolophidae (BPP 1.0; BS 95), the nodes subtending its relationship to 'core stromateoids' and the remaining pelagiarian families—particularly Arripidae and *Icosteus*—all received relatively low support.

Our series of ASTRAL-III species tree analyses resulted in two topologies that correspond to whether or not the input gene trees were subjected to branch contraction at various thresholds of node bootstrap support (Figure 4). The topology of species trees whose gene trees' branches were collapsed for nodes not exceeding 15%, 30% or 45% BS, all converged on an identical topology, and ASTRAL-III's metric of node support (local posterior probability [LPP]) differed slightly among these replicates. We present the tree and node support from the 15% threshold of node contraction in Figure 2c. Across all species tree analyses, *Amarsipus*

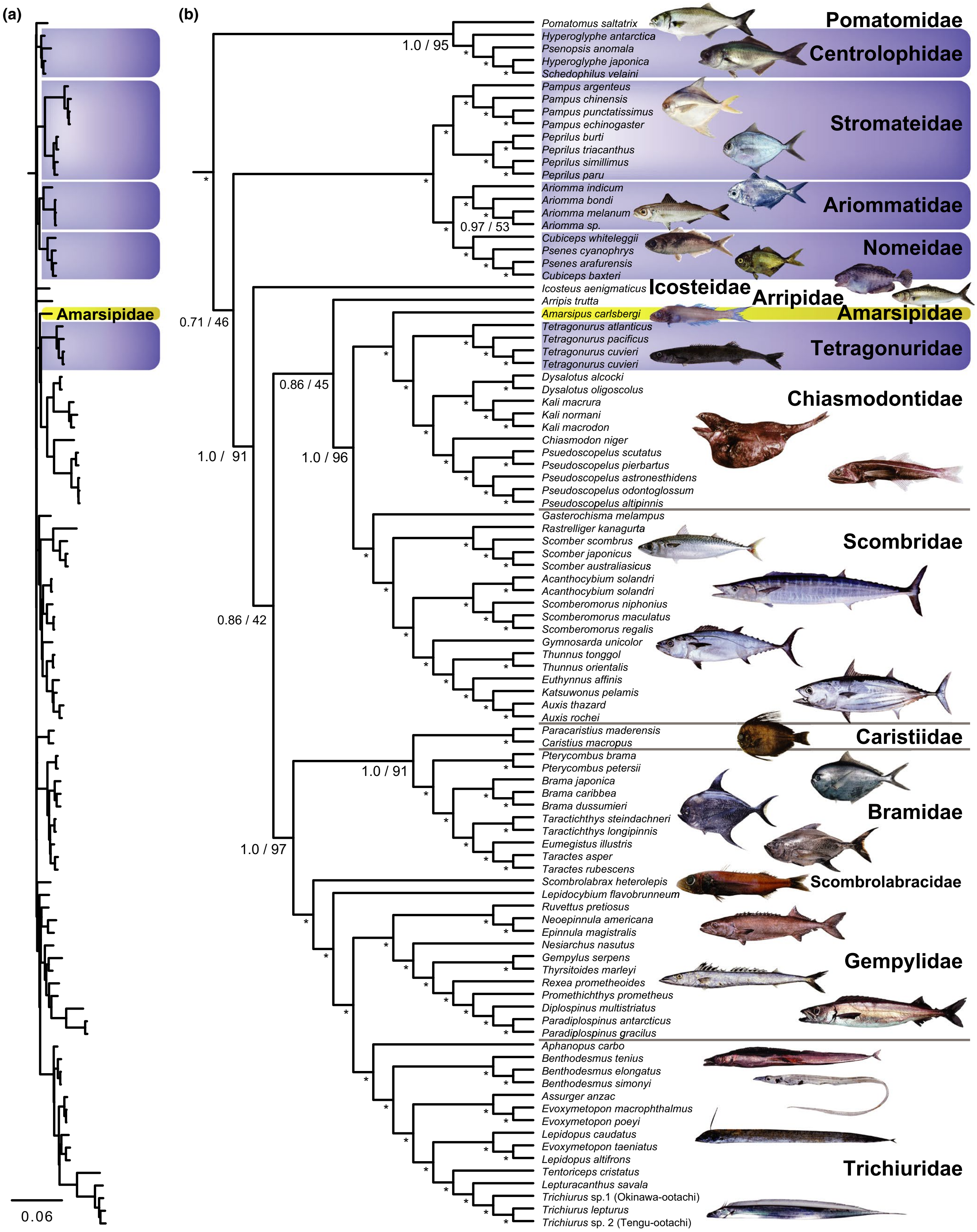

FIGURE 3 (a, b) Phylogeny of Pelagiaria inferred by analysis of 610 concatenated, partitioned UCE loci in Exabayes and IQTree. (a) Phylogenetic tree with branch lengths drawn relative to number of substitutions; (b) Same tree as in *A*, but with ultrametric branch length transformation and annotated to illustrate Bayesian and Maximum Likelihood node support. Support values are shown adjacent to each node, with ExaBayes Bayesian posterior probability (BPP) first, followed by IQTree maximum likelihood bootstrap support (BS). Nodes with both maximum BPP and BS support are indicated with an asterisk. *Amarsipus* is highlighted in yellow, and stromateoid families bearing a pharyngeal sac are highlighted in blue [Colour figure can be viewed at wileyonlinelibrary.com]

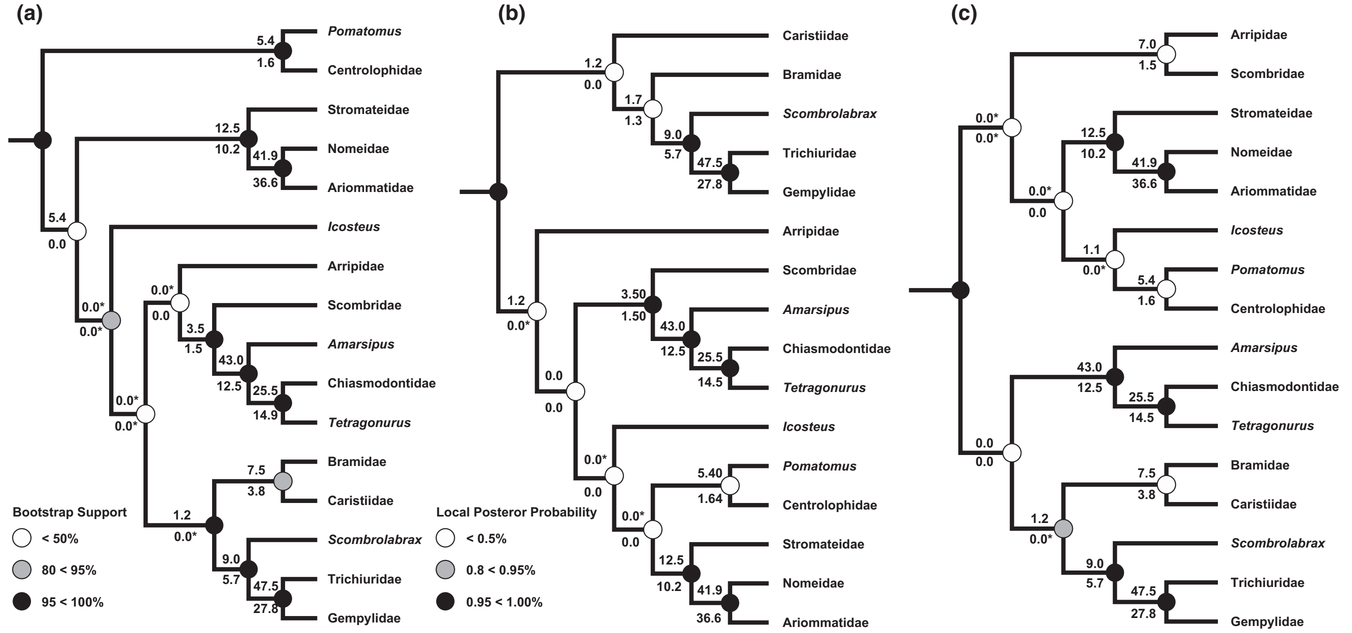

FIGURE 4 (a–c) Topologies inferred from concatenation and species tree analyses annotated with node support, concordance factors, and number of loci strongly supporting each node. (a) IQTree analysis of partitioned, concatenated UCE loci; (b) ASTRAL-III species tree analysis conducted without node-support filtering; (c) ASTRAL-III species tree conducted with gene trees for which nodes that have lower than 15% bootstrap support are collapsed. Support values are indicated with coloured discs on nodes, with black representing 95%–100% bootstrap support (BS) for IQTree or 0.95–1.0 Local Posterior Probability (LPP); grey indicating 80%–95% BS or 0.8–0.95 LPP; and white representing nodes with support values lower than 80% BS or 0.8 LPP. BUCKy-estimated concordance factors are indicated above each node, and the percentage of individual UCE loci that contain partitions corresponding to a node higher than 50% BS are listed below each node

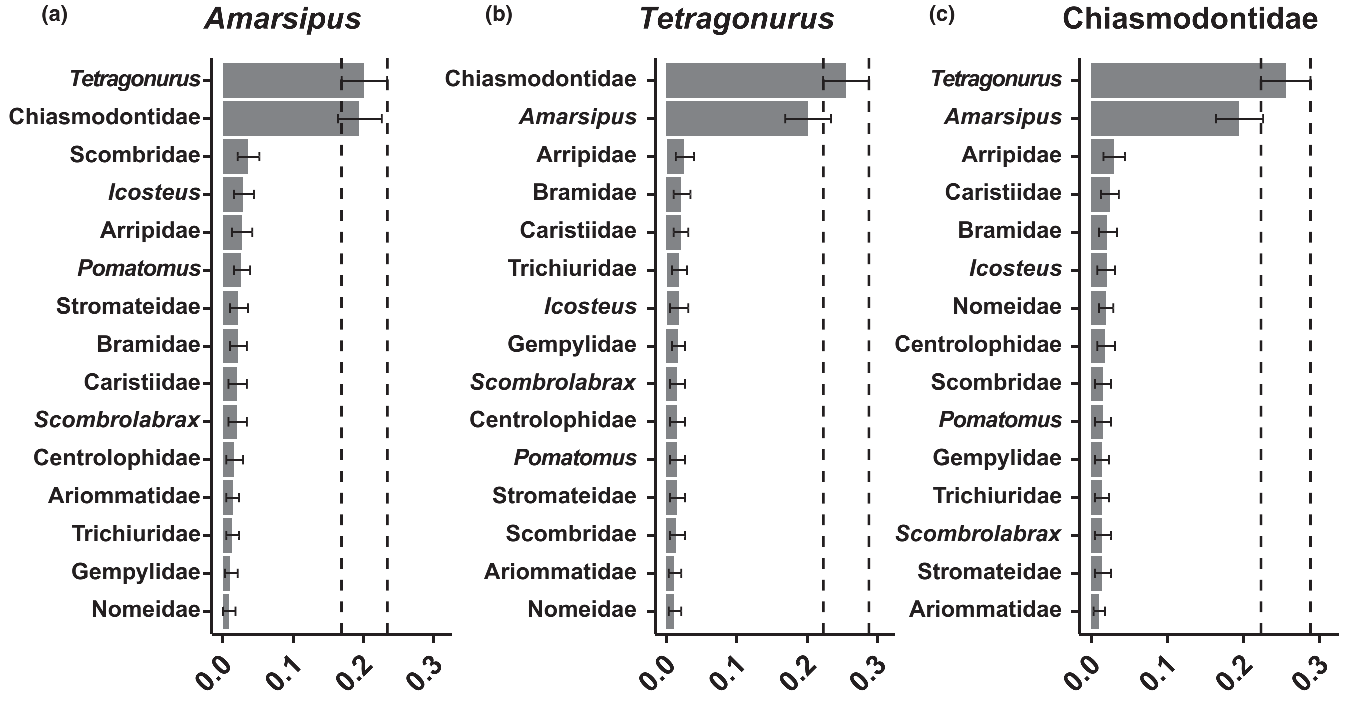

FIGURE 5 (a–c) BUCKy concordance factor estimates for the proportion of individual UCE gene trees in which *Amarsipus* (a), *Tetragonurus* (b) and Chiasmodontidae (c) appear in topological partitions with each Pelagiarian family

was inferred as sister to a clade including *Tetragonurus* and Chiasmodontidae with strong LPP support (Figure 4). As in the concatenated analysis, we also observed consistently high support for a *Scombrolabrax*-gempylid-trichiurid clade and a 'core stromateoid' clade, which appeared in each of the replicate ASTRAL-III analyses. A primary difference is that the node-collapsed species trees find *Icosteus* is sister to a clade containing *Pomatomus* + Centrolophiidae and 'core stromateoids', and this entire group sister to a clade containing Arripidae and Scombridae. In the species tree generated without filtering based on node bootstrap support, Scombridae is sister to the clade *Amarsipus* + *Tetragonuru s* + Chiasmodontidae, which is similar to the topology from concatenation analyses.

Examination of the posterior tree distribution of the concatenated ExaBayes analysis reveals that the clade comprising *Amarsipus*, *Tetragonurus* and Chiasmodontidae was present in all posterior trees examined (BPP = 1.00). The resulting Bayes factors, which consider the monophyly of Stromateoidei (BPP = 0.00, Bayes factor = 0.00/1.00 = 0.00) and the monophyly of fishes with a pharyngeal sac (BPP = 0.00, Bayes factor = 0.00/1.00 = 0.00), strongly support the clade comprising *Amarsipus*, *Tetragonurus* and Chiasmodontidae.

3.3 | Concordance of Loci and measures of UCE support

The close relationship between *Amarsipus, Tetragonurus* and Chiasmodontidae is supported by relatively high sample-wide concordance among topologies of individual UCE gene trees. A partition containing these three taxa occurs in 44.8% of loci (95% CI: 42.3%–47.3%; Figure 5, Table 1). The inter-relationships between these three lineages exhibit a moderate level of discordance, with similar percentages of loci inferring the three alternative topologies and with overlapping 95% credible intervals. In our data set, a sister relationship between *Tetragonurus* and Chiasmodontidae, to the exclusion of *Amarsipus,* is present in 25.5% [95% CI: 22.3%–28.8%] of loci. The alternative topologies, where *Amarsipus* occurs in a partition with either *Tetragonurus* or Chiasmodontidae, to the exclusion of the other, occur in 20.1% [95% CI: 16.9%–23.4%] and 19.4% [95% CI: 16.4%–22.6%] of loci, respectively. By contrast, the percentage of loci for which *Amarsipus* occurs in a partition with any of the other individual families of Pelagiaria is substantially lower, ranging between 0.9% and 3.5% (Figure 5).

In contrast to the similar concordance factors estimated for gene tree topologies that are nearly equally divided between the three alternative sets of relationships among *Amarsipus*, *Tetragonurus* and Chiasmodontidae (with the highest number resolving *Tetragonurus* + Chiasmodontidae), only the clade uniting *Tetragonurus* and Chiasmodontidae receives strong bootstrap support in more than a handful of individual UCE gene trees. A sister relationship between these two lineages, to the exclusion of *Amarsipus*, meets the threshold of 50% and 80% bootstrap support in 91 (15% of loci) and 38 (6% of loci) gene trees, respectively (Table 1). A sister relationship between *Amarsipus* and *Tetragonurus* meets the 50% bootstrap support in 4 gene trees, and 80% in one 1 tree (0.7% and 0.1% of loci, respectively). Similarly, only 4 gene trees have at least 50% bootstrap support for a sister relationship between *Amarsipus* and Chiasmodontidae, with only a single of these loci surpassing the 80% bootstrap threshold (representing 0.7% for BS of 50, and 0.1% of loci for BS of 80).

Patterns of sample-wide topological concordance among the remaining pelagiarian families are similar to those reported in Friedman et al. (2019). For instance, our data set has a relatively high frequency of occurrence for partitions that include Trichiuridae and Gempylidae (50.7% [95CI: 48.1–53.5], vs. 48.2% [95CI: 45.8–51.0] in Friedman et al. (2019)) and Ariommatidae-Nomeidae (45.1% [95CI: 42.3–47.8], vs. 44.5% [95CI: 42.0–47.2] in Friedman et al. (2019)). The 'rogue' lineages of Arripidae, *Icosteus*, Centrolophidae and Pomatomidae appeared in partitions with overlapping 95% confidence intervals with at least 7 of other pelagiarian families. For example, concordance estimates for a partition containing Arripidae and each of nine other pelagiarian families have overlapping 95% credible intervals, ranging between 3.1% and 6.7% of loci containing these alternative relationships. Scombridae, which in all of our molecular phylogenetic analyses, is resolved as a sister lineage of a clade containing *Amarsipus*, *Tetragonurus* and Chiasmodontidae (but with only modest support), has concordance factors with overlapping 95% credible intervals for eight pelagiarian families.

A clade composed of only the families traditionally classified as belonging to Stromateoidei appears in the MrBayes-generated posterior tree distributions of three UCE loci,

TABLE 1 Proportions of UCE loci supporting alternative relationships between *Amarsipus*, *Tetragonurus* and Chiasmodontidae. Sample-wide concordance factors represent the proportion of loci for which the partition was estimated to be the true topology, as estimated in BUCKy with MrBayes-inferred gene tree distributions. The proportion of loci exceeding either a 50% or 80% bootstrap support threshold were estimated using IQTree-inferred gene trees for each UCE locus

	Amarsipus*— *Tetragonurus	***Amarsipus*— Chiasmodontidae**	***Tetragonurus*— Chiasmodontidae**
Sample-wide concordance factor	0.201	0.194	0.255
Proportion of loci with >50 BS	0.007	0.007	0.149
Proportion of loci with >80 BS	0.002	0.003	0.062

although at a frequency low enough such that BUCKy estimates a probability that it reflects the true topology of none of these loci (concordance factor of 0.00 [95% CI = 0.0–0.003]). A clade containing all traditional stromateoid families plus Chiasmodontidae, to the exclusion of all other pelagiarian families, receives only a slightly higher concordance factor of 0.003 [95% CI = 0.0–0.008], occurring in the posterior distribution of 8 loci, and has a 0.975 probability of representing the true topology of only three loci. Likewise, a clade that includes only the stromateoid lineages that are known to have pharyngeal sacs (i.e. *Tetragonurus*, Ariommatidae, Centrolophidae, Nomeidae and Stromateidae) receives a concordance factor estimate of 0.00.

4 | DISCUSSION

This study provides the first genomic-scale analysis of the phylogenetic relationships of *Amarsipus*, and the second molecular study to contain sufficient taxonomic sampling of Pelagiaria to evaluate the relationships of taxonomic families classified in the Stromateoidei. We present several phylogenies inferred using concatenation and coalescent species tree summary methods (Figures 3 and 4), and explore concordance among loci to highlight confidence for a clade containing *Amarsipus*, *Tetragonurus* and Chiasmodontidae. The rapid increase in high-throughput sequencing for phylogenetic analyses has sparked debate about the most appropriate approaches for tree inference and interpretation of node support with large, genomic-scale data sets (e.g. Gatesy & Springer, 2014; Gatesy et al., 2019; Mendes & Hahn, 2018). Although coalescent species tree analyses attempt to model the independent evolutionary history of many unlinked loci, species tree accuracy is affected by high levels of ILS or erroneous gene tree inference—phenomena that can be exacerbated by 'anomaly zone' scenarios of rapid, deep divergences (Degnan & Rosenberg, 2006; Gatesy et al., 2019; Walker et al., 2018). Fossil-calibrated divergence time estimates from Alfaro et al. (2018) and Friedman et al. (2019) support a scenario of rapid diversification of major pelagiarian lineages beginning around the Cretaceous–Paleogene boundary (66 million years ago) and extending through the Paleocene. A series of rapid, successive divergence events among major lineages early in pelagiarian history create a phylogenetic scenario that is difficult to resolve with the simple addition of more loci and analysed in traditional concatenated or coalescent species tree analytical frameworks (e.g. Campbell et al., 2017, 2020). This is reflected in the relatively high levels of gene tree discordance, low node support and inferred topologies that are inconsistent with regard to the relationships among the oldest nodes within the pelagiarian phylogeny (Figure 2).

Campbell et al. (2018) provided the first molecular phylogenetic study of *Amarsipus*, which resolved it and *Tetragonurus* as sister lineages as well as non-monophyly of the Stromateoidei. The subsequent study by Friedman et al. (2019) investigated the relationships of Pelagiaria with a phylogenomic analysis utilizing nearly 1,000 UCE loci and identified several 'rogue' lineages (e.g. Arripidae, *Icosteus* and *Pomatomus*) due to the prevalence of discordant UCE gene tree topologies that resulted in their variable and weakly supported phylogenetic resolution across analyses. However, Friedman et al. (2019) did not include *Amarsipus* in their phylogenomic analyses.

The phylogenomic analysis of UCE data demonstrates that the phylogenetic resolution of *Amarsipus* as the sister lineage of a clade containing *Tetragonurus* and Chiasmodontidae is one of the most robustly supported relationships among major pelagiarian lineages by metrics of node support and gene tree topological concordance (Figures 3–5). Thus, *Amarsipus* is not a 'rogue' lineage. While the topologies of individual UCE loci in our data set contain partitions for each of the three possible relationships among *Amarsipus*, *Tetragonurus* and Chiasmodontidae at nearly equal frequency, the only topology that garnered strong bootstrap support from more than four loci was the sister relationship between *Tetragonurus* and Chiasmodontidae, which had bootstrap support greater than 50% in 91 loci (Table 1). This asymmetry between the nearly equal frequency of these alternative topologies versus disproportionate number of these gene trees inferred with strong support for a partition containing *Tetragonurus* and Chiasmodontidae may reflect that these two lineages have a longer, shared evolutionary history relative to *Amarsipus*, during which they would have accumulated concordant mutations that increase gene tree node support metrics. Among the remaining stromateoid lineages, the core clade of Ariommatidae, Nomeidae and Stromateidae also receives consistent and strong molecular support (Campbell et al., 2018; Friedman et al., 2019). While across the more inclusive pelagiarian clade some relationships may remain unresolved, the phylogenetic resolution of *Amarispus* and the non-monophyly of Stromateoidei are strongly supported in the phylogenomic analyses.

Previous phylogenetic analyses of morphological data resulted in different hypotheses regarding relationships of *Amarsipus* and the remaining stromateoid lineages. Haedrich (1969) and Horn (1984) hypothesized that *Amarsipus* is sister to all remaining stromateoids, a relationship that is consistent with a single origin of the modified stromateoid pharyngeal sac (Figure 2a). Doiuchi et al. (2004) analysed a larger morphological data set (36 characters, rather than the 27 considered in Horn's, 1984 study) and concluded that *Amarsipus* was nested within the stromateoids and represented a secondary loss of the pharyngeal sac (Figure 2b). As with the early molecular phylogenetic studies of Pelagiaria, an unforeseen but key weakness of these morphological analyses was insufficient taxonomic coverage of non-stromateoid pelagiarian lineages, and only Doiuchi et al. (2004) included one such representative, *Arripis*. Regardless of their lack of broader sampling within Pelagiaria, none of the previous morphological hypotheses are congruent with our UCE-based results in which the six families traditionally classified as stromateoids represent a polyphyletic group that variously share most recent common ancestry with Arripidae, Icosteidae, Pomatomidae and Scombridae, and perhaps the all other lineages of Pelagiaria (Figures 3 and 4).

In contrast to the historical uncertainty regarding the position of *Amarsipus* among acanthomorph fishes, our analysis of UCE loci provides clear support for a close relationship between *Amarsipus*, *Tetragonurus* and Chiasmodontidae and the non-monophyly of the traditional suborder Stromateoidei. The striking ecological and anatomical differences within the clade comprising *Tetragonurus* and Chiasmodontidae have been noted previously (Friedman et al., 2019), and resolution of *Amarsipus* as the sister lineage to this group only amplifies these contrasts. Unfortunately, our analyses do not resolve all of the backbone of pelagarian phylogeny, and there is phylogenetic uncertainty regarding the sister lineage of the strongly supported clade uniting *Amarsipus*, *Tetragonurus* and Chiasmodontidae. The pharyngeal sacs that are a feature of five of the six stromateoid families have a long history of being interpreted as evidence of shared evolutionary history among these lineages (Doiuchi et al., 2004; Haedrich, 1967; Horn, 1984). Strong support for the clade containing *Amarsipus, Tetragonurus* and Chiasmodontidae, and the associated non-monophyly of stromateoids highlights a more complicated evolutionary history of the pharyngeal sac. Although multiple losses or origins of the pharyngeal sac (and other morphological features of stromateoids) were unanticipated prior to the application of molecular phylogenetics, the lack of thorough taxonomic coverage in comparative morphological studies of pelagiarian lineages has left a gap in our understanding of the origin of these key morphological traits. This gap in comparative morphological examination of Pelagiaria remains, but represents an important area of inquiry for advancing the understanding of pelagiarian relationships. With modest diversity, mature genomic resources and many anatomically well-documented lineages, Pelagiaria is an ideal candidate for integrative studies that seek to reconcile the contrasting phylogenetic signals of morphological and molecular data sets (e.g. Girard et al., 2020).

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DATA AVAILABILITY STATEMENT

Raw read sequence data for *Amarsipus carlsbergi* is available from the NCBI Sequence Read Archive (SRX4707127). UCE raw read data from Friedman et al. (2019) are available on the NCBI Sequence Read Archive under BioProject number PRJNA561597. Individual UCE alignments and multilocus phylogenies generated in this study are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.w9ghx3fns.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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