Phylogenomic reappraisal of the Neotropical catfish family Loricariidae (Teleostei: Siluriformes) using ultraconserved elements

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ABSTRACT

Neotropical freshwaters host more than 6000 fish species, of which 983 are suckermouth armored catfishes of the family Loricariidae – the most-diverse catfish family and fifth most species-rich vertebrate family on Earth. Given their diversity and ubiquitous distribution across many habitat types, loricariids are an excellent system in which to investigate factors that create and maintain Neotropical fish diversity, yet robust phylogenies needed to support such ecological and evolutionary studies are lacking. We sought to buttress the systematic understanding of loricariid catfishes by generating a genome-scale data set (1041 loci, 328,330 bp) for 140 species spanning 75 genera and five of six previously proposed subfamilies. Both maximum likelihood and Bayesian analyses strongly supported the monophyly of Loricariidae. Our results also reinforced the established backbone of loricariid interrelationships: Delturinae as sister to all other analyzed loricariids, with subfamily Rhinelepinae diverging next, followed by Loricariinae sister to Hypostominae + Hypoptopomatinae. Previous DNA-based relationships within Hypostominae and Loricariinae were strongly supported. However, we evaluated for the first time DNA-based relationships among many Hypoptopomatinae genera and found significant differences with this subfamily's current genus-level classification, prompting several taxonomic changes. Finally, we placed our topological results within a fossil-calibrated temporal context indicating that early Loricariidae diversification occurred across the Cretaceous-Paleogene boundary ~65 million years ago (Ma). Our study lays a strong foundation for future research to focus on relationships among species and the macroevolutionary processes affecting loricariid diversification rates and patterns.

1. Introduction

1.1. General overview

Earth's freshwater ecosystems are extremely biodiverse, containing more than 13,000 fish species in about 2500 genera, or about 40–45% of all fishes (Lévêque et al., 2008). Of the six freshwater realms commonly recognized, the Neotropical realm (South America to central Mexico and the Caribbean Islands) is by far the most diverse with over 6000 fish species in more than 700 genera (Albert et al., 2011a; Fricke et al., 2019). The Neotropical realm also has the highest number of strictly freshwater families (43) and the most species-rich vertebrate fauna on Earth (Lundberg et al., 2000; Berra, 2001; Reis et al., 2003, 2016; Lévêque et al., 2005, 2008; Petry, 2008). Understanding the historical origins and evolutionary processes driving Neotropical species diversification has been a great challenge for evolutionary
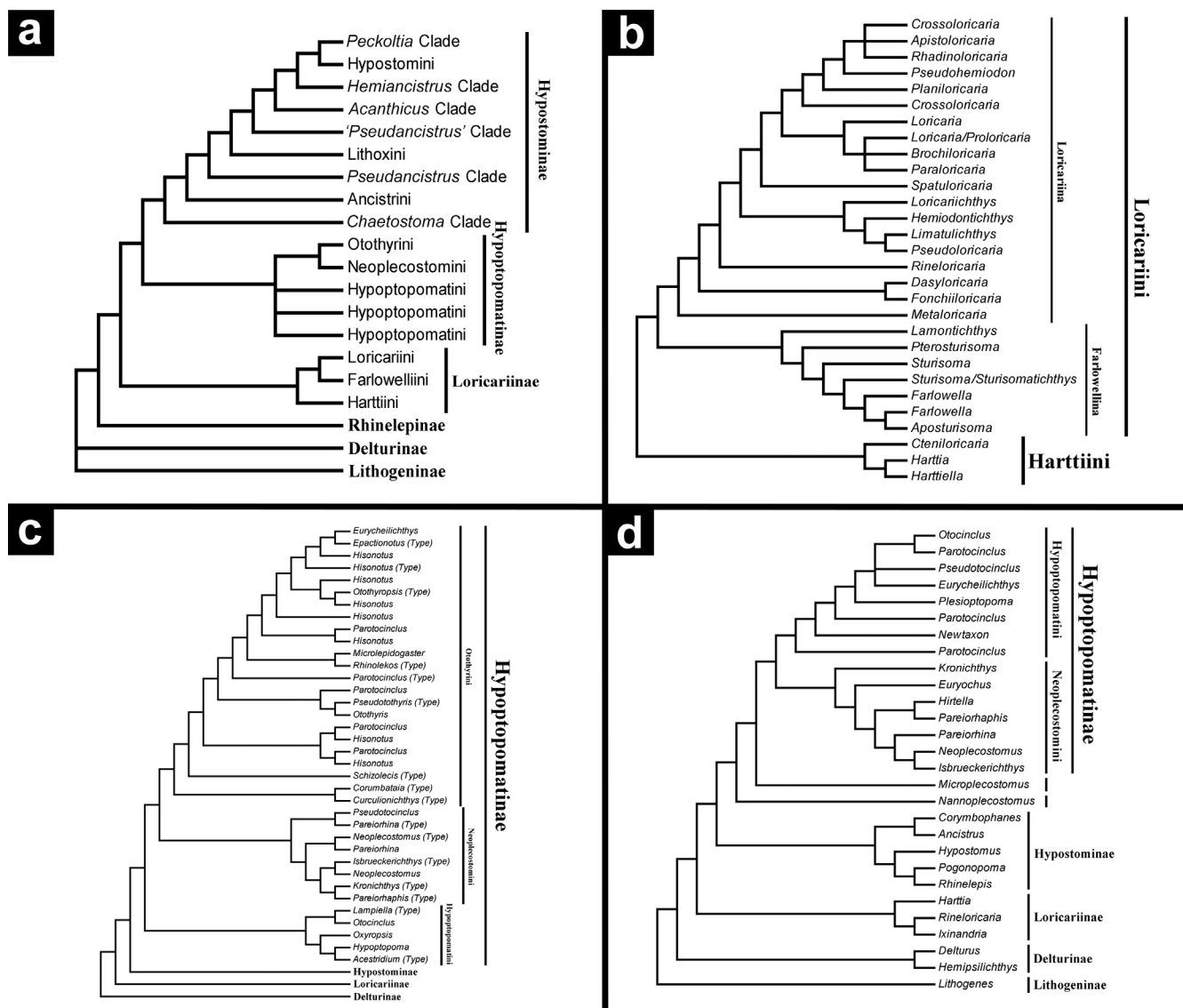
Fig. 1. (a) Phylogeny of Loricariidae based on Bayesian and maximum likelihood analyses of concatenated mitochondrial (16S, Cytb) and nuclear (Myh6, Rag1 and Rag2) markers with emphasis on the subfamily Hypostominae (modified from Lujan et al., 2015a). (b) Phylogeny of the subfamily Loricariinae based on maximum likelihood analysis of concatenated mitochondrial (12S, 16S) and nuclear (F-reticulon 4) markers (modified from Covain et al., 2016). (c) Phylogeny of Loricariidae based on maximum likelihood analysis of concatenated mitochondrial (16S, Cytb, COI) and nuclear (F-reticulon 4) markers with emphasis on the subfamily Hypoptopomatinae (modified from Roxo et al., 2014). "Type" denotes placement of type species for each genus. (d) Phylogeny of Loricariidae based on a maximum parsimony analysis of morphological characters with emphasis on the subfamily Hypoptopomatinae (modified from Pereira and Reis, 2017). Tree depiction and higer taxonomy was modified to match the broader concept of Hypoptopomatinae used in this study, inclusive of tribes Hypoptopomatini and Neoplecostomini, rather than treatment of these clades as separate subfamilies.

biologists. Recent geological/paleontological evidence (Malabarba et al., 2010; Wesselingh and Hoorn, 2011) and the development of advanced phylogenomic techniques (Lemmon et al., 2012; Faircloth et al., 2012) provide valuable new tools for inferring phylogenetic relationships and discerning the factors that have affected cladogenesis in Neotropical freshwater fishes (Faircloth et al., 2013; Harrington et al., 2016).

The Neotropical ichthyofauna is dominated by non-cypriniform otophysan fishes (i.e., Characiformes, Siluriformes and Gymnotiformes), which constitute roughly 77% of the total species richness (Albert et al., 2011a,b). Among Neotropical otophysan families, Loricariidae is the second most species rich with 983 currently valid species, after Characidae with 1180 species (Fricke et al., 2019). Loricariids range in body size from the miniature *Nannoplecostomus eleonorae* Ribeiro, Lima & Pereira 2012 maturing at 16.2 mm standard length (Ribeiro et al., 2012) to species reaching almost 40 times that

size (> 600 mm for *Panaque schaeferi* Lujan, Hidalgo & Stewart 2010 and > 625 mm for *Acanthicus hystrix* Spix & Agassiz, 1829; Lujan et al., 2010). Loricariid catfishes are easily distinguished from other fish groups by a combination of features, such as a body covered with ossified plates and external teeth called odontodes, and a ventral mouth with lips forming an oral disk used to adhere to solid substrates and winnow soft substrates while foraging (Schaefer and Lauder, 1986; Geerinckx et al., 2011). Loricariids occupy lotic to lentic habitats in hydrographic systems of all sizes throughout South America and southern Central America, from Andean streams over 3000 m above sea level to the vast lowland floodplains of the Pantanal and Amazonia, as well as estuarine ecosystems along the northern South American coast (Armbruster, 2004a; Lujan et al., 2015a).

1.2. Historical systematics of Loricariidae

Higher classification of the Loricariidae has a complex history going back more than a century (see Lujan et al., 2015a; Pereira and Reis, 2017) with significant early revisions by Eigenmann and Eigenmann (1890) and Regan (1904). Isbrücker (1980) assembled a comprehensive taxonomic catalog of Loricariidae in which he arranged taxa into six subfamilies: Lithogeninae, Neoplecostominae, Hypostominae, Ancistrinae, Hypoptopomatinae and Loricariinae. Howes (1983) was the first to use a cladistic analysis of myological and osteological data to coarsely resolve the following relationships between five loricariid subfamilies (omitting Lithogeninae): Hypostominae sister to a trichotomy composed of Neoplecostominae, Chaetostominae and Loricariinae + Hypoptopomatinae. Schaefer (1986, 1987) further expanded the cladistic analysis of Loricariidae osteology and retained the loricariid subfamilies proposed by Isbrücker (1980), but noted that Ancistrinae made Hypostominae paraphyletic. Schaefer (1987) placed the Lithogeninae as sister to all other members of Loricariidae, and considered the Neoplecostominae to be sister to all remaining subfamilies. In an early molecular study, Montoya-Burgos et al. (1998) provided evidence for the monophyly of Loricariidae but found poor resolution among the remaining subfamilies (Lithogeninae omitted). Armbruster (2004a) used morphological characters and extensive taxon sampling to propose *Lithogenes* + Astroblepidae sister to all loricariids, and *Delturus* + *Hemipsilichthys gobio* (Lütken, 1874) (then *Upsilodus victori*) as the first lineage to diverge within Loricariidae. Armbruster's (2004a) analysis also nested a monophyletic Hypoptopomatinae within Neoplecostominae and expanded Hypostominae to include taxa formerly assigned to subfamily Ancistrinae, which consequently became tribe Ancistrini. Reis et al. (2006) subsequently proposed the new subfamily Delturinae for *Delturus* and *Hemipsilichthys*. A recent multilocus phylogeny by Lujan et al. (2015a) found the first molecular support for placing Lithogeninae within Loricariidae (*vs.* sister to Astroblepidae). Although Lujan et al. (2015a) supported many of the other higher-level relationships proposed by Armbruster (2004a), they found significantly different relationships among many genera. Lujan et al. (2015a) also added two new subfamily-level clades: Rhinelepinae and a monotypic undescribed genus represented by '*Pseudancistrus*' *genisetiger* Fowler 1941 (see Fig. 1a for main phylogenetic relationships of Hypostominae proposed by Lujan et al. (2015a)).

Although recent multilocus studies by Lujan et al. (2015a) and Covain et al. (2016) have provided relatively robust and taxonomically comprehensive phylogenies to guide the genus-level classification of the Hypostominae and Loricariinae (respectively), some relationships in these species- and genus-rich clades remain weakly resolved. Relationships within Hypostominae (hereafter *sensu* Lujan et al., 2015a) are perhaps the most complex due to the large number of genera and species proposed for the subfamily (see Lujan et al., 2015a for summary). Armbruster (2004a) recognized five tribes in Hypostominae: Ancistrini, Corymbophanini, Hypostomini, Pterygoplichthini and Rhinelepini. Lujan et al. (2015a) restricted the composition of Ancistrini and Hypostomini and divided the remaining hypostomines among seven tribe-level clades: the *Chaetostoma* Clade, *Pseudancistrus* Clade, Lithoxini (then the *Lithoxus* Clade), '*Pseudancistrus*' Clade (not including '*Pseudancistrus*' *genisetiger*), *Acanthicus* Clade, *Hemiancistrus* Clade and *Peckoltia* Clade (Fig. 1a). Within Loricariinae, some studies have recognized three tribes: Harttiini, Farlowellini and Loricariini (Nijssen and Isbrücker, 1987; Lujan et al., 2015a). Others recognize two tribes (Harttiini and Loricariini) with the latter expanded to include taxa formerly in Farlowellini (Covain et al., 2008; Covain et al., 2016 see Fig. 1b).

Classification of species and genera traditionally assigned to subfamilies Hypoptopomatinae and Neoplecostominae are now among the most problematic in Loricariidae. Based on morphological characters, Schaefer (1997, 1998) considered Hypoptopomatinae to be composed of two monophyletic tribes, Hypoptopomatini and Otothyrini, with the

Neoplecostominae excluded from both. Based on molecular data, Chiachio et al. (2008) elevated the Otothyrini to a monophyletic subfamily more closely related to Neoplecostominae than Hypoptopomatinae. Cramer et al. (2011) subsequently used both nuclear and mitochondrial loci to analyze relationships among nearly all genera of Hypoptopomatinae, Neoplecostominae and Otothyrinae. Their analysis supported a monophyletic clade composed of all three subfamilies (treated as tribes), but none were supported as monophyletic. Likewise, the molecular study by Lujan et al. (2015a) supported a close relationship between the three subfamilies (again treated as tribes), and failed to group representatives of Hypoptopomatinae into a monophyletic clade. Subsequent molecular studies (Roxo et al., 2014, 2017; Silva et al., 2016) provided support for the monophyly of each of the three subfamilies with Hypoptopomatinae sister to Neoplecostominae + Otothyrinae (see Fig. 1c from Roxo et al., 2014). In a broad morphology-based analysis of Loricariidae, Pereira and Reis (2017, Fig. 1d) provided weak support for a clade composed of taxa assigned to Hypoptopomatinae, Neoplecostominae and Otothyrinae, and corroborated the monophyly of Neoplecostominae (minus *Microplecostomus* and *Pseudotocinclus*). Relationships between the few hypoptopomatines (*Otocinclus*, *Plesioptopoma*) and otothyrins (*Eurycheilichthys*, *Parotocinclus*) included in their study, however, were inconsistent with previous classifications derived from molecular evidence. Morphological and molecular analyses generally have agreed on the monophyly and composition of the Neoplecostominae, although only molecules support the inclusion of *Microplecostomus* and *Pseudotocinclus*. Furthermore, the assignment of two genera (*Euryochus* and *Hirtella*) to the subfamily by Pereira and Reis (2017) has not been tested with molecular data.

Here, we used high-throughput sequencing of ultraconserved elements (UCEs; Faircloth et al. 2012) with the newly designed ostariophysan bait set targeting thousands of loci from throughout the genome (Faircloth et al., in revision). UCEs have recently been used to explore problematic relationships within various animal groups, including fishes (Faircloth et al., 2013; Harrington et al., 2016; Chakrabarty et al., 2017; Alfaro et al., 2018; Burress et al., 2018). We generated a new genome-based matrix of UCEs much larger than any previous DNA-based analysis of the Loricariidae in order to test previous phylogenetic hypotheses and to better understand the evolution of this large Neotropical fish clade.

2. Material and methods

2.1. Taxon sampling

Our ingroup comprised 163 terminal taxa spanning 140 species (~15%) and 75 genera (~70%) distributed among all proposed subfamilies of Loricariidae except the Lithogeninae (due to lack of samples). Outgroup taxa included one species of Astroblepidae (*Astroblepus grixalvii* Humboldt, 1805), three Callichthyidae (*Corydoras aeneus* (Gill, 1858), *Aspidoras fuscoguttatus* Nijssen & Isbrücker 1976, *Hoplosternum littorale* (Hancock, 1828)), one Scoloplacidae (*Scoloplax dicra* Bailey & Baskin, 1976), and one Trichomycteridae (*Trichomycterus areolatus* Valenciennes, 1846 in Cuvier and Valenciennes, 1846). The tree was rooted using two Characidae: *Poptella paraguayensis* (Eigenmann, 1907) and *Hyphessobrycon compressus* (Meek 1904). Voucher specimens were fixed in 96% ethanol or 10% formalin, then transferred to 70% ethanol for permanent storage (see Table S1 for catalog and locality data). Institutional acronyms follow Sabaj (2016) with inclusion of LGC: Laboratório de Genética da Conservação, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil.

2.2. DNA extraction and sequencing

Whole genomic DNA was extracted from ethanol preserved muscle samples with the DNeasy Tissue Kit (Qiagen) and quantified using the

Qubit dsDNA broad range (BR) Assay Kit (Invitrogen, Life Technologies) following manufacturer's instructions. Library preparation, sequencing, and raw data processing were performed at Arbor Biosciences (AB; arborbiosci.com; Ann Arbor, MI, USA). Whole genomic DNA (concentration of 40 ng/µl) was first sheared with a QSonica Q800R instrument and selected to modal lengths of approximately 500 nt using a dual-step SPRI bead cleanup.

We used a probeset developed for ostariophysan fishes to generate sequence data for about 2700 UCE loci (Faircloth et al., in revision; http://doi.org/10.1101/432583). DNA libraries were prepared for the 171 specimens (163 ingroup taxa and 8 outgroup taxa) by modifying the Nextera (Epicentre Biotechnologies) library preparation protocol for solution-based target enrichment following Faircloth et al. (2012) and increasing the number of PCR cycles following the tagmentation reaction to 20 as recommended by Faircloth et al. (2013). AB staff used the Nextera library preparation protocol of *in vitro* transposition followed by PCR to prune the DNA and attach sequencing adapters (Adey et al., 2010), then used the Epicentre Nextera kit to prepare transposase-mediated libraries with insert sizes averaging 100 bp (95% CI: 45 bp) following Adey et al. (2010). AB staff then converted the DNA to Illumina sequencing libraries with a slightly modified version of the NEBNext(R) Ultra(TM) DNA Library Prep Kit for Illumina(R). After ligation of sequencing primers, libraries were amplified using KAPA HiFi HotStart ReadyMix (Kapa Biosystems) for six cycles using the manufacturer's recommended thermal profile and dual P5 and P7 indexed primers (see Kircher et al., 2012 for primer configuration).

After purification with SPRI beads, libraries were quantified with the Quant-iT(TM) Picogreen(R) dsDNA Assay Kit (ThermoFisher). AB staff then enriched pools comprising 100 ng each of eight libraries (800 ng total) using the MYbaits(R) Target Enrichment system (MYcroarray) following manual version 3.0. Sequencing was performed across two Illumina HiSeq paired-end 100 bp lanes using v4 chemistry.

2.3. Bioinformatics

Details of UCE sequence analyses are available online via the Phyluce document hub at: https://github.com/faircloth-lab/phyluce (Faircloth, 2016). All matrices used in the present study are available at figshare, doi: https://doi.org//10.6084/m9.figshare.5611306 (see Table 1 for information about data of each matrix), all raw sequence data are available at NCBI Sequence Read Archive (SRA) submissions

SUB4628240, SUB4627627, SUB4622505, SUB4630603, SUB4637928, SUB4705905, SUB4712035 (see Table S2 for information on reads). After sequencing, adapter contamination, low quality bases, and sequences containing ambiguous base calls were trimmed using the Illumiprocessor software pipeline (Faircloth, 2013; https://github.com/faircloth-lab/illumiprocessor). After trimming, we assembled Illumina reads into contigs on a species-by-species basis using Velvet (Zerbino and Birney, 2008) on VelvetOptimiser (https://github.com/Victorian-Bioinformatics-Consortium/VelvetOptimiser).

After sequence assembly, we used a custom Python program (match_contigs_to_probes.py), present in the phyluce software package (Faircloth, 2016), integrating LASTZ (Harris, 2007) to align species-specific contigs to our probe-UCE set. This last program creates a relational database of matches to UCE loci by taxon. We then used the get_match_counts.py program (also in Phyluce) to query the database and generate FASTA files for UCE loci that were identified across all taxa. A custom Python program (seqcap_align_2.py) was then used to align contigs using the MUSCLE alignment algorithm (Edgar, 2004) and to perform edge trimming (i.e., cutting edges of each alignment, eliminating highly variable and saturated regions, with poor phylogenetic signal for old groups) and internal trimming (i.e., cutting edges and internal portions of the alignments, discarding highly variable regions and parts of conserved regions). Effects of trimming can be hard to predict (Faircloth, 2016), so we explored tree topology and node support under both options. According to Faircloth (2016) edge trimming may be the best option when taxa are closely related (< 30–50 Ma) and internal trimming may be the best option when the taxa span a wider range of divergence times (> 50 Ma).

We also performed phylogenetic analyses with varying amounts of missing data keeping 60%, 75% and 85% of UCEs present in the complete alignment matrix, to explore the potentially strong effect that missing data can have on phylogenetic reconstruction (Hosner et al., 2016; Streicher et al., 2016).

2.4. Phylogenetic analyses of the concatenated matrix

We analyzed the concatenated dataset using maximum likelihood (ML) in RAxML v8.019 (Stamatakis, 2014) and Bayesian inference (BI) in ExaBayes v1.4 (Aberer et al., 2014) approaches on the 2 × 10 CPU, 256 GB *Zungaro* server at IBB-UNESP. For ML analyses, we compared the total data-partitioning schemes with models chosen by

Table 1

Distinct analyzed matrices (figshare DOI https://doi.org//10.6084/m9.figshare.5611306) resuming different schemes of data partitions and sequence data trimmings.

	Matrices (available at figshare)	Trimming	Total UCE loci	Total bp	Analysis	Available results
1	60% with kmeans data-partitioning schemes	Edge	1454	494,488	RAxML	Figure S1
2	75% with kmeans data-partitioning schemes	Edge	1041	328,330	RAxML	Figure S2
3	85% with kmeans data-partitioning schemes	Edge	471	102,064	RAxML	Figure S3
4	60% without partitions	Edge	1454	494,488	RAxML	Figure S4
5	*75% without partitions	Edge	1041	328,330	RAxML	Figure S5
6	85% without partitions	Edge	471	102,064	RAxML	Figure S6
7	60% without partitions	Edge	1454	494,488	Exabayes	Figure S7
8	75% without partitions	Edge	1041	328,330	Exabayes	Figure S8
9	85% without partitions	Edge	471	102,064	Exabayes	Figure S9
10	60% with kmeans data-partitioning schemes	Internal	1473	494,488	RAxML	Figure S10
11	75% with kmeans data-partitioning schemes	Internal	1054	328,330	RAxML	Figure S11
12	85% with kmeans data-partitioning schemes	Internal	478	102,064	RAxML	Figure S12
13	60% without partitions	Internal	1473	494,488	RAxML	Figure S13
14	75% without partitions	Internal	1054	328,330	RAxML	Figure S14
15	85% without partitions	Internal	478	102,064	RAxML	Figure S15
16	60% without partitions	Internal	1473	494,488	Exabayes	Figure S16
17	75% without partitions	Internal	1054	328,330	Exabayes	Figure S17
18	85% without partitions	Internal	478	102,064	Exabayes	Figure S18
19	75% without partitions	Edge	1454	328,330	Astral-II	Figure S19
20	*90% without partitions	Edge	187	26,410	Beast – Molecular clock	Figure S20

* Matrix used in the Discussion (Figs. 5–12).

PartitionFinder (Lanfear et al., 2012) using the kmeans algorithm (Frandsen et al., 2015) and the GTR + G model applied to the total matrix without partitions. The best tree search was performed under the parameter $-N = 5$ which specifies the number of alternative runs on distinct parsimony starting trees. The concatenated alignment was also used to perform bootstrap replicates using the autoMRE function for the extended majority-rule consensus tree criterion (available in RAxML v8; Stamatakis, 2014) to assess support for individual nodes. This option allowed the bootstrap convergence test to be conducted, which determines whether replicates are sufficient to obtain stable support values (Pattengale et al., 2010). The ML analysis was performed on 60%, 75% and 85% complete matrices with and without partitions (see Table 1 for all analyses). We also analyzed different matrices to compare edge vs. internal alignment trimmings (see Table 1 for all matrix schemes).

Bayesian analysis of the unpartitioned concatenated alignment was performed using ExaBayes (Aberer et al., 2014). We performed two independent runs, each with two chains (one cold and one heated) with 1,000,000 generations using the GTR + G model for different complementary matrices and alignment trimming analyses (see Table 1). Tree space was sampled every 100 generations to yield a total of 10,001 trees. Parameter estimates and ESS values were visualized in Tracer v 1.6 (Rambaut et al., 2014) and the last 7500 trees were sampled after checking results for convergence. This allowed us to visualize the log of posterior probabilities within and between independent runs and to ensure that the average standard deviation of split frequencies was < 1%, effective sample sizes (ESS) were > 200, and the potential scale reduction factor for estimated parameters was approximately 1.0. We generated the 50% most credible set of trees from the posterior distribution of possible topologies using the consensus algorithm of ExaBayes (burn-in: 25%; thinning: 500).

2.5. Coalescent-based species tree analysis

To account for coalescent stochasticity among individual UCE loci and to address the related problem where concatenated analyses can return highly supported but incorrect trees, we inferred a species tree from individual gene trees using a two-step process. First, we used PHYLUCE to resample loci available for at least 75% of taxa and used RAxML to analyze each of these alignments and generate a set of best trees. These best trees were then analyzed using ASTRAL-II (Mirarab and Warnow, 2015) to infer majority-rule species trees having a minimum clade frequency of 0.7. While ASTRAL is not a coalescent method strictly, it is statistically consistent with the multispecies coalescent model and scales well to large numbers of loci.

2.6. Pairwise comparisons of phylogenetic trees

The best way to combine information contained in numerous gene-trees for the same set of species remains an open problem in the field of the systematics. Despite the availability of different methods, we chose to use the R package "distory" (Chakerian et al., 2012) and the function "distinct.edges" to perform a pairwise comparison between phylogenetics trees generated by different analyses and matrix treatments. This method counts the number of branches between two phylogenetic trees, making it easy to recognize the total number of differences in the topology of large trees.

2.7. Time calibration

An uncorrelated relaxed molecular clock (lognormal) was estimated using BEAST v1.8.2 (Drummond et al., 2012). BEAST is unable to handle a data matrix > 20,000 bp in length, so we down-sampled our dataset to generate a 90% complete edge-trimmed matrix comprising 19,846 bp and 187 UCEs (Table 1). The best ML tree generated from the 75% complete edge-trimmed alignment was used as a fixed topology in

the Bayesian search so that only ages were estimated for each node.

We included two node calibrations to constrain divergence dates in our Loricariidae tree. First, a maximum age calibration point was assigned to the root of the tree (i.e., including all taxa), the most recent common ancestor (MRCA) of Characiformes and Siluriformes. This calibration was implemented as a normally distributed prior, with an age offset of 120 million years and a standard deviation of 14 million years. These date-estimate parameters were selected to match our current understanding of the timing of siluriform diversification. Fossil evidence and previous fossil-calibrated molecular clock analyses of Siluriformes (Lundberg, 1993; Sullivan et al., 2006; Lundberg et al., 2007) indicate an origin for the order during the Lower Cretaceous (145–100 Ma).

A second internal calibration was assigned to the first node within Corydoradinae (i.e., least inclusive node containing both C. aeneus and Aspidoras fuscoguttatus) based on the callichthyid fossil †Corydoras revelatus Cockerell 1925. †Corydoras revelatus is the oldest known loricarioid fossil assignable to an extant taxon. Cockerell (1925) described the fossil from the Maíz Gordo Formation (Giudici and Gascon, 1982), which was deposited during the lower Eocene about 56–52 Ma (Del Papa and Salfity, 1999). For this calibration, we implemented a lognormal prior offset to 55 Ma with a mean and standard deviation of 0.5.

We used a birth–death model prior for diversification likelihood values. The BEAST analysis was conducted under the HKY model of molecular evolution for the entire matrix and was run for 50 million generations with tree space sampled every 1000th generation. Stationarity and sufficient mixing of parameters (ESS > 200) were checked using Tracer v1.6 (Rambaut et al., 2014). A consensus tree was built using TreeAnnotator v1.8.2. All clade-age estimates are presented as the mean plus 95% highest posterior density (HPD) values.

3. Results and discussion

Sequencing and data filtering yielded an initial edge-trimmed aligned matrix comprising 756,476 base pairs (bp) and 2482 UCE loci for 171 specimens (163 Loricariidae and eight outgroup taxa). The total matrix included 79,682,706 characters, of which 61,797,668 were nucleotides and 17,885,038 (22.4%) were missing data. Mean locus length after alignment and trimming was 304 nucleotides (range: 100–1223 nt). Phylogenies inferred from the concatenated datasets were resolved with high statistical support for each node and exhibited similar topologies regardless of matrix completeness (60%: 1454 loci, 494,488 bp; 75%: 1041 loci, 328,330 bp; 85%: 471 loci, 102,064 bp), method of phylogenetic inference (ML, BI and Astral-II), and whether or not we partitioned the UCE matrix.

Therefore, we base our discussion exclusively on results of the ML and BI analyses (Figs. 2–5) of the edge-trimmed, 75% complete, concatenated, unpartitioned matrix. These analyses yielded phylogenies with strong support for nearly all nodes (ML > 95%, BI > 0.99), except for 13 nodes where bootstrap support fell between 50% and 95% (indicated by arrows in Fig. 2).

In a pairwise comparison of results from different analyses and data matrices, the Astral-II species tree was the most topologically distinct, with results of the concatenated ML and BI analyses being very similar to each other. Differences in the tree topology of ML and BI from Astral-II are discussed below. In a comparison of ML and BI analyses of data matrices with different levels of completeness (60%, 75% or 85%), the results from the 85% complete matrix were the most distinct, with results from the 60% and 75% complete matrices being very similar. The use of different data partitioning schemes had less influence on tree topology than other analyzed parameters, such as edge vs. internal sequence trimming and different methods of phylogenetic inference (ML vs. BI vs. Astral-II). Topological differences among trees were highly variable and unrelated to previous phylogenetic hypotheses. See Table S3 for a pairwise comparison of the total number of branches that differed between tree topologies and Figs. S1–S19 for all trees and
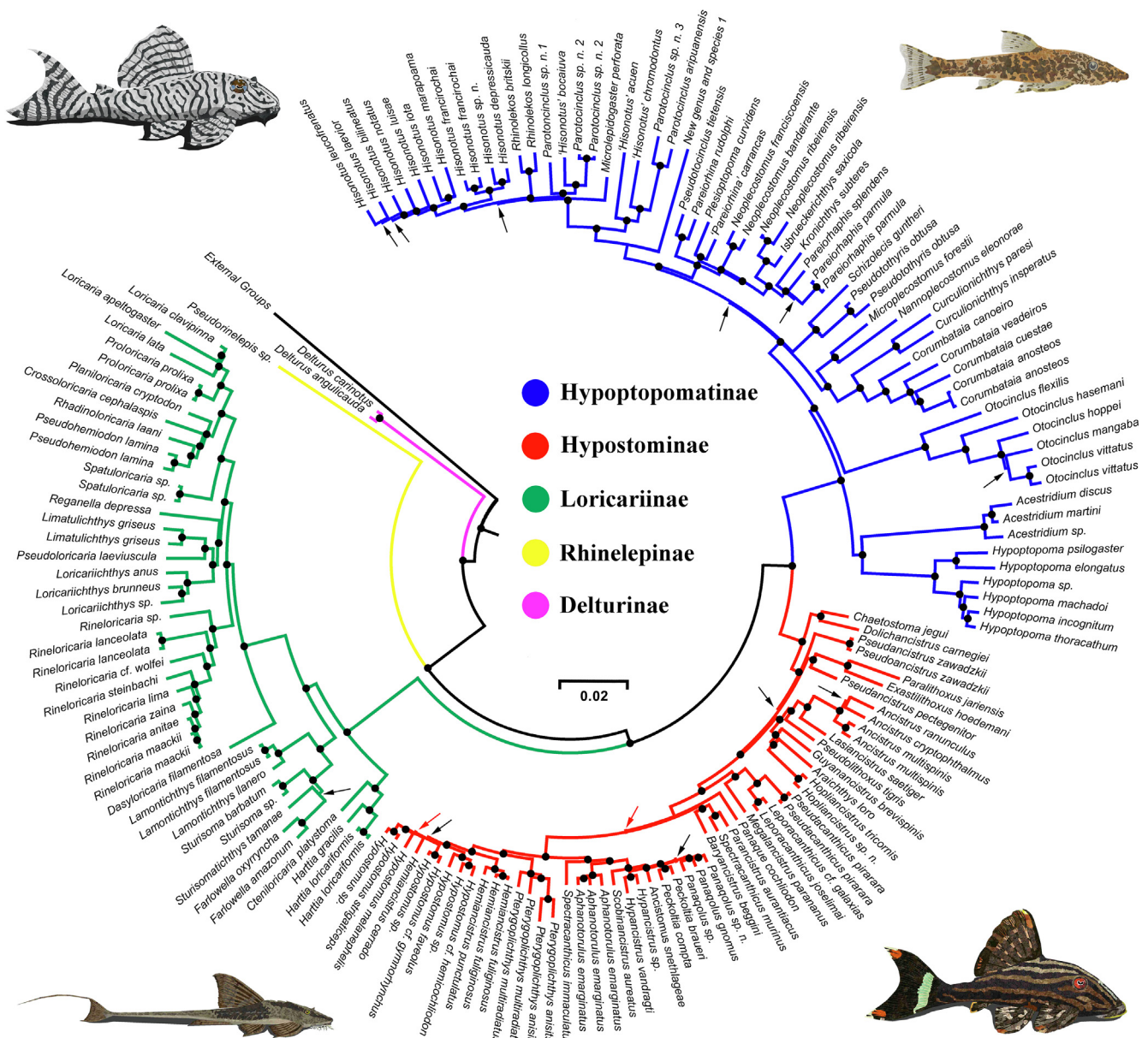
Fig. 2. Phylogeny of Loricariidae based on a maximum likelihood analysis of a concatenated alignment of 1041 UCE loci from 163 specimens representing 140 species and 75 genera. All nodes had bootstrap values > 50%. Black dots denote nodes with bootstrap values > 95%; black arrows denote 13 nodes with bootstrap values between 50% and 95%. Bayesian analysis of the same concatenated alignment of 1041 UCE loci (75% complete, edge-trimmed, unpartitioned; data S8) produced the same topology (Fig. S8). Red arrows indicate nodes with BI < 0.95. Fish illustrations by Mitsuhiro Iwamoto.

specific differences among them.

3.1. Basal relationships

Both maximum likelihood and Bayesian inference strongly supported the monophyly of Loricariidae (Fig. 2; ML > 95%, BI = 1) corroborating previous molecular (Roxo et al., 2014, 2017; Lujan et al., 2015a; Covain et al., 2016; Silva et al., 2016) and morphological studies (Armbruster, 2004a, 2008). Our results strongly supported the monophyly of four loricariid subfamilies (ML > 95%, BI = 1): Delturinae, Loricariinae, Hypostominae (including taxa formerly placed in Ancistrinae and Chaetostominae) and Hypoptopomatinae (including taxa formerly placed in Neoplecostominae and Otothyrinae). However, our sampling of early-diverging lineages was limited. Specifically, we did not analyze Lithogeninae (previously placed in a trichotomy with Delturinae and a clade containing all other loricariids) and 'Pseudancistrus'

genisetiger (previously placed in a trichotomy with Rhinelepinae and a clade containing all other loricariids except Lithogeninae and Delturinae) (Lujan et al., 2015a).

The subfamily Delturinae, represented by *Delturus angulicauda* (Steindachner, 1877) and *D. carinotus* (La Monte, 1933), was sister to all other loricariids analyzed in concordance with previous morphological (Armbruster, 2004a) and molecular (Lujan et al., 2015a) hypotheses. The second lineage to diverge inside Loricariidae was the subfamily Rhinelepinae, represented in this analysis by the single species *Pseudorinelepis genibarbis* (*Rhinelepis* was not included in the present study). Rhinelepinae was sister to a clade in which Loricariinae was sister to Hypostominae + Hypoptopomatinae (ML > 95%, BI = 1).

3.1.1. Timetree estimation of Loricariidae lineages

We obtained a time-calibrated phylogeny for all major clades of Loricariidae that is one of the most taxonomically comprehensive to
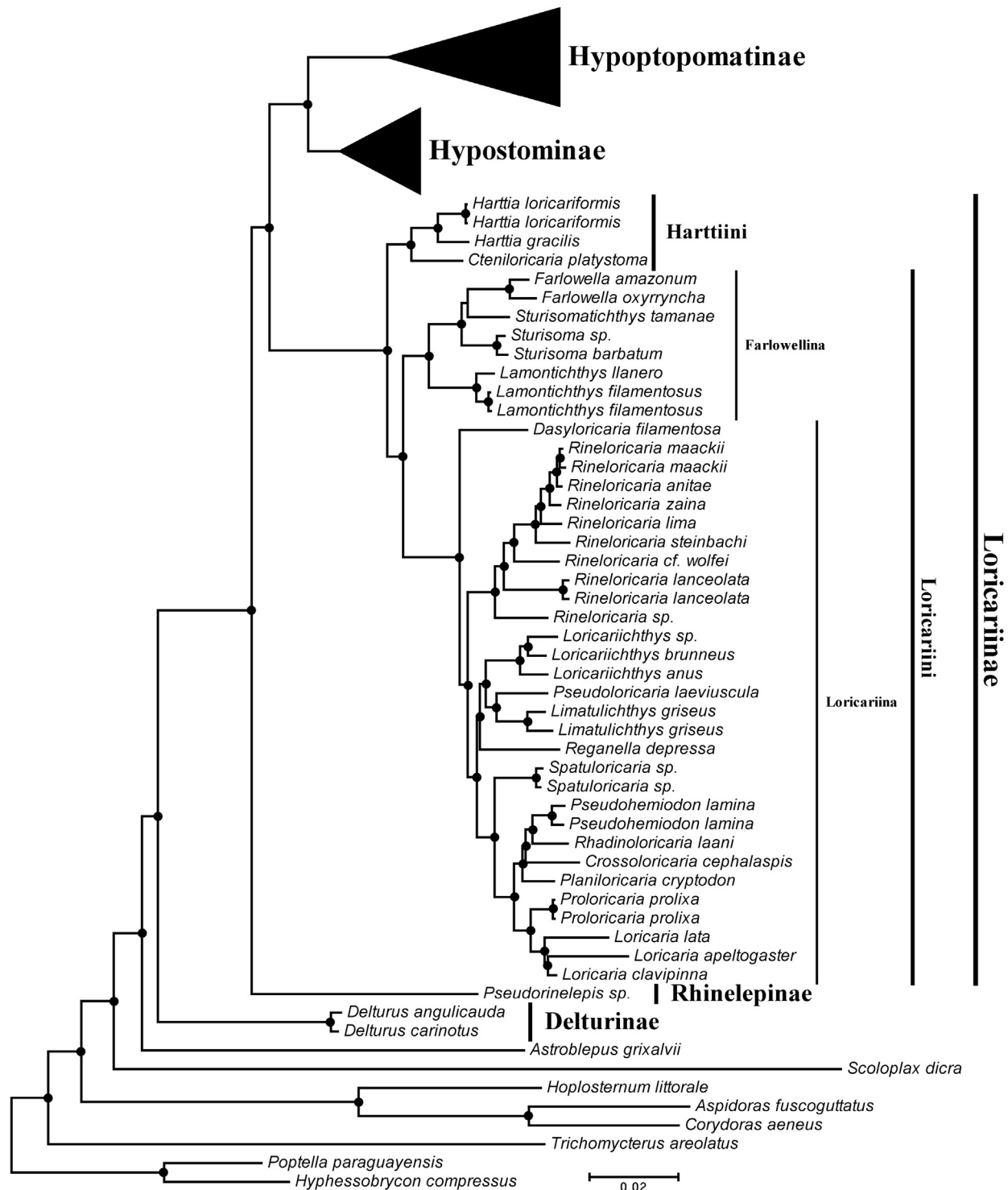
Fig. 3. Partial maximum likelihood tree showing outgroups and interspecific relationships within the subfamilies Delturinae, Rhinelepinae and Loricariinae. Black dots indicate node support values > 95% from 1000 bootstrap pseudoreplicates. Bayesian analysis of the same concatenated alignment of 1041 UCE loci (75% complete, edge-trimmed, unpartitioned; data S8) produced the same topology (Fig. S8) with all nodes having BI = 1.

date (Fig. 6) with a tree topology that parallels earlier ones for Loricariinae (Covain et al., 2016), Hypostominae (Lujan et al., 2015b; Silva et al., 2016b) and Hypoptopomatinae (Roxo et al., 2014; Silva et al., 2016a). Mean substitution rate for the entire dataset was estimated to be 0.04% substitutions per million years.

According to our time-tree estimation, Loricariidae (excluding

subfamily Lithogeninae, not examined) originated during the Late Cretaceous-Paleogene boundary, at approximately 65.4 Ma (46.4–86.6 Ma 95% HPD; Fig. 6). The subfamily Delturinae, represented by *Delturus angulicauda* and *D. carinotus*, originated during the Paleocene, approximately 58.6 Ma (41.2–77.6 Ma 95% HPD). The remaining subfamilies (Figs. S21–S23) originated during the Eocene,
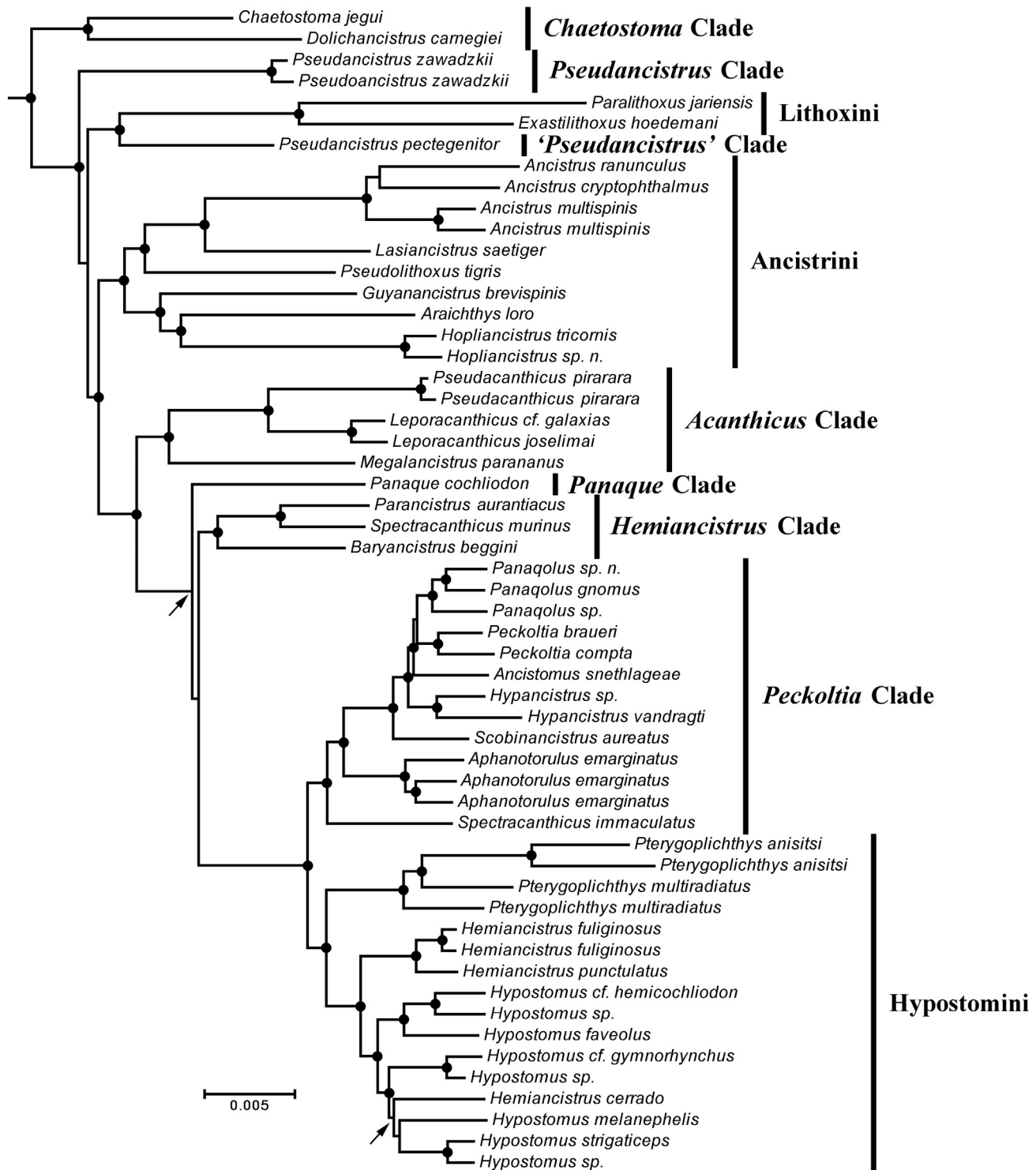
Fig. 4. Partial maximum likelihood tree showing outgroups and interspecific relationships within the subfamily Hypostominae. Black dots indicate node support values > 95% from 1000 bootstrap pseudoreplicates. Bayesian analysis of the same concatenated alignment of 1041 UCE loci (75% complete, edge-trimmed, unpartitioning; data S8) produced the same topology (Fig. S8). Black arrows indicate nodes with BI < 0.95.

with Rhinelepinae approximately 46.6 Ma (33.3–61.8 Ma 95% HPD), Loricariinae approximately 42.4 Ma (30.1–56.2 Ma 95% HPD) and Hypostominae + Hypoptopomatinae approximately 35.8 Ma (24.8–47.9 Ma 95% HPD), corroborating dates of origin previously proposed by Roxo et al. (2014) and Silva et al. (2016a,b).

3.2. Subfamily Loricariinae

Our analyses (Fig. 3) supported a topology for the subfamily Loricariinae that was similar to that of the recent multilocus phylogeny by Covain et al. (2016). We follow Covain et al. (2016) by recognizing two tribes, Harttiini (represented by *Harttia loricariformis* Steindachner,
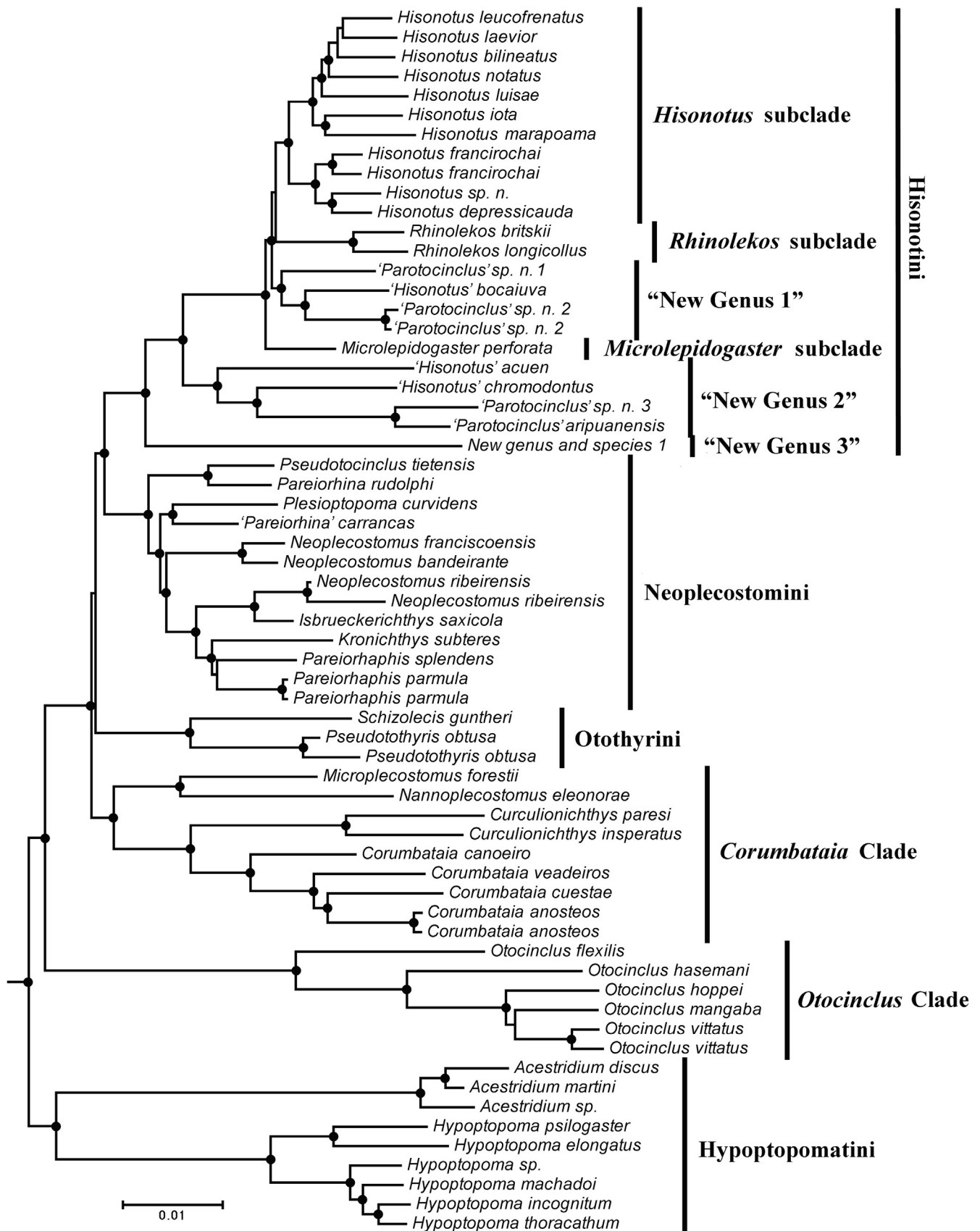
Fig. 5. Partial maximum likelihood tree showing outgroups and interspecific relationships within the subfamily Hypoptopomatinae. Black dots indicate node support values > 95% from 1000 bootstrap pseudoreplicates. Bayesian analysis of the same concatenated alignment of 1041 UCE loci (75% complete, edge-trimmed, unpartitioned; data S8) produced the same topology (Fig. S8) with all nodes having BI = 1.
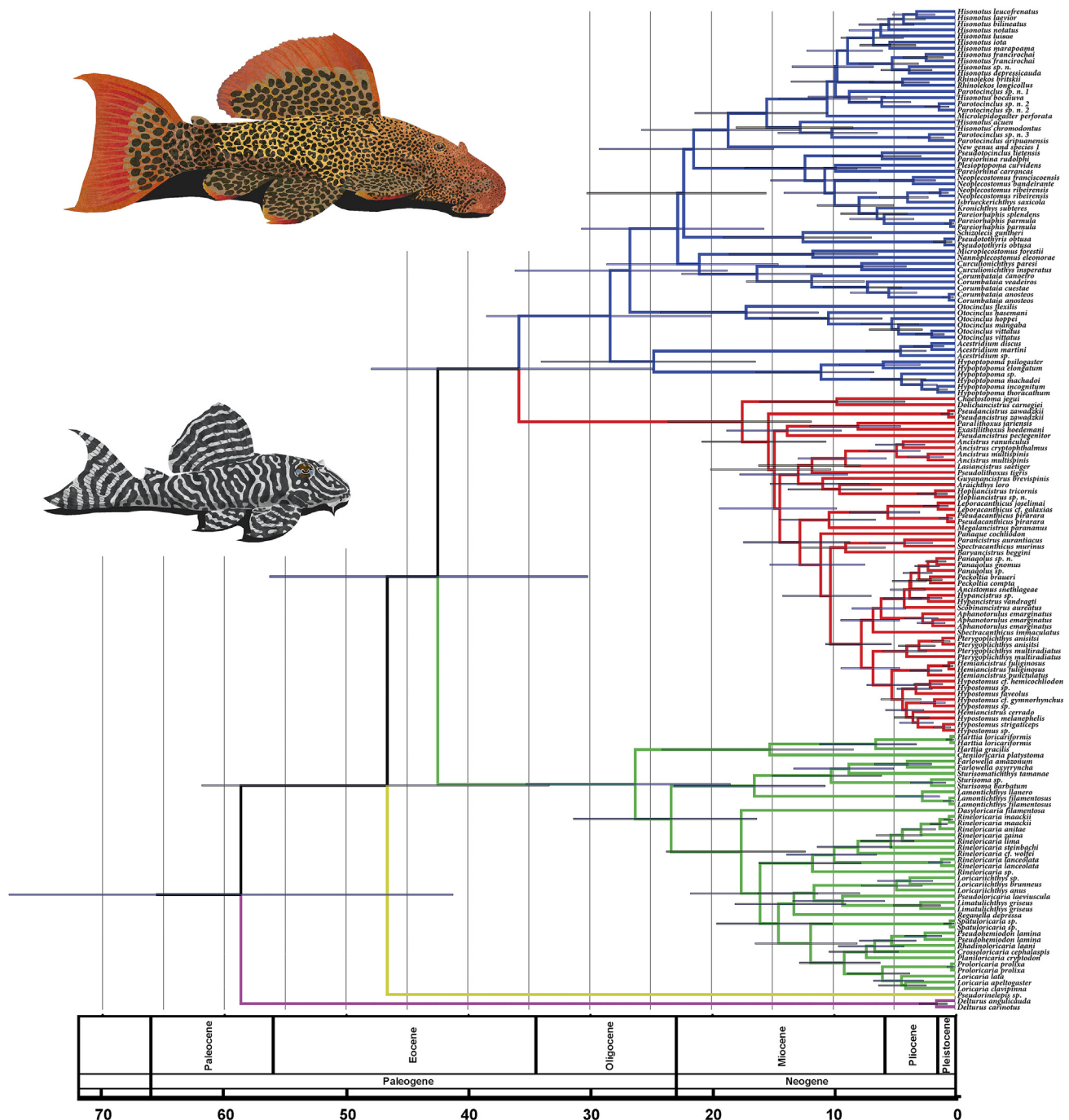
Fig. 6. Time-calibrated phylogeny for Loricariidae based on a BEAST analysis of 187 UCE loci present for at least 90% of 163 specimens representing 140 species and 75 genera. Total alignment length = 19,846 bp. Node bars show the 95% highest posterior distribution of ages. Branch colors highlight members of five major loricariid subfamilies: Delturinae (pink), Rhinelepinae (yellow), Loricariinae (green), Hypostominae (red), and Hypoptopomatinae (blue). Fish illustrations by Mitsuhiro Iwamoto. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1877, *H. gracilis* Oyakawa, 1993 and *Cteniloricaria platystoma* (Günther, 1868); *Harttiella* not examined) and Loricariini, both of which were monophyletic with strong statistical support in our analysis (ML > 95%, BI = 1). Within Loricariini, the two subtribes recognized by Covain et al. (2016), Farlowellina and Loricariina (*sensu* Covain et al., 2016) were also monophyletic. Farlowellina (ML > 95%, BI = 1) was represented by four genera in our study (*Farlowella*, *Lamontichthys*, *Sturisoma* and *Sturisomatichthys*) compared to the six assigned to that group by Covain et al. (2016; *Aposturisoma* and *Pterosturisoma* not examined here). Loricariina (ML > 95%, BI = 1) was represented here by 13 of the 23 genera previously assigned to that group.

3.2.1. Tribe Harttiini

Covain et al. (2016) found that the tribe Harttiini included the genera *Harttia*, *Cteniloricaria* and *Harttiella* and excluded members of the Farlowellina, which had been included in Harttiini by Isbrücker (1979) and Rapp Py-Daniel (1997). Our analysis, which included *Harttia* and *Cteniloricaria*, corroborated the exclusion of Farlowellina from Harttiini.

3.2.2. Subtribe Farlowellina

Within Farlowellina, the four analyzed genera were monophyletic (i.e., *Farlowella*, *Sturisomatichthys*, *Sturisoma* and *Lamontichthys*).

Relationships among members of Farlowellina were also similar to those in Covain et al. (2016), wherein *Lamontichthys* was the first group to diverge and the remaining clade was composed of *Sturisoma* sister to *Farlowella* + *Sturisomatichthys*. Astral-II recovered *Sturisoma* as being sister to *Farlowella* with these two groups sister to *Sturisomatichthys*.

Covain et al. (2016) recovered *Sturisoma* and *Sturisomatichthys* as paraphyletic, and thereby restricted the genus *Sturisoma* to the *cis*-Andean region and expanded *Sturisomatichthys* to contain all trans-Andean species of *Sturisoma* and *Sturisomatichthys*. In Armbruster (2004a, 2008), the genera *Sturisoma*, *Sturisomatichthys* and *Lamontichthys* were closely related to species of the genus *Harttia*, a hypothesis rejected by the present and previous molecular works (Montoya-Burgos et al., 1998; Covain et al., 2008; Rodriguez et al., 2011; Lujan et al., 2015a; Covain et al., 2016).

3.2.3. Subtribe Loricariina

Relationships within Loricariina were the same in ML, BI and Astral-II analyses. We analyzed thirteen genera in the species-rich subtribe Loricariina. *Dasyloricaria* was the first group to diverge; however, we did not analyze *Metaloricaria* – the first group to diverge in Covain et al. (2016) followed by *Fonchiiloricaria* + *Dasyloricaria*.

The second lineage to diverge within Loricariina was *Rineloricaria*, the most species-rich genus of Loricariinae with about 63 valid (Eschmeyer, 2018) and numerous undescribed species. Corroborating previous studies, *Ixinandria steinbachi* (Regan, 1906) (currently valid as *Rineloricaria steinbachi*) was closely related to species of the genus *Rineloricaria*. However, three other genera also treated as synonyms of *Rineloricaria* (*Hemiloricaria*, *Fonchiiichthys*, *Leliella*) and *Fonchiiloricaria* were not examined.

Our results for the *Loricariichthys* group (including *Limatulichthys*, *Loricariichthys* and *Pseudoloricaria*) also largely corroborated those of Covain et al. (2016). However, *Hemiodontichthys* and *Furcodontichthys* (Covain and Fisch-Muller, 2007; Covain et al., 2016) were not examined. The monotypic genus *Reganella* was sister to the *Loricariichthys* group in our analysis. This contrasts previous hypotheses placing *Reganella* within the *Pseudohemiodon* group (Covain and Fisch-Muller, 2007; Covain et al., 2016).

The genus *Spatuloricaria* was sister to the *Loricaria* group + the *Pseudohemiodon* group, corroborating the studies of Covain et al. (2016) and Rodriguez et al. (2011). However, relationships within the *Pseudohemiodon* group slightly differed. In the present study, *Planiloricaria* was the first lineage to diverge and *Crossoloricaria* (represented by *C. cephalaspis* Isbrücker (1979), a trans-Andean species) was sister to *Pseudohemiodon* + *Rhadinoloricaria*. In Covain et al. (2016), the first group to diverge comprised exclusively trans-Andean *Crossoloricaria*.

3.3. Subfamily Hypostominae

Hypostominae was monophyletic in our analysis (ML > 95%, BI = 1; Fig. 4) and internal relationships within this subfamily differed only slightly from the more taxonomically representative phylogeny by Lujan et al. (2015a). Our analysis resolved hypostomines into the same nine subclades identified in Lujan et al. (2015a). At this level, the only difference was in placement of the genus *Panaque*. In our analysis, *Panaque* was represented by the single trans-Andean species *Panaque cochliodon* (Steindachner, 1879). We found moderate support for *Panaque* being sister to a large clade comprising the *Hemiancistrus* Clade + (Hypostomini + *Peckoltia* Clade) in ML and BI analyses of the unpartitioned 75%-complete edge-trimmed alignment, but strong support for this relationship in the Astral-II analysis of the unpartitioned 75%-complete edge-trimmed alignment and most other analyses (e.g., ML analysis of 60%-complete edge-trimmed alignment with the kmeans data-partition). Lujan et al. (2015a) analyzed both trans- and cis-Andean *Panaque*, and resolved *P. cochliodon* as the first species to diverge. Their analysis found weak support for *Panaque* as the sister to the *Hemiancistrus* Clade only with *Panaque* + *Hemiancistrus* Clade sister to

Hypostomini + *Peckoltia* Clade.

Within Hypostominae, only six nodes had moderate support (i.e., ML = 50–95%, BI = 1), those describing relationships between (1) the Lithoxini + '*Pseudancistrus*' Clade and remaining clades, (2) the *Panaque* Clade and other members of the Hypostominae, (3) species *Ancistrus ranunculus* Muller et al. (1994) and *A. cryptophthalmus* Reis, 1987, (4) genera *Peckoltia* and *Panaqolus*, (5) *Hemiancistrus cerrado* de Souza et al. (2008) and (6) *Hypostomus melanephelis* Zawadzki et al. (2015) and other members of the genus *Hypostomus*. In the Astral-II analysis, *Hemiancistrus cerrado* was sister to *Hypostomus* sp. and *Hypostomus* cf. *gymnorhynchus*, which differed from analyses of the concatenated alignment in which *Hypostomus melanephelis* was sister to *Hypostomus* sp. and *Hypostomus* cf. *gymnorhynchus*.

The *Chaetostoma* Clade, represented in our analysis by the genera *Chaetostoma* and *Dolichancistrus*, was the first group to diverge, followed by the *Pseudancistrus* Clade, represented by a single species, *Pseudancistrus zawadzkii* Silva, Roxo, Britzke and Oliveira (2014) Lithoxini was strongly monophyletic (ML > 95%, BI = 1) and represented by two species: *Exastilithoxus hoedemani* Isbrücker and Nijssen (1985) and *Paralithoxus jariensis* (Silva, Covain, Oliveira and Roxo, 2017). Lithoxini was sister to the '*Pseudancistrus*' Clade, represented by the single species '*Pseudancistrus*' *pectegenitor* Lujan, Armbruster and Sabaj (2007).

The tribe Ancistrini *sensu* Lujan et al. (2015a) was represented in our analysis by *Ancistrus*, *Guyanancistrus*, *Hopliancistrus*, *Lasiancistrus*, *Pseudolithoxus*, and the recently described *Araichthys* (Zawadzki et al., 2016). Monophyly of this clade was strongly supported (ML > 95%, BI = 1), as was monophyly of the *Acanthicus* Clade (ML > 95%, BI = 1) represented by the genera *Leporacanthicus*, *Megalancistrus* and *Pseudacanthicus*.

Our results strongly supported monophyly of the *Peckoltia* Clade containing *Panaqolus*, *Peckoltia*, *Hypancistrus*, *Scobinancistrus*, *Aphanotorulus* (senior synonym of *Squaliforma*) and *Spectracanthicus* (ML > 95%, BI = 1). This clade was sister to Hypostomini, which was also monophyletic (ML > 95%, BI = 1). Hypostomini contained the genera *Pterygoplichthys*, *Hypostomus* and three species of '*Hemiancistrus*' ('*H.*' *fuliginosus* Cardoso & Malabarba, 1999, '*H.*' *punctulatus* Cardoso & Malabarba, 1999 and '*H.*' *cerrado*).

3.3.1. Chaetostoma Clade

The tribe-level *Chaetostoma* Clade (*sensu* Lujan et al., 2015b) was represented in our analyses by the genera *Chaetostoma* and *Dolichancistrus*. Lujan et al. (2015a,b) also placed *Andeancistrus*, *Cordylancistrus*, *Leptoancistrus* and *Transancistrus* in this clade. Armbruster (2004a, 2008) provided strong morphological support for monophyly of the same *Chaetostoma* Clade, but considered it closely related to members of the Lithoxini (*Lithoxus* and *Exastilithoxus*). Molecular results consistently reject this hypothesis.

3.3.2. Pseudancistrus Clade

As in Lujan et al. (2015a) the *Pseudancistrus* Clade (comprising only the genus *Pseudancistrus sensu stricto*) was the second lineage to diverge within Hypostominae. It was represented in our analyses by only one species, *P. zawadzkii* (Silva et al., 2014), although a molecular phylogeny and taxonomic revision by Covain and Fisch-Muller (2012) and subsequent species description by Silva et al. (2014) identified six additional congeners.

3.3.3. Tribe Lithoxini

Lujan et al. (2018) recently proposed the tribe Lithoxini for members of the *Lithoxus* Clade (*sensu* Armbruster, 2004a, 2008, and Lujan et al., 2015a). Their phylogenetic analysis recognized four genera with the monotypic *Avalithoxus* as the first to diverge, followed by *Exastilithoxus* sister to *Lithoxus* + *Paralithoxus*. Our analysis included two species of Lithoxini: *Exastilithoxus hoedemani* and the recently described *Paralithoxus jariensis* (Silva et al., 2017).

3.3.4. 'Pseudancistrus' Clade

The 'Pseudancistrus' Clade (*sensu* Lujan et al., 2015a), represented in our analysis by the single species '*Pseudancistrus*' *pectegenitor*, was sister to the Lithoxini. That relationship is consistent with one previous molecular analysis (Covain and Fisch-Muller, 2012), but not supported by another with greater taxonomic sampling (Lujan et al., 2015a). Both studies found '*P.' pectegenitor* to be sister to '*P.' sidereus*, but the latter study weakly grouped this '*Pseudancistrus*' Clade with one composed of Hypostomini and the *Acanthicus*, *Hemiancistrus* and *Peckoltia* clades. None of the molecular analyses support *Pseudancistrus* (*sensu lato*, Armbruster, 2008) as monophyletic.

3.3.5. Tribe Ancistrini

Morphology-based phylogenetic and systematic analyses have traditionally grouped loricariid species having enlarged and highly evertible cheek odontodes in either the subfamily Ancistrinae (Isbrücker, 1980) or tribe Ancistrini (Armbruster, 2004a, 2008). However, molecular analyses (Montoya-Burgos et al., 1998, 1998; Cramer et al., 2011; Lujan et al., 2015a) have consistently rejected the monophyly of these taxa, finding instead that the entire evertible cheek spine mechanism has been lost several times, creating a suite of highly homoplastic characters that strongly influence morphology-based analyses. To resolve this, Lujan et al. (2015a) restricted Ancistrini to ten genera that are most closely related to the genus *Ancistrus*. Our analyses found the Ancistrini Clade to comprise the genera *Ancistrus*, *Lasiancistrus*, *Pseudolithoxus*, *Guyanancistrus*, *Hopliancistrus* and the monotypic, recently described genus *Araichthys*. Lujan et al. (2015a) also included within Ancistrini the genera *Lithoxancistrus*, *Paulasquama*, *Neblinichthys*, *Dekeyseria* and *Corymbophanes*, which were not examined here.

Within Ancistrini, the genus *Ancistrus* was sister to *Lasiancistrus* forming a clade sister to *Pseudolithoxus*, corroborating previous morphological and molecular studies (e.g., Armbruster, 2004a, 2008; Covain and Fisch-Muller, 2012; Lujan et al., 2015a; Silva et al., 2016).

Zawadzki et al. (2016) assigned their new monotypic genus *Araichthys* to Ancistrini since it shares all five characters diagnostic of the tribe *sensu* Armbruster (2004a, 2008). Zawadzki et al. (2016) also suggested that *Araichthys* might be closely related to the genus *Neblinichthys*, although our analysis did not examine *Neblinichthys* and placed *Araichthys* sister to *Hopliancistrus*. *Guyanancistrus* was sister to *Hopliancistrus* + *Araichthys* in our analysis, supporting *Guyanancistrus* as a valid genus and corroborating previous molecular analyses (Covain and Fisch-Muller, 2012; Lujan et al., 2015a; Fisch-Muller et al., 2018).

3.3.6. Acanthicus Clade

Monophyly of the *Acanthicus* Clade, comprising *Acanthicus*, *Leporacanthicus*, *Megalancistrus* and *Pseudacanthicus*, was previously supported by both morphological (Armbruster, 2004a, 2008) and molecular (Montoya-Burgos et al., 1998; Hardman, 2005, Cramer et al., 2011, Lujan et al., 2015a) phylogenetic studies. In our study, *Megalancistrus* was the first to diverge and formed the sister group to *Pseudacanthicus* + *Leporacanthicus* (*Acanthicus* not examined).

3.3.7. Panaque Clade

The *Panaque* Clade is represented in our analysis by the single species *P. cochliodon*, which was found to be sister to a clade comprising the *Hemiancistrus* Clade + (*Peckoltia* Clade + Hypostomini); however, node support for this relationship was moderate and differed from relationships found by Lujan et al. (2015a) and Lujan et al. (2017) in which *Panaque* was weakly supported as sister to the *Hemiancistrus* Clade exclusively.

3.3.8. Hemiancistrus Clade

Hemiancistrus has long been a large and poorly defined genus comprising any Hypostominae species that lacked the distinguishing synapomorphies of other better-diagnosed genera. Cladistic analyses based on morphology (Armbruster 2004a, 2008) and molecules (Lujan

et al., 2015a, 2017) consistently failed to support the monophyly of *Hemiancistrus*. Molecular data suggest that *Hemiancistrus* is monotypic and restricted to its type species *H. medians* (Kner, 1854) which is nested among the genera *Parancistrus*, *Spectracanthicus*, *Baryancistrus* and a clade of upper Orinoco '*Hemiancistrus*' and '*Baryancistrus*' (Lujan et al., 2015a). This phylogenetic position is distant from other putative congeners, such as '*H.' fuliginosus*, '*H.' meizospilos* Cardoso and da Silva, 2004, '*H.' votouro* Cardoso and da Silva, 2004, '*H.' punctulatus*, '*H.' aspidolepis* (Günther, 1867), '*H.' maracaiboensis* Schultz, 1944, '*H.' landoni* Eigenmann, 1916 and '*H.' pankimpuju* Lujan and Chamon, 2008. Although we did not examine *H. medians*, the '*Hemiancistrus*' species *fuliginosus*, *punctulatus* and *cerrado* were more closely related to species of *Hypostomus* in our molecular analysis, which is consistent with studies by Cramer et al. (2011) and Lujan et al. (2015a).

Prior morphological and molecular analyses have strongly disagreed on the phylogenetic placement of *Spectracanthicus*. Morphology placed *Spectracanthicus* as sister to a clade containing *Leporacanthicus*, *Pseudacanthicus*, *Megalancistrus* and *Acanthicus*, a relationship driven in part by the shortening of tooth rows, reductions in tooth number, and other related changes in the oral jaws (Armbruster, 2004a, 2008). The molecular study by Lujan et al. (2015a) placed *Spectracanthicus* among the generally wider-jawed genera *Baryancistrus* and *Parancistrus*, but did not include the type species of the genus, *S. murinus* Nijssen and Isbrücker (1987), which had been included in the morphological studies. Our analysis was the first molecular study to include *S. murinus*, and our results still grouped *Spectracanthicus* with *Baryancistrus* and *Parancistrus*. This relationship suggests that the oral jaw characters are homoplastic and likely subject to evolutionary convergence related to trophic ecology, with narrower-jawed species being generally more carnivorous and wider-jawed species more herbivorous/detritivorous (Lujan et al., 2012). Among all genera of Hypostominae, only species of *Baryancistrus*, *Parancistrus* and *Spectracanthicus* have a posterior expansion of the dorsal-fin membrane that attaches to either the adipose-fin spine (e.g., *Parancistrus*) or to one of the azygous plates preceding the adipose-fin spine (e.g., *B. longipinnis* (Kindle, 1895)). Thus, this interdorsal membrane is a valuable characteristic for inferring the shared phylogenetic history of these taxa.

3.3.9. Peckoltia Clade

We found the *Peckoltia* Clade to contain the genera *Ancistomus*, *Panaqolus*, *Peckoltia*, *Hypancistrus*, *Scobinancistrus*, *Aphanotorulus* and '*Spectracanthicus*' *immaculatus*, corroborating the results of Lujan et al. (2015a). The *Peckoltia* Clade *sensu* Lujan et al. (2015a) is the most genus-rich tribe-level clade within Hypostominae and includes the monotypic cis-Andean genera *Peckoltichthys* and *Pseudoqolus*, the genus *Isorineloricaria*, which contains cis- and trans-Andean species, and a still undescribed trans-Andean genus containing '*Hemiancistrus*' *landoni* and '*H.' furtivus* Provenzano and Barriga Salazar (2017) (Lujan et al., 2015a, 2017), none of which were examined here.

Our topology for relationships within the *Peckoltia* Clade differs from that of Lujan et al. (2015a, 2017). The species '*Spectracanthicus*' *immaculatus* Chamon and Rapp Py-Daniel (2014) was the first lineage to diverge, followed by *Aphanotorulus*, which was recently revised by Ray and Armbruster (2016) to include *Squaliforma* as a junior synonym. In Lujan et al. (2015a, 2017), *Aphanotorulus* is closer to the base of the *Peckoltia* Clade, subtended only by '*Hemiancistrus*' *landoni* (not examined here). In our analysis, *Scobinancistrus* was the third lineages to diverge, followed by *Hypancistrus*, then *Ancistomus* sister to *Panaqolus* + *Peckoltia*. Relationships among those genera were well resolved and well supported relative to Lujan et al. (2015a, 2017), although those studies also included the monotypic genera *Peckoltichthys* and *Pseudoqolus* in the *Peckoltia* Clade, neither of which were examined here. In contrast to this study, Lujan et al. (2015a, 2017) found consistently strong support for *Ancistomus* and *Scobinancistrus* as sister taxa, forming a clade sister to *Panaqolus*. Our results corroborate the synonymization of *Micracanthicus* with *Hypancistrus* (Lujan et al., 2017).

Table 2
Nomenclatural changes within the Hypoptopomatinae.

	Original description	New combination
1	*Epactionotus bilineatus* Reis and Schaefer, 1998	*Hisonotus bilineatus* (Reis and Schaefer, 1998)
2	*Epactionotus gracilis* Reis and Schaefer, 1998	*Hisonotus gracilis* (Reis and Schaefer, 1998)
3	*Epactionotus itaimbezinho* Reis and Schaefer, 1998	*Hisonotus itaimbezinho* (Reis and Schaefer, 1998)
4	*Eurycheilichthys luisae* Reis, 2017	*Hisonotus luisae* (Reis, 2017)
5	*Gymnotocinclus anosteos* Carvalho, Lehmann A. & Reis, 2008a	*Corumbataia anosteos* (Carvalho, Lehmann A. & Reis, 2008a)
6	*Gymnotocinclus canoeiro* Roxo, Silva, Ochoa, Zawadzki, 2017	*Corumbataia canoeiro* (Roxo, Silva, Ochoa, Zawadzki, 2017)
7	*Microlepidogaster longicolla* Calegari and Reis, 2010	*Rhinolekos longicollum* (Calegari and Reis, 2010)
8	*Otothyropsis marapoama* Ribeiro, Carvalho and Melo, 2005	*Hisonotus marapoama* (Ribeiro, Carvalho & Melo, 2005)

3.3.10. Tribe Hypostomini

The tribe Hypostomini was narrowly restricted by Lujan et al. (2015a) to include only the widespread genera *Hypostomus* and *Pterygoplichthys* and two geographically restricted clades, the first containing '*Hemiancistrus*' *aspidolepis* and '*H.*' *maracaiboensis* from northwestern South America and Panama, and the second containing '*Hemiancistrus*' *fuliginosus*, '*H.*' *meizospilos*, '*H.*' *punctulatus* and '*H.*' *votouro* from the Uruguay and Laguna dos Patos basins in Argentina, Uruguay and southeastern Brazil. *Pterygoplichthys* was monophyletic in our analysis, corroborating the morphological and molecular results of Montoya-Burgos (2003), Armbruster (2004a), Cardoso et al. (2012) and Lujan et al. (2015a). As in Lujan et al. (2015a), *Pterygoplichthys* was the first group to diverge inside Hypostomini, forming the sister group to *Hemiancistrus* and *Hypostomus* + a clade containing '*Hemiancistrus*' species from southeastern South America (northwestern South American species '*H.*' *aspidolepis* and '*H.*' *maracaiboensis* not examined here).

3.4. Subfamily Hypoptopomatinae

Taxonomic limits of Hypoptopomatinae have waxed and waned since its inception as a major division within Loricariidae by Eigenmann and Eigenmann (1890). Composition of the Hypoptopomatinae largely depends on whether two groups are treated as constituent tribes (Neoplecostomini, Otothyrini) or separate subfamilies (Neoplecostominae, Otothyrinae). Our analysis strongly supported a clade composed of taxa historically assigned to the subfamilies Hypoptopomatinae, Neoplecostominae, and Otothyrinae. However, the relationships among those taxa did not permit a clear molecular delimitation of either Neoplecostominae or Otothyrinae at the subfamilial level. Therefore, we treat all neoplecostomine and otothyrine species as part of a single, broadly circumscribed subfamily Hypoptopomatinae. Within this Hypoptopomatinae *sensu lato*, we identified six major clades whose interrelationships (Fig. 5) were more consistent with the results of previous molecular studies (Chiachio et al., 2008; Cramer et al., 2011; Roxo et al., 2014, 2017; Silva et al., 2016) than results based exclusively on morphological data (Martins et al., 2014; Pereira and Reis, 2017).

3.4.1. Hypoptopomatini and Otocinclus Clade

Our results identified *Hypoptopoma* + *Acestridium* as the first clade to diverge from all other Hypoptopomatinae (Fig. 5), followed by a clade composed of five species of *Otocinclus*. Previous molecular studies have found *Otocinclus* to be sister to *Hypoptopoma* (Chiachio et al., 2008) or the currently monotypic genus *Lampiella* (Roxo et al., 2014; Silva et al., 2016). Roxo et al. (2014) found strong support for a clade composed of *Acestridium*, *Hypoptopoma*, *Lampiella*, *Otocinclus* and *Oxyropsis*. The absence of *Lampiella* and *Oxyropsis* from the present analyses may account for the lack of support for a similar clade. Alternatively, Rodriguez et al. (2015) provided morphological evidence for a sister relationship between *Acestridium* and the monotypic genus *Niobichthys* (Schaefer and Provenzano, 1998), which has not been analyzed in any molecular phylogenetic study.

3.4.2. Corumbataia Clade

The third group to diverge in Hypoptopomatinae was the *Corumbataia* Clade comprising the genera *Corumbataia*, *Curculionichthys*, *Nannoplecostomus* and *Microplecostomus*. All nodes within this clade had strong statistical support (ML > 95%, BI = 1), and the interrelationships supported the synonymization of *Gymnotocinclus* (Carvalho et al., 2008a) with *Corumbataia* (Britski, 1997). Carvalho et al. (2008a) proposed *Gymnotocinclus* as a new genus based on four features thought to be uniquely derived within Hypoptopomatinae: extreme reduction of body dermal plates, absence of lateral connecting bone, absence of bifid hemal spines on abdominal vertebrae posterior to the first anal-fin proximal radial and dorsally or anteriorly curved odontode tips on posteriormost dermal plates on caudal peduncle. Based on molecular data, Roxo et al. (2017) described a second species of *Gymnotocinclus* (*G. canoeiro*), but noted that this species lacked all of the features previously used to diagnose the genus. Therefore, Roxo et al. (2017) proposed a new diagnosis for *Gymnotocinclus* based on two morphological characters that were shared: absence of dermal plates on the snout tip, and maxillary barbel adnate to lower lip. This study supported a clade composed of the two nominal species of *Gymnotocinclus* and three species of *Corumbataia* with *G. anosteos* (type species of *Gymnotocinclus*) sister to *C. cuestae* (type species of *Corumbataia*). Therefore, we consider *Gymnotocinclus* to be a junior synonym of *Corumbataia*, and transfer the species *G. anosteos* and *G. canoeiro* to *Corumbataia* (Table 2). The condition of having maxillary barbel adnate to lower lip serve to diagnose the genus *Corumbataia*.

Our study supported a sister-group relationship between *Corumbataia* and the recently described genus *Curculionichthys*, corroborating previous molecular works (Roxo et al., 2014, 2017; Silva et al., 2016). Our study also supported a sister-group relationship between two recently described monotypic genera, *Microplecostomus* and *Nannoplecostomus*. Based on a phylogenetic analysis of morphological data, Ribeiro et al. (2012) found *Nannoplecostomus* to be a distinct lineage within Loricariidae that was sister to Hypostominae (*sensu* Armbruster, 2008), despite *Nannoplecostomus* having characters traditionally diagnostic of both Hypoptopomatinae and the tribe Hypostomini. Our study firmly places *Nannoplecostomus* in Hypoptopomatinae as the sister to *Microplecostomus*. Alternatively, Pereira and Reis (2017) provided morphological evidence to support *Nannoplecostomus* and *Microplecostomus* as successive sister taxa to a clade composed of Hypoptopomatinae + Neoplecostominae.

3.4.3. Tribe Otothyrini

After *Corumbataia* Clade, the next lineage to diverge was the monophyletic tribe Otothyrini (ML > 95%, BI = 1) comprising *Pseudotothyris obtusa* (Miranda Ribeiro, 1911) and the monotypic genus *Schizolecis*. This relationship was not well supported by our concatenated ML (83%) and Astral II species tree (0.54) analyses, but was well supported by our concatenated BI analysis (BI = 1). In general, across all analyses, BI presented higher support for this relationship than ML. Furthermore, this relationship is at odds with previous molecular studies that found no support for a close relationship between *Pseudotothyris* and *Schizolecis* (Cramer et al., 2011; Roxo et al., 2014,

2017; Silva et al., 2016). Instead, our results partially corroborate morphological evidence for a sister-group relationship between *Schizolecis* and *Pseudotothyris* + *Otothyris* (Schaefer, 1998; Martins et al., 2014). Martins et al. (2014: Appendix 1, node 28) proposed 15 synapomorphies for a clade containing *Schizolecis*, *Pseudotothyris* and *Otothyris*. Therefore, the tribe Otothyrini may be restricted to the genera *Otothyris*, *Pseudotothyris* and *Schizolecis* based on the 15 synapomorphies proposed by Martins et al. (2014).

3.4.4. Tribe Neoplecostomini

Our study recognized within Hypoptopomatinae *sensu lato* a clade that has historically been recognized as a distinct subfamily Neoplecostominae (e.g., Pereira and Reis, 2017). Although we found strong support (ML > 95%, BI = 1) for monophyly of this clade, its recognition at the subfamily level would necessitate the erection of subfamilies for additional clades within Hypoptopomatinae *sensu lato*. Thus, we downgrade Neoplecostomini to the level of tribe.

Relationships within the Neoplecostomini were very similar to those of previous molecular studies (e.g., Cramer et al., 2011; Roxo et al., 2014, 2017; Silva et al., 2016). Congruencies included the non-monophyly of *Pareiorhina* and *Neoplecostomus*. The type species of *Pareiorhina* (*P. rudolphi*) was sister to *Pseudotocinclus tietensis* (its junior synonym, *P. intermedius* being the type species of *Pseudotocinclus*). Based on morphology, Martins et al. (2014) similarly found *P. tietensis* to be unrelated to other species of *Pseudotocinclus*. Likewise, a species of *Neoplecostomus* (*N. ribeirensis*) was more closely related to species of *Isbrueckerichthys*, *Kronichthys* and *Pareiorhaphis* than to other *Neoplecostomus* (i.e., *N. bandeirante* + *N. franciscoensis*). Although Pereira and Reis (2017) did not include *N. bandeirante* in their analysis, they provided strong morphological evidence for nesting *N. franciscoensis* + *N. ribeirensis* deep within a monophyletic *Neoplecostomus*.

Our results conflicted with the morphology-based results of Reis et al. (2012) and Pereira and Reis (2017) by finding the monotypic genus *Plesioptopoma* sister to '*Pareiorhina*' *carrancas* (ML and BI), forming a clade nested within Neoplecostomini. Reis et al. (2012) noted similarities between *Plesioptopoma* and the neoplecostomine genus *Kronichthys* (e.g., narrow elongate body, premaxillary and dentary tooth series strongly curved medially), yet Pereira and Reis (2017) excluded *Plesioptopoma* from subfamily Neoplecostominae because it lacks one exclusive synapomorphy: anteriormost pleural ribs connected to vertebral centra via ligament (*vs.* posterior ribs articulated directly). The Astral-II analysis also placed *Plesioptopoma* within Neoplecostomini; however, this genus was sister to a large clade containing *Neoplecostomus*, *Pareiorhaphis*, *Isbrueckerichthys*, *Pareiorhina* and *Kronichthys* species.

Our placement of the genus *Pareiorhaphis* also differed from hypotheses based on morphology (Armbruster, 2004a, 2008; Pereira and Reis, 2017). In our study, *Pareiorhaphis* + *Kronichthys* was sister to *Isbrueckerichthys* + *Neoplecostomus ribeirensis*. In contrast, Pereira and Reis (2017) found *Pareiorhaphis* to be sister to the monotypic genus *Hirtella*, and found *Kronichthys* to be sister to all other Neoplecostominae. Pereira and Reis (2017) also found another monotypic genus, *Euryochus*, as sister to all Neoplecostominae except *Kronichthys*. Phylogenetic placements of *Hirtella* and *Euryochus* within the Neoplecostomini have not been tested with molecular data. Our ML and BI analyses recovered the genus *Pareiorhaphis* as monophyletic; however, Astral-II found this genus to be paraphyletic, with *P. splendens* being sister to *Kronichthys subteres*.

3.4.5. Tribe Hisonotini Roxo & Silva

We newly erect the tribe Hisonotini (type genus *Hisonotus*) within subfamily Hypoptopomatinae to include three nominal genera (*Hisonotus*, *Microlepidogaster*, *Rhinolekos*) traditionally recognized in the subfamily Otothyrinae (e.g., Cramer et al., 2011; Roxo et al., 2014), plus three lineages treated herein as "New Genus 1, 2 and 3", each with high statistical support (ML > 95%, BI = 1). The tribe Hisonotini still

lacks a morphological definition and further phylogenetic analyses are necessary to corroborate our strong molecular-based hypothesis. Our "New Genus 1" contains the species '*Hisonotus*' *bocaiuva* (Roxo et al., 2013), '*Parotocinclus*' sp. n. 1 and '*Parotocinclus*' sp. n. 2. Previous molecular studies have grouped both of the *Parotocinclus*-like species with two additional species of *Parotocinclus* from the São Francisco (*P. prata* Ribeiro, Melo and Pereira, 2002, and *P. robustus* Lehmann and Reis, 2012), as well as *Microlepidogasterar arachas* Martins, Calegari and Langeani, 2013 and two other undescribed species (*Microlepidogaster* sp. 1 and 2). The "New Genus 2" contains the species '*Hisonotus*' *acuen* Silva, Roxo and Oliveira, 2014, '*H.*' *chromodontus* Britski and Garavello, 2007, '*Parotocinclus*' sp. n. 3 and '*P.*' *aripuanensis* Garavello, 1988. The "New Genus 3" comprises a single undescribed genus and species from the rio São Francisco basin in northeastern Brazil.

3.4.5.1. Microlepidogaster and Rhinolekos subclades.
Eigenmann and Eigenmann (1889) proposed *Microlepidogaster* as a monotypic genus for their new species *M. perforata*. Schaefer (1998) provided the first diagnosis of *Microlepidogaster* and maintained it as monophyletic: neural spine of 7th vertebra not contacting the nuchal plate, dorsal-fin position shifted posteriorly relative to 7th vertebra; first dorsal-fin proximal radial articulating with neural spine of 9th vertebra; and rostrum without enlarged odontodes, plates forming lateral rostral margins thin. Calegari and Reis (2010) described a second species of *Microlepidogaster*, *M. longicolla*, and re-diagnosed the genus accordingly: dorsal fin shifted posteriorly with the compound 1st pterygiophore articulating with neural spine of at least the 8th vertebral centrum (i.e., vertebrae 8 or 9 in *M. perforata* and 10 or 11 in *M. longicolla*). Our study did not support a close relationship between *Microlepidogaster perforata* and *M. longicolla*. Instead, *M. longicolla* was grouped with the type species of *Rhinolekos*, *R. britskii*. Although relationships among species of *Microlepidogaster* and *Rhinolekos* remain unclear (Martins et al., 2013, 2014), we transfer *Microlepidogaster longicolla* Calegari and Reis, 2010 and *Microlepidogaster arachas* Martins, Calegari & Langeani 2013 to *Rhinolekos* (Table 2). Our decision for the latter species is based on the morphological evidence provided by Martins et al. (2014).

3.4.5.2. Hisonotus subclade.
Within Hisonotini, the *Hisonotus* subclade is composed of six nominal species (including the type species *Hisonotus notatus* Eigenmann and Eigenmann, 1889), three species transferred from other genera, and one possibly undescribed species. The nominal species newly assigned here to *Hisonotus* are: *Eurycheilichthys luisae* Reis, 2017 and the type species for both *Epactionotus* (*Epactionotus bilineatus* Reis and Schaefer, 1998) and *Otothyropsis* (*Otothyropsis marapoama* Ribeiro, Carvalho and Melo, 2005) (Table 2). Our results corroborate previous molecular studies (Cramer et al., 2011; Roxo et al., 2014, 2017; Silva et al., 2016), which nested additional species of *Otothyropsis*, *Epactionotus* and *Eurycheilichthys* (including the type species *E. pantherinus* (Reis and Schaefer, 1992)) within *Hisonotus*. Therefore, based on the evidence from molecular data, we consider *Otothyropsis*, *Epactionotus* and *Eurycheilichthys* to all be junior synonyms of *Hisonotus*. Thus, *Hisonotus* now contains at least the following 25 species: *H. aky* (Azpelicueta et al., 2004), *H. armatus* Carvalho, Lehmann, Pereira and Reis, 2008b, *H. bilineatus* (ex *Epactionotus*), *H. carreiro* Carvalho and Reis, 2011, *H. charrua* Almiron, Azpelicueta, Casciotta and Litz, 2006, *H. depressicauda* (Miranda Ribeiro, 1918), *H. francirochai* (Ihering, 1928), *H. gracilis* (ex *Epactionotus*), *H. iota* Carvalho and Reis, 2009, *H. itaimbezinho* (Reis and Schaefer, 1998) (ex *Epactionotus*), *H. laevior* Cope, 1894, *H. leucofrenatus* (Miranda Ribeiro, 1908), *H. leucophrys* Carvalho and Reis, 2009, *H. limulus* (Reis and Schaefer, 1998) (ex *Eurycheilichthys*), *H. luisae* (ex *Eurycheilichthys*), *H. marapoama* (ex *Otothyropsis*), *H. megaloplax* Carvalho and Reis, 2009, *H. montanus* Carvalho and Reis, 2009, *H. nigricauda* (Boulenger, 1891), *H. notatus*, *H. notopagos* Carvalho & Reis, 2011, *H. paulinus* (Regan, 1908), *H. pantherinus* (ex *Eurycheilichthys*), *H. taimensis* (Buckup, 1981), *H. prata* Carvalho and Reis, 2011 and *H. ringueleti* Aquino, Schaefer and

Miquelarena, 2001. Four additional species of *Hisonotus* remain unexamined by molecular studies, but are likely also members of *Hisonotini*: *H. brunneus* Carvalho and Reis, 2011, *H. heterogaster* Carvalho and Reis, 2011, *H. hungy* Azpelicueta, Almirón, Casciotta and Koerber, 2007, and *H. vireo* Carvalho and Reis, 2011. Finally, we consider *Microlepidogaster depressinotus* Miranda Ribeiro, 1918, to be a junior synonym of *Hisonotus paulinus* (Regan, 1908) (Table 2) (H.A. Britski, personal communication).

The remaining species of the genus *Eurycheilichthys* (i.e., *E. apocremnus* Reis (2017), *E. castaneus* Reis (2017), *E. coryphaenus* Reis (2017), *E. pantherinus, E. paucidens* Reis (2017), *E. planus* Reis (2017), *E. vacariensis* Reis (2017), *Otothyropsis* (i.e., *O. alicula* Lippert, Calegari and Reis (2014), *O. biamnicus* Calegari et al. (2013), *O. dialeukos* Calegari et al. (2017), *O. piribebuy* Calegari et al. (2011), *O. polyodon* Calegari, Lehmann and Reis (2013) and *Microlepidogaster* (i.e., *M. arachas, M. dimorpha* Martins and Langeani (2011), *M. discontenta* Calegari, Silva and Reis (2014), *M. discus* Martins, Rosa and Langeani (2014) and *M. negomata* Martins, Cherobim, Andrade and Langeani (2017) still need to be analyzed in a phylogenetic context to better understand their placement in Hypoptopomatinae and relationships to members of the *Hisonotus* subclade as delimited herein.

Acknowledgments

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2019.02.017.

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