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Evolutionary history of Heptapteridae catfishes using ultraconserved elements (Teleostei, Siluriformes)

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Abstract

Heptapteridae is composed of 228 valid species allocated in 24 genera, making it the most diverse family within superfamily Pimelodoidea, a clade endemic to the Neotropical freshwaters. Heptapterids are widely distributed from southern Mexico to the Pampas of Argentina and occupy a variety of habitats generally in small- to medium-sized rivers. To evaluate the phylogenetic relationships of Heptapteridae, we used a matrix with 1,319 ultraconserved elements (UCEs) from the genome from 56 specimens spanning 42 species and 24 genera of Heptapteridae and 19 related siluriform taxa. Maximum likelihood, Bayesian and coalescent-based analyses strongly supported the monophyly of Heptapteridae and confirmed previous hypotheses of a sister relationship between Heptapteridae and *Conorhynchos conirostris*. We provide the evidence to recognize two subfamilies: (1) Rhamdiinae (*Goeldiella*, *Rhamdella*, *Rhamdia*, *Brachyrhamdia*, *Pimelodella*) and (2) Heptapterinae; with two tribes: Brachyglaniini new tribe (*Gladioglanis*, *Myoglanis*, *Brachyglanis* and *Leptorhamdia*) and Heptapterini (*Mastiglanis*, *Chasmocranus*, *Cetopsorhamdia*, *Pariolius*, *Phenacorhamdia*, *Nemuroglanis*, *Imparfinis*, *Taunayia*, *Rhamdioglanis*, *Acentronichthys*, *Rhamdiopsis* and *Heptapterus*). Inside Heptapterini, we recognize five subclades and provide putative morphological synapomorphies. This paper represents the first molecular hypothesis of intergeneric and interspecific relationships helping to better delineate heptapterid taxa.

KEYWORDS

catfishes, freshwater fishes, phylogenomics, Pimelodoidea, ultraconserved elements

1 | INTRODUCTION

Catfishes (Siluriformes) belong to the superorder Ostariophysi, a major group of predominantly freshwater teleosts that also includes Gonorynchiformes, Cypriniformes, Characiformes and Gymnotiformes (Arcila et al., 2017; Betancur et al., 2017; Nelson et al., 2016). Siluriformes is composed of 3,995 species classified into 502 genera and 39 families (Fricke et al., 2020). Based on estimates in Chapman (2009), approximately one in three freshwater

fishes and one in 16 vertebrates is a catfish. Siluriformes are distributed throughout freshwater and coastal marine habitats of the Americas, Africa, Madagascar, Eurasia, southeast Asia, Japan and Australia (Diogo, 2004), while the rich fossil record expands the geographic range to western North America, North Africa, Saudi Arabia and Antarctica (El-Sayed et al., 2017; Gayet & Meunier, 2003; Grande & Eastman, 1986; Lundberg, 1975).

Heptapteridae contains 228 valid species in 24 genera (Fricke et al., 2020) distributed from southern Mexico to the Pampas of central Argentina at the southernmost limit to the Neotropical region (Thomas & Sabaj, 2020). Heptapterids are commonly found in small- to medium-sized rivers (Bockmann & Guazzelli, 2003) where they occupy a variety of habitats such as rocky bottoms (*Cetopsorhamdia*, *Chasmocranus*, *Heptapterus*, *Imparfinis*, *Phenacorhamdia*, *Rhamdioglanis*), submerged vegetation (*Cetopsorhamdia*, *Rhamdiopsis*), and sandy beaches (*Imparfinis*, *Mastiglanis*) (Bockmann and Guazzelli, 2003; F.A. Bockmann, personal observation).

Heptapteridae includes many catfish taxa long classified together in the family Pimelodidae (Bockmann and Guazzelli, 2003). Lundberg and McDade (1986) provided the first phylogenetic evidence for a monophyletic subgroup within Pimelodidae equivalent to Heptapteridae composed of *Brachyglanis*, *Brachyrhamdia*, *Cetopsorhamdia*, *Goeldiella*, *Heptapterus*, *Imparfinis*, *Myoglanis*, *Nannorhamdia*, *Pariolius*, *Pimelodella*, *Rhamdella*, *Rhamdia* and *Typhlobagrus*. Ferraris (1988) termed this group the *Brachyrhamdia* clade and Lundberg et al. (1988) expanded it to include *Acentronichthys*, *Caecorhamdella*, *Caecorhamdia*, *Chasmocranus*, *Horiomyzon*, *Imparales*, *Leptorhamdia*, *Medemichthys*, *Nemuroglanis* and *Phenacorhamdia*. Lundberg et al. (1991) expanded this group yet again to include *Gladioglanis*, *Phreatobius* and *Rhamdiopsis* and formally named it as the subfamily Rhamdiinae Bleeker 1862 within Pimelodidae. Silfvergrip (1996) correctly pointed out that Heptapterinae Gill 1861 has priority over Rhamdiinae for naming this group. Bockmann and Guazzelli (2003) firmly established the family-level status of Heptapteridae and assembled a comprehensive checklist of nominal valid and synonymous species and genera.

Phylogenetic-based studies have largely focussed on relationships between heptapterid taxa and other members of the superfamily Pimelodoidea (de Pinna, 1998; Hardman, 2005; Lundberg et al., 2000; Lundberg & McDade, 1986; Sullivan et al., 2006, 2013). Molecular studies support the monophyly of Heptapteridae (minus *Phreatobius*) as well as revealed its close relationship with *Conorhynchos conirostris* (Sullivan et al., 2006, 2013). Molecular evidence places *Phreatobius* within Pimelodoidae, but more closely related to Pimelodidae and Pseudopimelodidae than to Heptapteridae and *Conorhynchos* (Sullivan et al., 2013). Bockmann (1998), in an unpublished thesis, performed a morphological phylogenetic analysis of Heptapteridae, including 72 family terminals (then including *Phreatobius*) and 278 characters. Bockmann and Miquelarena (2008) presented a phylogeny of Heptapteridae focussing on its large internal clades, corroborating Bockmann's (1998) hypothesis that *Goeldiella* is the earliest divergent genus of the family. The monophyly of several genera of Heptapteridae has been rejected (Bockmann, 1998), implying that numerous new ones should be described to reflect relationships between their species (Bockmann, 1998; Bockmann & Slobodian, 2017). Although bearing a high overall resolution, the Heptapteridae phylogeny built by Bockmann (1998) still has some uncertainties, such as the affinities between the three higher clades of the *Nemuroglanis* subclade and the internal relationships of some of its genera. Sullivan et al. (2006), in their Siluriformes phylogeny based on *rag1* and *rag2* nuclear gene sequences, found a monophyletic Heptapteridae, although represented by six terminals only (representing *Goeldiella*, *Imparfinis*, *Pimelodella*, *Rhamdia* and possibly a new genus), this family being the sister group of the genus *Conorhynchos*. Employing the same nuclear genes plus the *12S* and *16S* rRNA genes from the mitochondrial genome, Sullivan et al. (2013) generated a hypothesis of phylogenetic relationships for the superfamily Pimelodoidea (Heptapteridae, Pimelodidae and Pseudopimelodidae), which provided strong support for the monophyly of Heptapteridae, represented by nine terminals, each corresponding to a genus of the family. This latter molecular phylogeny, although bearing a very limited family sample, is notably congruent with the topology obtained by Bockmann (1998), mainly with respect to the following aspects: the close relationship between *Gladioglanis* and *Myoglanis*, the monophyly of the *Nemuroglanis* subclade, having *Chasmocranus* and *Cetopsorhamdia* as early-divergent genera and *Acentronichthys* and *Heptapterus sympterygium* belonging to a more apical clade of this group; and the non-monophyly of *Imparfinis*. However, there are some incongruities that need to be clarified: *Goeldiella* as the sister group of the other heptapterids in the morphological analysis whereas this genus is the sister group of the clade *Gladioglanis* + *Myoglanis* in the molecular analysis; and *Cetopsorhamdia* as the most basal genus within the *Nemuroglanis* subclade in morphological phylogeny while this genus constitutes an unresolved node together with *Chasmocranus* and the group formed by the remaining members of that subclade in molecular phylogeny. Briñoccoli et al. (2018) performed a phylogenetic reconstruction of Heptapteridae based on the mitochondrial *COI* gene. This analysis, despite having greater representativeness of the family (29 terminals representing at least 10 valid and two new genera), was based on a reduced number

of base pairs (bp) and most of the sequences were obtained from the GenBank, of heptapterids whose identification has not been confirmed. In order to elucidate such divergences between the different phylogenetic hypotheses, we use target capture of thousands of ultraconserved elements (UCEs) to perform a phylogenetic analysis on the densest set of heptapterid taxa assembled for a molecular analysis to date.

2 | MATERIAL AND METHODS

2.1 | Taxon sampling

Ingroup sampling comprised 56 terminal taxa spanning 42 species (24 described and 18 undescribed) and 24 genera (20 described and four undescribed). This represents 10.5% of all valid species and 83% of all valid genera. Related taxa included *Conorhynchos conirostris* (1) and 18 species of the siluriform families Ariidae (1), Aspredinidae (1), Callichthyidae (1), Doradidae (2), Ictaluridae (1), Loricariidae (1), Pimelodidae (5) and Pseudopimelodidae (5). Trees were rooted in *Charax metae* (Characiformes). Voucher specimens for tissue samples were fixed in 10% formalin and transferred to 70% ethanol for permanent storage (see Table S1 for catalogue and locality data). Institutional acronyms follow Sabaj (2020).

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. We used a newly developed probeset for Ostariophysi to capture sequence data of about 2,700 UCEs (Faircloth et al., 2020). Library preparation, sequencing, and data pipeline were performed by Arbor Biosciences staff (Ann Arbor, MI, USA) using the following protocol: DNA libraries were prepared for the 75 specimens (56 ingroup and 19 outgroup) 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 (Faircloth et al., 2013). The Nextera library preparation protocol of in vitro transposition was used followed by PCR to prune the DNA and attach sequencing adapters, and the Epicentre Nextera kit was used to prepare transposase-mediated libraries with insert sizes averaging 100 bp (95% CI: 45 bp) following Adey et al. (2010).

To prepare the libraries, whole genomic DNA (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. Illumina sequencing libraries were prepared 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). After purification with SPRI beads, libraries were quantified with the Quant-iT (TM) Picogreen(R) dsDNA Assay kit (ThermoFisher). Pools were enriched comprising 100 ng each of eight libraries (800 ng total) using the MYbaits(R) Target Enrichment system (MYcroarray) following manual version 3.0. After capture cleanup, the bead-bound library was resuspended in the recommended solution and amplified for 10 cycles using a universal P5/P7 primer pair and KAPA HiFi reagents. After purification, each captured library pool was quantified with PicoGreen, and combined with all other pools in projected equimolar ratios prior to sequencing. Sequencing was performed across two Illumina HiSeq paired-end 100 bp lanes using v4 chemistry.

2.3 | Raw data analysis

After sequencing, adapter contamination, low-quality bases and sequences containing ambiguous base calls were trimmed using the Illumiprocessor software pipeline developed by Faircloth et al. (2013; https://github.com/faircloth- lab/illumiprocessor). After trimming, we assembled Illumina reads into contigs on a species-by-species basis using ABySS pipeline (Simpson et al., 2009; https://github.com/bcgsc/abyss). We then used a custom python program (match_contigs_to_probes.py) implemented in PHYLUCE (Faircloth, 2016) integrating LASTZ (Harris, 2007) to align species-specific contigs to the 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 included 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 (Edgar, 2004) and to perform edge trimmings. We also performed phylogenetic analyses with varying amounts of data (70%, 80% 90% of UCEs present in the complete alignment matrices) to explore the potentially strong effect of missing data on tree reconstruction (Hosner et al., 2016; Streicher et al., 2016). All matrices are available at Figshare (https://doi.org/10.6084/m9.figshare.12753257). Information about data in each matrix is summarized in Table 1; species read information is presented in Table S2. All sequences are available

TABLE 1 Parameters of matrices analysed in the present study (https://doi.org/10.6084/m9.figshare.12753257)

	Matrices	Trimming	UCE loci	Total bp	Analysis	Trees
1	70% with data-partitioning schemes[a]	Edge	1,319	728,019	RAxML	Figure S1
2	80% with data-partitioning schemes	Edge	1,107	639,813	RAxML	Figure S2
3	90% with data-partitioning schemes	Edge	723	432,292	RAxML	Figure S3
4	70% with data-partitioning schemes	Edge	1,319	728,019	ExaBayes	Figure S4
5	80% with data-partitioning schemes	Edge	1,107	639,813	ExaBayes	Figure S5
6	90% with data-partitioning schemes	Edge	723	432,292	ExaBayes	Figure S6
7	70% with data-partitioning schemes	Edge	1,319	728,019	ASTRAL	Figure S7
8	80% with data-partitioning schemes	Edge	1,107	639,813	ASTRAL	Figure S8
9	90% with data-partitioning schemes	Edge	723	432,292	ASTRAL	Figure S9

[a]The matrix used in the manuscript.

at NCBI Sequence Read Archive (SRA) submissions: SAMN18821754-SAMN18821828. Details on UCE sequence analyses are available online via PHYLUCE documentation (Faircloth, 2016).

2.4 | Phylogenetic analyses

Phylogenetic analyses were performed during approximately two months in three independent clusters: the 2 × 20 CPU, 128 GB *Brycon* and 2 × 10 CPU, 256 GB *Zungaro* servers at LBP/UNESP, and the 256 × 3,104 CPU, 4,096 GB servers at NCC/GridUNESP. We analysed the concatenated datasets using maximum likelihood (ML; RAxML v8; Stamatakis, 2014), Bayesian (BI; ExaBayes v1.4; Aberer et al., 2014) and coalescent-based analyses (ASTRAL-II; Mirarab & Warnow, 2015). We used a data-partitioning scheme of each UCE using the program PFinderUCE-SWSC-EN (Tagliacollo & Lanfear, 2018) with models chosen by PartitionFinder v2 (Lanfear et al., 2012). The RAxML analysis was performed on partitioned 70%, 80% and 90% complete matrices (see Table 1 for all matrix schemes). Five alternative runs on distinct parsimony starting trees were performed to find the best ML tree in RAxML v8. Pseudoreplicates of the ML analysis were obtained using the autoMRE function for the extended majority-rule consensus tree criterion available in RAxML v8 to assess bootstrap support for individual nodes. This option allows the bootstrap convergence test to be conducted, which determines if bootstrap replicates are getting stable support values (Pattengale et al., 2010).

BI of the concatenated alignment was performed using ExaBayes (Aberer et al., 2014) in two independent runs with two chains each, one cold and one hot chain, of 1,000,000 generations using the partition scheme for 70%, 80% and 90% complete matrices (Table 1). Tree space was sampled every 100 generations to yield 10,001 trees. Parameter estimates and ESS values were visualized in Tracer v1.6 (Rambaut et al., 2014) and the last 7,500 trees were sampled after checking results for convergence. This allowed us to visualize the log of posterior probability within and between independent runs and to ensure that the average standard deviation of split frequencies was <1%, the 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).

To account for coalescent stochasticity among individual UCEs and to address the problem of highly supported but incorrect trees in concatenated analyses (Mirarab et al., 2014), we estimated a species tree from individual gene trees using a two-step process. First, we used phyluce to resample the 70%, 80% and 90% complete matrices by loci and generated a best tree using RAxML for each of those matrices. Then, we used ASTRAL-II (Mirarab & Warnow, 2015) to infer species trees from each of the best tree subsets of loci and generated a majority-rule consensus

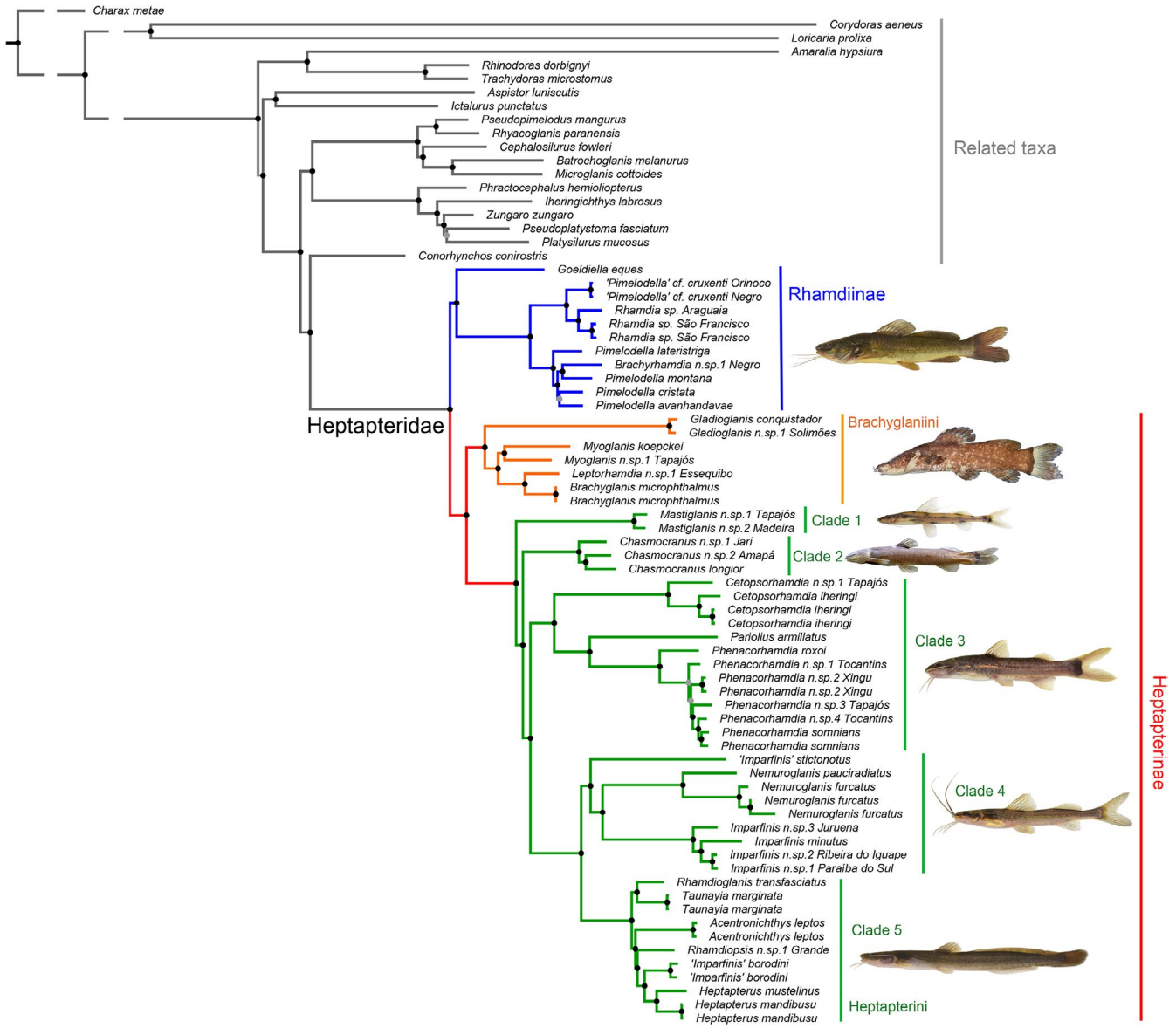

FIGURE 1 Maximum likelihood tree of Heptapteridae based on the 70% complete matrix including 1,319 loci of ultraconserved elements (728,019 bp). Black nodes indicate 100% bootstrap values from 1,000 bootstrap pseudoreplicates; grey nodes indicate <85% bootstrap values. Tree topology includes 56 specimens of Heptapteridae representing 42 species (24 described and 18 undescribed) and 24 genera (20 described and four undescribed). From top to bottom, figured specimens represent the genera: *Rhamdia*, *Brachyglanis*, *Mastiglanis*, *Chasmocranus*, *Cetopsorhamdia*, *Imparfinis* and *Heptapterus*

tree of the results (minimum clade frequency = 0.7). Although ASTRAL-II is not strictly a coalescent method, it is statistically consistent with the multispecies coalescent model (Nute et al., 2018) and scales well with larger numbers of loci.

3 | RESULTS AND DISCUSSION

3.1 | Major clades of Heptapteridae

The final data set included 75 terminals, with the 70% complementary matrix containing 1,319 loci (728,019 bp), the 80% complete matrix containing 1,107 loci (639,813 bp) and the 90% complete matrix containing 723 loci (432,292 bp) (Supporting Information). Partition-UCE yielded 857 partitions for the 70% matrix, 759 partitions for the 80% matrix, and 561 partitions for the 90% matrix. Phylogenetic resolution inferred from the concatenated data set has strongly supported clades regardless of matrix completeness (70%, 80%, or 90%) or method of analysis (ML, BI, or ASTRAL-II) (Figures S1–S9). Disagreements mainly involve the ASTRAL-II analysis wherein the 90% complementary matrix showed the highest number of differences (7 nodes) compared to the main topology chosen for discussion (70% concatenated matrix with data partitioning of UCEs and ML

analysis). Overall, the ASTRAL-II presents the highest number of differences compared to the ML and the BI (Table S4). Details of the differences among each analysis can be observed in Figures S1–S9.

ML, BI, and ASTRAL-II analyses strongly support the monophyly of Heptapteridae (Figure 1), corroborating previous molecular (Arcila et al., 2017; Briñoccoli et al., 2018; Hardman, 2005; Sullivan et al., 2006, 2013) and morphological studies (Bockmann, 1994, 1998; Bockmann & Miquelarena, 2008; Lundberg et al., 1991). Our results also place Heptapteridae as sister group to *Conorhynchos* and this clade sister to Pimelodidae + Pseudopimelodidae, in accordance with other recent molecular hypotheses based on multilocus data (Sullivan et al., 2006, 2013).

Our phylogeny reveals two major clades within Heptapteridae ranked here as subfamilies: Rhamdiinae and Heptapterinae (Figure 1 and Figures S1–S9). The molecular phylogeny herein obtained is rather congruent with the morphological ones by Bockmann (1998) and Bockmann and Miquelarena (2008), differing mainly with regard to the genera that diverged earlier (*Goeldiella*, *Brachyrhamdia*, *Pimelodella*, and *Rhamdia*; *Rhamdella* has not been studied herein), which are successively closer to the clades formed by the remaining heptapterids. In this study, they were recovered as a monophyletic group.

3.2 | Relationships within the subfamily Rhamdiinae

Rhamdiinae Bleeker, 1862

Type genus: *Rhamdia* Bleeker, 1858

Included genera: *Brachyrhamdia* Myers 1927, *Goeldiella* Eigenmann and Norris 1900, *Pimelodella* Eigenmann and Eigenmann 1888 (senior synonym of *Caecorhamdella* Borodin 1927, *Typhlobagrus* Miranda Ribeiro 1907), *Rhamdia* Bleeker 1858 (senior synonym of *Caecorhamdia* Norman 1926, *Pimelenotus* Gill 1858, *Pteronotus* Swainson 1839), and *Rhamdella* Eigenmann and Eigenmann 1888.

Rhamdiinae has two putative morphological synapomorphies: (1) tip of the parapophysis of vertebra 4 distally branched (modified from Bockmann, 1998, character 141, state 1) and (2) posterior cartilage of basipterygium extended posteriorly as a long projection (modified from Bockmann, 1998, character 190, state 0).

We restrict the subfamily Rhamdiinae to the genera *Brachyrhamdia*, *Goeldiella*, *Pimelodella* and *Rhamdia* (Figure 1). Such an arrangement has no parallel in morphological analysis (cf. Bockmann, 1998; Bockmann & Miquelarena, 2008; Slobodian, 2017), but equivalent clades including these genera have been recovered by Hardman (2005), Lundberg et al. (2007), and Sullivan et al. (2006, 2013) and also comprising *Rhamdella* by Briñoccoli et al. (2018).

The monotypic *Goeldiella* is the earliest genus to split in Rhamdiinae, followed by a clade that diverges into two sister clades, one composed of "*Pimelodella*" cf. *cruxenti* and *Rhamdia* and one composed of *Brachyrhamdia* and *Pimelodella*. Morphological studies alternatively support *Goeldiella* as sister to the clade containing all other Heptapteridae (Bockmann, 1998; Bockmann & Miquelarena, 2008). Bockmann and Miquelarena (2008) interpreted the rectangular shape of hypobranchial 1 and presence of anterolateral projection of hypobranchial 3 as synapomorphies for a clade composed of all heptapterids except *Goeldiella*. Based on our topology, those characters either become synapomorphies for Heptapteridae that are reversed in *Goeldiella* or are interpreted as independent acquisition in the Rhamdiinae exclusive of *Goeldiella* and in Heptapterinae. However, the branch subtending the node joining *Goeldiella* to the other rhamdiins is extremely short and its collapse would result in a polytomy at the base of Heptapteridae composed of *Goeldiella*, Rhamdiinae and Heptapterinae.

Pimelodella is paraphyletic in our analysis as "*Pimelodella*" cf. *cruxenti* is sister to *Rhamdia* and *Brachyrhamdia* n. sp. in nested inside the group formed by the remaining species of *Pimelodella* (*P. cristata*, *P. lateristriga* and *P. avanhandavae*). Given the topology herein recovered, a new genus should be erected for "*P.*" cf. *cruxenti*. Several authors have questioned the validity of *Brachyrhamdia* due to its morphological similarity with *Pimelodella* (Bockmann, 1998; Innes & Myers, 1950; Lundberg & McDade, 1986; Sands, 1985; Schultz, 1944), and because it is phylogenetically nested within *Pimelodella* (Bockmann & Miquelarena, 2008; Slobodian, 2013; Slobodian & Bockmann, 2013). Our molecular analysis is consistent with that view; however, we refrain from any taxonomic changes because our phylogeny does not include the type species of *Brachyrhamdia* (*B. imitator*) and the great diversity of the genus *Pimelodella* (cf. Slobodian, 2017) is herein underrepresented. We also did not analyse *Rhamdella*, but we rely on the molecular reconstruction by Briñoccoli et al. (2018), which included this genus, and on morphological evidence herein provided for placing it in this subfamily.

3.3 | Relationships within the subfamily Heptapterinae Gill 1861

Included genera: *Acentronichthys* Eigenmann and Eigenmann 1889, *Brachyglanis* Eigenmann 1912, *Chasmocranus* Eigenmann 1912, *Cetopsorhamdia* Eigenmann and Fisher 1916, *Gladioglanis* Ferraris and Mago-Leccia 1989, *Heptapterus* Bleeker 1858, *Imparfinis* Eigenmann and Norris 1900 (senior synonym of *Nannorhamdia* Regan 1913), *Leptorhamdia* Eigenmann 1918, *Mastiglanis*

Bockmann 1994, *Myoglanis* Eigenmann 1912, *Nemuroglanis* Eigenmann and Eigenmann 1889 (senior synonym of *Imparales* Schultz 1944 and *Medemichthys* Dahl 1961), *Pariolius* Cope 1872, *Phenacorhamdia* Dahl 1961, *Rhamdioglanis* Ihering 1907, *Rhamdiopsis* Haseman 1911, *Taunayia* Miranda Ribeiro 1918, and likely *Horiomyzon* Stewart 1986 and *Nannoglanis* Boulenger 1887.

Heptapterinae possesses 12 putative morphological synapomorphies: (1) skull roof mostly smooth, poorly ornamented (Bockmann, 1998, character 1, state 1); (2) supraoccipital process very short, not extending far beyond the posterior region of the neurocranium, and narrow (modified from Bockmann, 1998, character 45, state 2); (3) proximal extremity of ceratobranchials 1–2 nearly as large as their medial regions (Bockmann, 1998, character 106, state 1); (4) proximal cartilaginous head of ceratobranchial 4 laterally straight (Bockmann, 1998, character 108, reversion to state 0); (5) distal cartilage of the ceratobranchial 5 short, as long as the distal cartilages of ceratobranchials 1–4 (Bockmann, 1998, character 110, state 1); (6) uncinate process of epibranchial 3 with a broad base (Bockmann, 1998, character 113, state 1); (7) arborescent portion of the posterior ramus of the transverse process of vertebra 4 separated in two branches (Bockmann, 1998, character 138, state 1); (8) neural and haemal spines of posterior vertebrae sloped 35° or less in relation to the vertebral column (Bockmann, 1998, character 149, state 1); (9) 3 or 2 sutural dentations on coracoidean portion of the complex bone of pectoral girdle (Bockmann, 1998, character 161, state 1); (10) distal cartilage of the external anterior process of basipterygium expanded (de Pinna, 1993, character 211, state 1; Bockmann, 1998, character 161, state 1); (11) mesial cartilages of basipterygia fused along midline (de Pinna, 1993, character 209, state 1; Bockmann, 1998, character 188, state 1); and (12) orbital rim around the eye absent or much reduced (Lundberg et al., 1991; Bockmann, 1998, character 276, state 1; Bockmann & Miquelarena, 2008).

Our phylogenetic analysis (Figure 1 and Figures S1–S9) supports the recognition of a large subfamily Heptapterinae divided here into two tribes: Brachyglaniini and Heptapterini.

3.3.1 | Relationships within Brachyglaniini, new tribe

Brachyglaniini Silva & Bockmann

Type genus: *Brachyglanis* Eigenmann, 1912

Included genera: *Brachyglanis* Eigenmann 1912, *Gladioglanis* Ferraris and Mago-Leccia 1989, *Leptorhamdia* Eigenmann 1918, and *Myoglanis* Eigenmann 1912.

Brachyglaniini shares at least 10 synapomorphies that support its monophyly, namely: (1) posterior portion of lateral ethmoid half the length of the anterior portion (Bockmann, 1998, character 25, state 1); (2) dorsal margin of quadrate straight (Bockmann, 1998, character 79, reversion to state 0); (3) second dorsal-fin ray flattened and short, much shorter than the third, first branched, ray (Bockmann, 1998, character 153, state 1); (4) external margin of the pectoral spine with very conspicuous dentations (Bockmann, 1998, character 179, state 1); (5) dentations on the external margin of the pectoral spine forwardly oriented (Bockmann, 1998, character 180, state 1); (6) posterior process of the schiatic cartilage near the basipterygium midline (Bockmann, 1998, character 189, state 1); (7) foramen on frontal for exit of the epiphyseal branch of the supraorbital laterosensory canal very large (Bockmann, 1998, character 237, state 1); (8) exit of the epiphyseal branch of the supraorbital laterosensory canal dorsally oriented (Bockmann, 1998, character 238, state 1); (9) left and right epiphyseal branches of the supraorbital laterosensory canals not fused together, each opening into its own pore on the skin surface (Bockmann, 1998, character 239, state 1); and (10) parietal branch of the supraorbital laterosensory canal absent (Bockmann, 1998, character 241, state 1).

Our analysis supports the monophyly of a major heptapterid lineage composed of the genera *Brachyglanis*, *Gladioglanis,* *Leptorhamdia* and *Myoglanis*, with *Gladioglanis* as the earliest group to diverge. Based on morphology, Bockmann (1998) proposed a similar clade composed of the same genera plus *Phreatobius cisternarum*. Within this group, a subclade composed of *Brachyglanis*, *Myoglanis* and *Leptorhamdia* is supported by several morphological synapomorphies including the invasion of the *adductor mandibule* muscle onto the skull roof (Bockmann, 1998; Lundberg et al., 1991). Although our analysis did not include *Phreatobius*, Sullivan et al. (2006, 2013) effectively removed this genus from Heptapteridae on the basis of molecular evidence, placing it in its own family Phreatobiidae. Thus, we propose here that the invasion of the *adductor mandibule* muscle onto the skull roof is a characteristic of Brachyglaniini being a homoplasy in Phreatobiidae.

3.3.2 | Relationships within the tribe Heptapterini

Heptapterini Gill, 1861

Type genus: *Heptapterus* Bleeker, 1858

Included genera: *Acentronichthys* Eigenmann and Eigenmann 1889, *Cetopsorhamdia* Eigenmann and Fisher 1916, *Chasmocranus* Eigenmann 1912, *Heptapterus* Bleeker 1858, *Imparfinis* Eigenmann and Norris 1900 (senior synonym of *Nannorhamdia* Regan 1913), *Mastiglanis* Bockmann 1994, *Nemuroglanis* Eigenmann and Eigenmann 1889 (senior synonym of *Imparales* Schultz 1944 and *Medemichthys* Dahl 1961), *Pariolius* Cope 1872, *Phenacorhamdia* Dahl 1961, *Rhamdioglanis* Ihering 1907, *Rhamdiopsis* Haseman 1911, and *Taunayia* Miranda Ribeiro

1918. *Horiomyzon* Stewart 1986 and *Nannoglanis* Boulenger 1887 are tentatively placed in this group.

Heptapterini has 12 synapomorphies: (1) nasal long (Bockmann, 1994, 1998, character 22, state 1); (2) anterior and posterior ceratohyals connected via a synchondral joint only, lacking a medial dentate suture (Bockmann, 1998, character 94, state 1); (3) pharyngobranchial 3 with a bony lamina on mesial margin (Bockmann, 1998, character 117, state 1); (4) neural spine of vertebra 4 approximately straight, not covering the neural spine of vertebra 5 (Bockmann, 1994, 1998, character 133, state 1); (5) arborescent portion of the posterior branch of the transverse process of vertebra 4 with a deep notch, clearly separating two main arms (Bockmann, 1994, 1998, character 138, state 3); (6) posterior branch of the transverse process of vertebra 4 with posterior laminar projection with triangular shape, which extends to the distal end of the transverse process of vertebra 5 (Ferraris, 1988; Bockmann, 1998, character 140, state 1); (7) ascending process of the scaphium absent (Bockmann, 1998, character 142, state 1); (8) distal part of the posterior portion of transforming process of the tripus abruptly forward directed (Bockmann, 1998, character 143, state 1); (9) first dorsal-fin ray (spinelet) missing (Ferraris, 1988; Bockmann, 1998, character 151, state 1); (10) postcleithral process very short or absent (Bockmann, 1998, character 158, state 1); (11) posteroventral process of coracoid keel absent (Bockmann, 1994, 1998, character 163, state 1); and (12) first ray of the pectoral fin weakly ossified, with very evident segmentation, rigid at most to its basal half (Stewart, 1986; Bockmann, 1998, character 176, state 2).

Our analysis supported the recognition of a large tribe, Heptapterini, divided here into five clades. Our Heptapterini is equivalent to the *Nemuroglanis* subclade proposed by Ferraris (1988) and subsequently expanded (Bockmann, 1994, 1998; Bockmann & Castro, 2010; Bockmann & Miquelarena, 2008) to include: *Acentronichthys*, *Cetopsorhamdia*, *Chasmocranus*, *Heptapterus*, *Horiomyzon*, *Imparfinis*, *Mastiglanis*, *Nannoglanis*, *Nannorhamdia*, *Nemuroglanis* (including synonyms *Imparales* and *Medemichthys*), *Pariolius*, *Phenacorhamdia*, *Phreatobius*, *Rhamdioglanis*, *Rhamdiopsis* and *Taunayia*. Our analysis included all genera currently assigned to the *Nemuroglanis* subclade except *Horiomyzon* and *Nannoglanis*. However, as these genera are nested within the *Nemuroglanis* subclade according to Bockmann's (1998) morphological analysis, their inclusion can be assumed.

Clade 1

Clade 1 is sister to all remaining members of Heptapterini and contains one genus (*Mastiglanis*) with three nominal species, *M. asopos* (type species), *M. durantoni* and *M. yaguas*, plus at least five undescribed species (Almeida, 2019; Bockmann, 1994; Faustino-Fuster & Ortega, 2020; de Pinna & Keith, 2019). According to Bockmann (1994), there is morphological evidence to suggest an early-divergent position for *Mastiglanis* within the so-called *Nemuroglanis* subclade. In all members of the subclade except *Mastiglanis* and *Nemuroglanis*, the triangular posterior lamina of the complex centrum transverse process has at its distal angle an additional notch (vs. fully straight in *Mastiglanis* and *Nemuroglanis*). Furthermore, the medial notch separating the two symmetrical arms of the posterior limb of vertebra 4 is shallow in *Mastiglanis* versus deeply forked in all members of the *Nemuroglanis* subclade including *Nemuroglanis* (Bockmann, 1994; Bockmann & Ferraris, 2005). Bockmann and Ferraris (2005), however, rejected the basal position of *Mastiglanis* in favour of one grouping the genus together with *Nemuroglanis*, *Imparfinis* and *Horiomyzon* as proposed by Bockmann (1998). Although our molecular analysis did not include *Horiomyzon*, we found no support for grouping *Mastiglanis* with *Nemuroglanis* and *Imparfinis*.

Clade 2

After the Clade 1, the next lineage to diverge is the Clade 2 that comprises *Chasmocranus longior* (type species) and a putative undescribed species of *Chasmocranus* from the Rio Jari of the Amazonas basin. Bockmann (1998) proposed *Chasmocranus* as sister to a clade formed by *Pariolius*, "*Imparfinis*" *microps,* and *Phenacorhamdia* based on a synapomorphy related to the gas bladder (character 139: state 2). Our phylogenetic analysis resolved *Chasmocranus* as sister to the remaining clades of Heptapterini, indicating the independent acquisition or loss of this character.

Clade 3

The Clade 3 includes three genera, namely: *Cetopsorhamdia* sister to *Pariolius* + *Phenacorhamdia*. Conversely, DoNascimento and Milani (2008) proposed a sister relationship between *Phenacorhamdia* and *Chasmocranus* based on distinctive bifid hemal spines of the vertebrae immediately above insertion of the anal-fin pterygiophores. Our molecular analysis, however, placed *Phenacorhamdia* sister to *Pariolius,* suggesting that this condition is homoplastic. Bockmann (1998) also recognized a phylogenetic proximity between *Pariolius* and *Phenacorhamdia* in a clade that also included "*Imparfinis*" *microps* and an undescribed species (neither included in the present study). Within *Cetopsorhamdia*, our phylogeny clearly separates *C. iheringi* from an undescribed species from the Rio Tapajós. Within *Phenacorhamdia*, *Phenacorhamdia roxoi* from Rio Paranapanema basin is sister to a clade composed of *P. somnians* and up to four new species from Tapajós, Tocantins and Xingu rivers of the Amazon basin.

Clade 4

Clade 4 is composed of three lineages: "*Imparfinis*" *stictonotus* sister to a clade containing *Nemuroglanis* and species of *Imparfinis*. Bockmann (1998) and Bockmann and Ferraris (2005) proposed a monophyletic group within the *Nemuroglanis* subclade composed of *Horiomyzon*, *Imparfinis*, *Mastiglanis* and *Nemuroglanis*, based on one synapomorphy: borders of contact between the frontals, sphenotics, pterotic and supraoccipital mostly continuous and smooth. This clade was not recovered in our analysis. Our results, instead, place *Mastiglanis* at the base of Heptapterinae, which suggests that the character above is likely plesiomorphic and reversed in Clade 4.

Our results also corroborate the polyphyly of *Imparfinis* as hypothesized by Bockmann (1998). "*Imparfinis*" *stictonotus* and "*Imparfinis*" *borodini* are not closely related to typical species of *Imparfinis*, which probably include *I. piperatus*, the type species of the genus. "*Imparfinis*" *stictonotus* is an independent lineage sister to *Nemuroglanis* plus true *Imparfinis*, while "*Imparfinis*" *borodini* is sister to the clade *Heptapterus* + "*H*". *mandimbusu*, in the Clade 5. The need for a new generic name to accommodate "*Imparfinis*" *stictonotus* was suggested by Bockmann (1998), which was included in "Heptapteridae genus C" by Bockmann and Slobodian (2017).

Clade 5

The Clade 5 includes *Acentronichthys*, "*Imparfinis*" *borodini* (belonging to an undescribed genus according to Bockmann, 1998 and Bockmann & Slobodian, 2017), *Heptapterus*, *Rhamdioglanis*, *Rhamdiopsis* and *Taunayia*, (Figure 1). The first lineage to diverge in Clade 5 is composed of *Rhamdioglanis transfasciatus* and *Taunayia marginata*, and a major group formed by *Acentronichthys leptos*, which is the sister group to a clade containing an undescribed species of *Rhamdiopsis* from the Grande river and "*Imparfinis*" *borodini* + (*Heptapterus* + "*H*." *mandimbusu*). Bockmann (1998) found one synapomorphy (charater 186: state 1) related to the length of anteromedial arm of basipterygium that is shared by members of our Clade 5. The most derived clade in our phylogeny groups *Heptapterus mustelinus*, "*Heptapterus*" *mandimbusu* and "*Imparfinis*" *borodini*. Bockmann (1998) found the same monophyletic group ("Clade 94") supported by the presence of a hypertrophied *levator operculi*, inserting right below the dorsal margin of the opercle, invading its lateral surface (Arratia, 1992). Furthermore, *H. mustelinus* and "*H*." *mandimbusu* (which belongs to a new genus sensu Bockmann, 1998) were found to be sister groups, while they were left unresolved in a polytomy together with "*Imparfinis*" *borodini* in Bockmann (1998). The latter species was treated in a new genus by Bockmann (1998), which was included in "Heptapteridae genus D" by Bockmann and Slobodian (2017).

4 | CONCLUSIONS

This paper represents the first molecular hypothesis of intergeneric and interspecific relationships within Heptapteridae, and the first attempt to identify monophyletic groups to help classify the heptapterid species that are well known but remain formally undescribed. Although our phylogeny represents only about 10.5% of the species richness of the family, we analysed 20 of 24 (83%) of all nominally valid heptapterid genera and employed a genome-based method to generate phylogenetic reconstructions. As such, our results provide a sound framework for stabilizing heptapterid taxonomy. Future projects involve the inclusion of unsampled genera and species, and further explore the evolutionary history of the family with macroevolution and biogeographic approaches.

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SUPPORTING INFORMATION

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

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