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Phylogenomics of the bumblebee catfishes (Siluriformes: Pseudopimelodidae) using ultraconserved elements

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Abstract

Neotropical catfishes of the family Pseudopimelodidae comprise 53 species allocated to seven genera widely distributed in South America from northwestern Colombia and Venezuela to Argentina and Uruguay. Intergeneric relationships based on morphology-based phylogenies are conflicting, and the interspecific relationships remain incipient. We conducted the first molecular phylogeny of the family by analyzing sequence data from ultraconserved elements (UCEs) of the genome for 33 specimens of Pseudopimelodidae and 19 related taxa. Phylogenetic relationships were accessed by concatenated matrices using Bayesian inference and, maximum likelihood, and the coalescent approach by a species tree analysis. The phylogeny with 868 UCE loci and 906,689 bp strongly support the monophyly of Pseudopimelodidae, and the arrangement of two major subclades herein classified as subfamilies Pseudopimelodinae and the newly proposed Batrochoglaninae. Pseudopimelodinae is composed by *Cruciglanis* sister to *Pseudopimelodus* and *Rhyacoglanis*, whereas the new subfamily Batrochoglaninae is composed by *Cephalosilurus* and *Lophiosilurus* as sister to *Batrochoglanis* and *Microglanis*. Pseudopimelodinae is supported by five morphological synapomorphies and Batrochoglaninae supported by three such synapomorphies. The results of this study will surely guide future research aiming to delimit and describe species within the monophyletic groups.

KEYWORDS
biodiversity, fish evolution, Neotropical region, systematic

1 | INTRODUCTION

Catfishes, order Siluriformes, occur in freshwater habitats on all continents, and a few groups are found in estuarine and saltwater environments (Hardman, 2005). The recent diversity of the order is composed of an estimated 3915 species in 500 genera and 39 families (Fricke et al., 2021). In the freshwaters of South America, catfishes are represented by over 2500 species (Fricke et al., 2021) allocated to 15 families in five major monophyletic lineages: Loricarioidei, Diplomystidae, Cetopsidae, Aspredinoidea, and Pimelodoidea (Sullivan et al., 2006). One of the most species-rich clades of siluriforms is the superfamily Pimelodoidea containing *Conorhynchos*

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(monotypic), Heptapteridae (228 species), Phreatobiidae (three species), Pimelodidae (114 species), and Pseudopimelodidae (53 species) (Fricke et al., 2021; Sullivan et al., 2013).

Pseudopimelodidae, known as bumblebee catfishes, are characterized by small eyes covered by skin, short maxillary and mental barbels, wide mouth, relatively small head, dorsal- and pectoral-fin spines serrate, and color patterns often including dark blotches over the head and body (Shibatta, 1998, 2003) (Figure 1). They are widely distributed throughout South America, from the La Plata basin in Argentina to Lago Maracaibo in Venezuela and trans-Andean rivers of northwestern Colombia (Shibatta & Vari, 2017). Some species of *Batrochoglanis* and *Microglanis* are popular in the aquarium trade (Shibatta, 2003) and *Lophiosilurus*, a Rio São Francisco endemic, is used in aquaculture (Costa et al., 2015; Sato et al., 2003). In addition, pseudopimelodids have been in the subjects of various studies on development (Guimarães-Cruz et al., 2009), cytogenetics (Gouveia et al., 2018; Martinez et al., 2004), mitogenomics (Carvalho et al., 2016), internal anatomy (Abrahão et al., 2018, 2021; Abrahão & Shibatta, 2015; Birindelli & Shibatta, 2011), and biogeography (Rangel-Medrano et al., 2020; Souza-Shibatta et al., 2018).

Pseudopimelodidae is currently divided into seven genera: *Batrochoglanis* Gill, 1858; *Cephalosilurus* Haseman, 1911; *Cruciglanis* Ortega-Lara & Lehmann, 2006; *Lophiosilurus* Steindachner, 1889; *Microglanis* Eigenmann, 1912; *Pseudopimelodus* Bleeker, 1858, and *Rhyacoglanis* Shibatta & Vari, 2017. The systematic understanding of the family was recently improved with the descriptions of two genera (Ortega-Lara & Lehmann, 2006; Shibatta & Vari, 2017), and multiple species, especially in *Batrochoglanis* (Shibatta, 2019; Shibatta & Pavanelli, 2005), *Microglanis* (e.g., Sarmento-Soares et al., 2006; Ruiz, 2016; Shibatta, 2016; Terán et al., 2016; Souza-Shibatta et al., 2018), and *Pseudopimelodus* (Restrepo-Gómez et al., 2020). Sixteen out of the 53 valid species of Pseudopimelodidae were described in the last 10 years (Fricke et al., 2021).

Pseudopimelodids were first recognized as monophyletic by Lundberg et al. (1991) and corroborated as such by morphological and molecular studies (Arcila et al., 2017; Hardman, 2005; de Pinna, 1998; Shibatta & Vari, 2017; Sullivan et al., 2006, 2013). In their descriptions of *Cruciglanis* (Ortega-Lara & Lehmann, 2006) and *Rhyacoglanis* (Shibatta & Vari, 2017), the authors used morphological data to hypothesize phylogenetic relationships among pseudopimelodid genera (Figure 2a,b). The major conflict between those

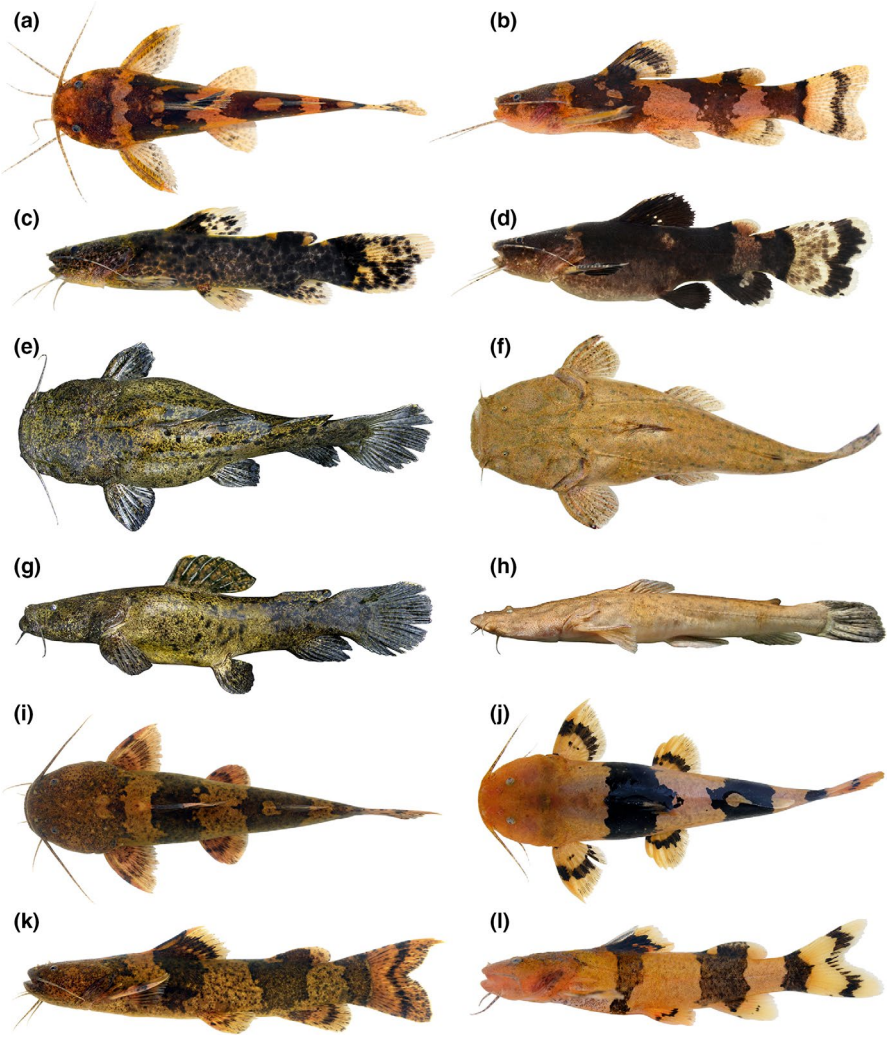

FIGURE 1 Representatives of genera of Pseudopimelodidae: *Microglanis* (a, b); *Batrochoglanis* (c, d); *Cephalosilurus* (e, g); *Lophiosilurus* (f, h); *Pseudopimelodus* (i, k); and *Rhyacoglanis* (j, l)

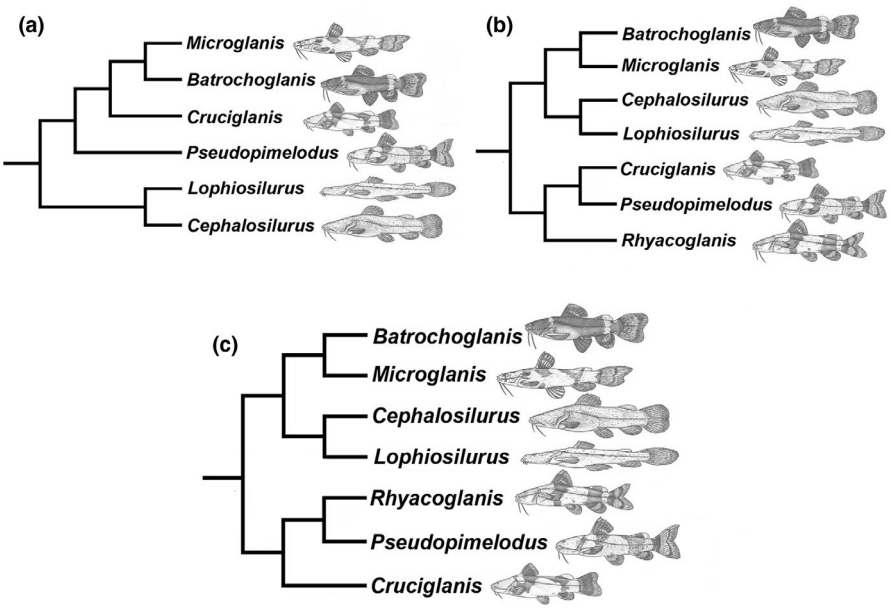

FIGURE 2 Hypotheses of intergeneric relationships within Pseudopimelodidae. (a) Phylogeny based on morphology modified from Ortega-Lara and Lehmann (2006); (b) phylogeny based on morphology modified from Shibatta and Vari (2017); (c) present study

phylogenies involved the placement of *Cephalosilurus* + *Lophiosilurus* either as the sister lineage of all members of the family (Ortega-Lara & Lehmann, 2006) or the sister group to *Batrochoglanis* + *Microglanis* (Shibatta & Vari, 2017). Furthermore, *Cruciglanis* was supported either as the sister group to *Batrochoglanis* + *Microglanis* (Ortega-Lara & Lehmann, 2006) or *Pseudopimelodus* (Shibatta & Vari, 2017). However, these studies included few ingroup species and did not aim to test their interspecific relationships.

New and informative morphological characters were developed in comparative studies of the gas bladder (Birindelli & Shibatta, 2011) and brain (Abrahão et al., 2018). Although phylogenetic analyses of gas bladder morphology resulted in two distinct hypotheses based on choice of outgroup, both topologies supported a sister group relationship between *Cruciglanis* and *Pseudopimelodus*. This relationship is similarly supported by two putative synapomorphies associated with brain morphology (Abrahão et al., 2018). In the most recent phylogenetic study of pseudopimelodids, Rangel-Medrano et al. (2020) used partial sequences from two molecular markers (*cytochrome c oxidase subunit I* and *recombination activation subunit 2*) to analyze *Pseudopimelodus* from trans- and cis-Andean basins in Colombia. Their phylogenetic analysis included all valid genera of Pseudopimelodidae but with few species aside from *Pseudopimelodus*, and supported the same topology proposed by Shibatta and Vari (2017).

Considering the conflicting hypotheses over intergeneric relationships and the incomplete understanding of interspecific relationships, we conducted a phylogenetic analysis of Pseudopimelodidae based on all seven genera and 36% of the species diversity, and the largest DNA dataset assembled for the family. We used the newly designed ostariophysan probe set to capture 2708 nuclear loci of ultraconserved elements (UCEs) (Faircloth et al., 2012, 2020) to test previous hypotheses of intergeneric and interspecific relationships within Pseudopimelodidae (Ortega-Lara & Lehmann, 2006; Rangel-Medrano et al., 2020; Shibatta & Vari, 2017).

2 | MATERIALS AND METHODS

2.1 | Taxon sampling

Ingroup sampling included 33 specimens spanning all seven genera and 21 species, (19 valid plus two undescribed), representing 36% of the valid species diversity of Pseudopimelodidae (Table 1). Related taxa included 18 species of the siluriform families Pimelodidae (six species), Heptapteridae (six species), Ariidae (one species), Aspredinidae (one species), Callichthyidae (one species), Doradidae (two species), and Ictaluridae (one species; Table 1). Related taxa were chosen based on a previous phylogenetic hypothesis within Siluriformes (Sullivan et al., 2006). Trees were rooted in the most distant taxon *Charax metae* (Characiformes: Characidae).

2.2 | DNA extraction and sequencing

Tissue samples were taken from fresh voucher specimens and preserved in 95% ethanol. Vouchers were then fixed in 10% formaldehyde and transferred to 70% ethanol for permanent storage (see Table 1 for catalog and locality data). Institutional codes follow Sabaj (2020). Whole genomic DNA was extracted from tissue 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 for 2708 UCE loci (Faircloth et al., 2020). Library preparation, sequencing, and data pipelining were performed at Arbor Biosciences (AB) using the following protocol: DNA libraries were prepared for the 52 specimens (33 ingroup, 18 related taxa, and one outgroup taxon) 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

TABLE 1 Distinct analyzed matrices based on different schemes of data partitions and sequence data trimmings

	Matrices	Trimming	Total UCE loci	Total bp	Analysis	Figures
1	70% with data-partitioning schemes	Edge	868	906,689	RAxML	Figure S1
2	80% with data-partitioning schemes	Edge	781	811,025	RAxML	Figure S2
3	90% with data-partitioning schemes	Edge	634	603,209	RAxML	Figure S3
4	70% with data-partitioning schemes	Edge	868	906,689	Exabayes	Figure S4
5	80% with data-partitioning schemes	Edge	781	811,025	Exabayes	Figure S5
6	90% with data-partitioning schemes	Edge	634	603,209	Exabayes	Figure S6
7	70% with data-partitioning schemes	Edge	868	906,689	ASTRAL	Figure S7
8	80% with data-partitioning schemes	Edge	781	811,025	ASTRAL	Figure S8
9	90% with data-partitioning schemes	Edge	634	603,209	ASTRAL	Figure S9

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, 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).

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 to prepare the libraries. 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 (Kircher et al., 2012). 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. After capture cleanup, the bead-bound library was re-suspended 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 algorithm (Edgar, 2004) and to perform edge trimmings (i.e., cutting edges of each alignment, eliminating highly variable and saturated regions). We also performed phylogenetic analyses on three matrices with varying amounts of data (70%, 80%, and 90% of UCEs present in the complete alignment matrices) to explore the potential effects of missing data on tree reconstructions (Hosner et al., 2016; Streicher et al. 2016). All matrices are available in Figshare [https://doi.org/10.6084/m9.figshare.14182865]. Information about data for each matrix is summarized in Table 1; species read information is presented in Table S1. All sequences are available at NCBI Sequence Read Archive (SRA) submissions: SAMN18849693-SAMN18849744. Details on UCE sequence analyses are available online in the PHYLUCE documentation (Faircloth, 2016).

2.4 | Phylogenetic analyses

We analyzed the Pseudopimelodidae dataset, with 52 specimens, using maximum likelihood (ML; RAxML v8; Stamatakis, 2014), Bayesian (BI; ExaBayes v1.4; Aberer et al., 2014), and coalescent tree (ASTRAL-II; Mirarab & Warnow, 2015) approaches. For all analyses, we partitioned the UCE data using the Partition-UCE (Tagliacollo & Lanfear, 2018) and performed model selection in PartitionFinder (Lanfear et al., 2012). The RAxML analysis was performed on 70%, 80%, and 90% complete matrices using partitions with edge-trimming alignment (Table 2). Five alternative runs using GTRGAMMA model and distinct parsimony-starting trees were performed to find the best ML tree. Pseudo-replicates applied the autoMRE function for the extended majority-rule consensus tree criterion available in RAxML v8 (Stamatakis, 2014) to assess bootstrap support for branches. This option allows tests for bootstrap convergence, determining if pseudo-replicates are getting stable support values (Pattengale et al., 2010).

TABLE 2 Species and specimens included in present study

	Species	Collection	Specimen number	Locality (river basin/city/state/country)	Geographic coordinates
1	*Amaralia hypsiura*	LBP 10891	50203	Madeira basin/Porto Velho/RO/Brazil	–
2	*Aspistor luniscutis*	LBP 4583	19083	Atlantic coastal drainage/São Vicente/SP/Brazil	–
3	*Batrochoglanis melanurus*	LBP 8501	41749	Paraguay basin/Cáceres/MT/Brazil	S 15°19′53.5″ W 57°11′31.1″
4	*Batrochoglanis raninus*	LBP 17990	72464	Amazon basin/Itacoatiara/AM/Brazil	S 03°07′07.0″ W58°27′14.7″
5	*Batrochoglanis villosus*	LBP 7312	32725	Negro basin/São Gabriel da Cachoeira/AM/Brazil	N 00°04′66.5″ W 66°49′54.6″
6	*Batrochoglanis villosus*	LBP 9157	42523	Guamá basin/Capitão Poço/PA/Brazil	S 01°34′28.3″ W 47°02′03.5″
7	*Batrochoglanis villosus*	LBP 12121	51810	Madeira basin/Porto Velho/AM/Brazil	S 9°12′42.1″ W 64°20′08.6″
8	*Batrochoglanis villosus*	LBP 12127	51823	Madeira basin/Porto Velho/AM/Brazil	S 9°12′42.1″ W 64°20′08.6″
9	*Batrochoglanis villosus*	LBP 15681	64479	Xingu basin/Ribeirão Cascalheira/MT/Brazil	S 13°09′13.6″ W 51°55′18.7″
10	*Brachyglanis microphtalmus*	LBP 7106	34644	Negro basin/São Gabriel da Cachoeira/AM/Brazil	N 00°03′38.1″ W 66°51′00.7″
11	*Brachyplatystoma filamentosum*	LBP 5171	26646	Amazon basin/Belém/PA/Brazil	S 01°18′20″ W 48°36′28″
12	*Cephalosilurus apurensis*	LBP 3034	19182	Orinoco basin/Caicara del Orinoco/Venezuela	N 07°38′11.6″ W 66°19′04.2″
13	*Cephalosilurus fowleri*	LBP 11275	48788	São Francisco basin/Gararu/SE/Brazil	S 09°51′23.0″ W037°06′30.3″
14	*Cetopsorhamdia iheringi*	LBP 8053	37803	Paraná basin/Delfim Moreira/MG/Brazil	S 22°26′56.2″ W 45°20′47.2″
15	*Charax metae*	LBP 18653	61598	Orinoco basin/Granada/Colombia	N 03°29′26.62″ W 73°44′34.10″
16	*Cheirocerus goeldii*	LBP 21845	83779	Negro basin/Iranduba/AM/Brazil	S 03°08′41″ W 59°54′38″
17	*Corydoras nattereri*	LBP 1266	11102	Ribeira do Iguape basin/Miracatu/SP/Brazil	–
18	*Cruciglanis pacifici*	LBP 24323	91524	Cauca basin/Buenaventura/Colombia	S 03°44′30.0″ W76°58′11.0″
19	*Heptapterus mustelinus*	LBP 13129	55150	Uruguai basin/Augusto Pestana/RS/Brazil	S 28°32′03.2″ W 53°58′03.9″
20	*Ictalurus punctatus*	LBP 2165	15148	Pisciculture/Brazil	–
21	*Leiarius marmoratus*	LBP 9787	53207	Amazon basin/Iquitos/Peru	S 03°42′ W 73°13′
22	*Lophiosilurus alexandri*	LBP 276	4235	São Francisco basin/Três Marias/MG/Brazil	S 18°13′66.1″ W 45°14′85.7″
23	*Microglanis* n.sp.1	LBP 9944	46688	Orinoco basin/Cabruta/Venezuela	N 7°52′04.1″ W 66°12′40.1″
24	*Microglanis* n.sp.1	LBP 2260	15738	Orinoco basin/Caicara del orinoco/Venezuela	N 07°32′22.4″ W 66°08′29.2″
25	*Microglanis* cf. *parahybae*	LBP 3471	16096	Macaé basin/Macaé/RJ/Brazil	S 22°14′07.0″ W 41°51′44.6″
26	*Microglanis cottoides LP*	LBP 14459	60608	Laguna dos Patos basin/Caraá/RS/Brazil	S 29°46′34.1″ W 50°26′34.1″
27	*Microglanis cottoides PS*	LBP 3659	21728	Passa Sete basin/Morretes/PR/Brazil	S 25°31′14.9″ W 48°47′52.7″
28	*Microglanis cottoides RI*	LBP 7393	35386	Ribeira do Iguape basin/Itapeúna/SP/Brazil	S 24°35′41.1″ W 48°12′53.3″
29	*Microglanis garavelloi*	LBP 3907	22539	Paraná basin/Avaré/SP/Brazil	S 23°01′27.4″ W 48°49′41.0″
30	*Microglanis leptostriatus*	LBP 23996	–	São Francisco basin/Jaíba/MG/Brazil	S 15°19′31.61″ W 43°39′51.11″
31	*Microglanis leptostriatus*	LBP 19492	76356	São Francisco basin/Pirapóra/MG/Brazil	S 17°20′56.6″ W 44°57′08.7″
32	*Microglanis malabarbai*	LBP 13151	55106	Uruguai basin/Uruguaiana/RS/Brazil	S 29°30′49.2″ W 56°43′28.7″
33	*Microglanis oliveirai*	LBP 1852	13269	Araguaia basin/Barra do Garça/MT/Brazil	S 15°32′54.2″ W 52°12′17.7″
34	*Microglanis poecilus*	LBP 4083	23505	Juruá basin/Mâncio Lima/AC/Brazil	S 07°34′28.8″ W 72°55′24.9″

(Continues)

TABLE 2 (Continued)

	Species	Collection	Specimen number	Locality (river basin/city/state/country)	Geographic coordinates
35	*Microglanis poecilus*	LBP 8612	43447	Arinos basin/Diamantino/MT/Brazil	S 14°08′39.8″ W 56°05′48.6″
36	*Microglanis poecilus*	LBP 14085	58490	Tapajós basin/Itaituba/PA/Brazil	S 04°55′58.8″ W 56°51′51.6″
37	*Microglanis poecilus*	LBP 15497	63828	Branco basin/Mucajaí/RR/Brazil	N 02°54′49.9″ W 60°52′15.7″
38	*Microglanis sparsus*	LBP 15909	65598	Xingu basin/Canarana/MT/Brazil	S 13°31′34.1″ W 52°43′52.5″
39	*Nemuroglanis pauciradiatus*	LBP 7001	34054	Negro basin/São Gabriel da Cachoeira/AM/Brazil	N 00°01′19.9″ W 67°10′19.2″
40	*Phenacorhamdia roxoi*	LBP 8247	38276	Paraná basin/São Miguel Arcanjo/SP/Brazil	S 23°59′49″ W 48°00′57″
41	*Phractocephalus hemioliopterus*	LBP 12883	54064	Tapajós basin/Itaituba/PA/Brazil	S 04°33′09.7″ W 56°17′59.6″
42	*Pseudopimelodus mangurus*	LBP 6560	31516	Paraguay basin/Barra do Bugre/MT/Brazil	S 15°04′37″ W 57°10′51″
43	*Pseudoplatystoma punctifer*	LBP 12822	54009	Tapajós basin/Itaituba/PA/Brazil	S 04°29′11.1″ W 56°17′22.1″
44	*Rhamdia quelen*	LBP 6515	31616	São Francisco basin/Santana do Riacho/MG/Brazil	S 19°23′06.0″ W 43°39′33.3″
45	*Rhinodoras dorbignyi*	LBP 21876	84491	Paraná basin/Ipameri/GO/Brazil	S 17°18′41″ W 47°30′09″
46	*Rhyacoglanis paranensis*	LBP 8083	37227	Paraná basin/Campo Mourão/PR/Brazil	S 23°40′29.0″ W 52°07′08.0″
47	*Rhyacoglanis paranensis*	LBP 11743	60260	Paraná basin/Rio Paranaíba/MG/Brazil	S 19°11′58.0″ W 46°21′49.0″
48	*Rhyacoglanis pulcher*	AUFT 4072	46789	Amazon basin/Rio Maranõn/Peru	–
49	*Rhyacoglanis seminiger*	LBP 13260	69410	Tapajos basin/Diamantino/MT/Brazil	S 13°59′04.1″ W 57°04′01.7″
50	*Rhyacoglanis* n.sp.1	LBP 15906	65589	Xingu basin/Canarana/MT/Brazil	S 13°31′34.1″ W 52°43′52.5″
51	*Sorubimichthys planiceps*	LBP 22301	86401	Solimões basin/Tabatinga/AM/Brazil	S 04°17′32.8″ W 69°54′55.5″
52	*Trachydoras microstomus*	LBP 6898	33244	Negro basin/São Gabriel da Cachoeira/AM/Brazil	S 00°08′15.6″ W 67°05′05.7″

BI of the concatenated alignment was performed using ExaBayes (Aberer et al., 2014) on two independent runs, each with two chains, (one cold and one hot), of 1,000,000 generations using the partition schemes for all three complete matrices (Table 2). 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., 2018), and the last 7500 trees were sampled after checking results for convergence (25% burn-in). This procedure allowed us to visualize the posterior probability log within and between independent runs and 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).

We inferred a coalescent tree analysis from individual gene trees using a two-step process accounting for coalescent stochasticity among individual UCE loci and addressing the related problem where concatenated analyses can return highly supported but incorrect trees process. First, we used PHYLUCE to resample the 70%, 80%, and 90% complete matrices by loci and generated a best tree using RAxML bootstraped for each locus in 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 tree of the results (minimum clade frequency 0.7). Although ASTRAL is not strictly a coalescent method, it is statistically consistent with the multi-species coalescent model (Nute et al., 2018) and scales well for a high number of loci.

3 | RESULTS AND DISCUSSION

Sequencing and data filtering yielded a 70% complete matrix with 868 loci and 906,689 bp; an 80% complete matrix with 781 loci and 811,025 bp; and a 90% complete matrix with 634 loci and 603,209 bp (Table 2). Phylogenetic resolution inferred from the concatenated datasets was strongly supported regardless of matrix completeness (70%, 80%, or 90%) or method of analysis (ML or BI; Figures S1–S8). The results of the concatenated ML trees and BI analyses showed identical topologies. Disagreements involve the ASTRAL analysis

with two distinct nodes compared to the main topology chosen for discussion (70% complete matrix with data partitioning of UCEs and ML analysis). Details of differences among each analysis can be observed in Figures S1–S9.

Results support the monophyly of Pimelodoidea (Figure 3) with Heptapteridae sister to Pimelodidae + Pseudopimelodidae as supported by previous morphological and genetic studies (Arcila et al., 2017; Hardman, 2005; Sullivan et al., 2006, 2013); however, our analyses did not include pimelodoids *Conorhynchos* and Phreatobiidae. Importantly, all phylogenetic reconstructions strongly support the monophyly of Pseudopimelodidae (Figure 2) again corroborating previous morphological (Lundberg et al., 1991; Ortega-Lara & Lehmann, 2006; de Pinna, 1998; Shibatta & Vari, 2017) and genetic studies (Arcila et al., 2017; Hardman, 2005; Silva et al., 2021; Sullivan et al., 2006, 2013).

Internally, our phylogeny revealed two major clades of Pseudopimelodidae classified here as Pseudopimelodinae Lundberg et al. 1991, and Batrochoglaninae new subfamily. This two-clade arrangement agrees exactly with those recently based on morphology (Shibatta & Vari, 2017) and molecules (Rangel-Medrano et al., 2020), but provide a new hypothesis of interspecific relationships (Figure 2).

3.1 | Relationships within Pseudopimelodinae Lundberg et al. 1991

Included genera: *Cruciglanis* Ortega-Lara, 2006; *Pseudopimelodus* Bleeker, 1858 (type genus); *Rhyacoglanis* Shibatta & Vari, 2017.

Diagnosis. Pseudopimelodinae is distinguished within Pseudopimelodidae by five morphological synapomorphies: (a) pectoral-fin spine covered with thick (vs. thin) skin (Shibatta & Vari, 2017: character 3, state 0); (b) tip of pectoral-fin spine bifurcate (vs. pointed) (Shibatta & Vari, 2017: character 29, state 1); (c) gas bladder small, dumbbell-shaped (vs. large, heart-shaped) (Birindelli & Shibatta, 2011; Shibatta & Vari, 2017, character 35, state 1); (d)

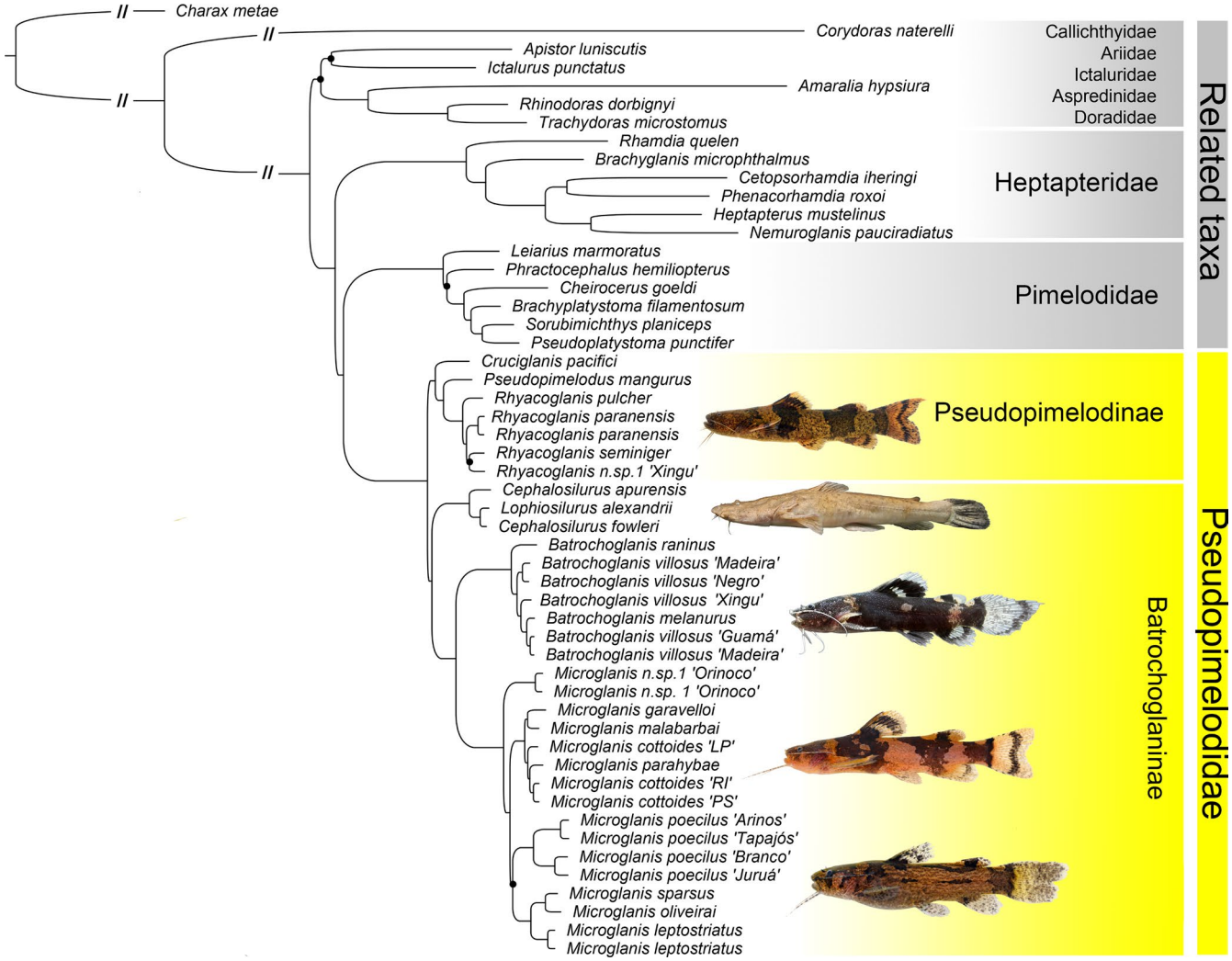

FIGURE 3 Maximum likelihood tree of Pseudopimelodidae based on the 70% complete matrix (868 loci; 906,689 bp). Nodes without symbols represent 100% support from 1000 bootstrap pseudo-replicates; nodal support between 84% and 99% denoted by black circles. LP, Laguna dos Patos; PS, Passa Sete River; RI, Ribeira de Iguape River

pseudotympanum opening small (vs. large) (Birindelli & Shibatta, 2011; Shibatta & Vari, 2017, character 38, state 1); (e) anterior portion of the *cerebellum* extremely prolonged, extending beyond mesencephalon, by less than half the length of telencephalon (vs. moderately prolonged, extending only as far as boundary between the mesencephalon and telencephalon and not contacting the latter) (Abrahão et al., 2018).

Pseudopimelodinae is herein restricted to the genera *Cruciglanis*, *Pseudopimelodus*, and *Rhyacoglanis* (Figures 2 and 3). In our results, the monotypic *Cruciglanis* is sister to *Pseudopimelodus* + *Rhyacoglanis*. Morphological (Shibatta & Vari, 2017) and genetic (Rangel-Medrano et al., 2020) analyses support a monophyletic group composed of the same three genera, but with *Rhyacoglanis* sister to *Cruciglanis* + *Pseudopimelodus*. According to Shibatta and Vari (2017), the sister group relationship between *Cruciglanis* and *Pseudopimelodus* is supported by the shared presence of a dark band on the predorsal region (vs. predorsal region light in *Rhyacoglanis*) and pectoral fin with seven branched rays (vs. usually six in *Rhyacoglanis*). However, Shibatta and Vari (2017) also noted some variation in the number of branched pectoral-fin rays in *Rhyacoglanis* with some specimens from the Rio Madeira having seven branched pectoral-fin rays. Give the UCEs phylogeny, the absence of a dark band on the predorsal region in *Rhyacoglanis* might be interpreted as a secondary loss within Pseudopimelodidae.

In the phylogeny of Shibatta and Vari (2017), *Rhyacoglanis paranensis* (upper Paraná basin) was sister to a clade of species from the Amazon and Orinoco basins, with *Rhyacoglanis epiblepsis* sister to *Rhyacoglanis annulatus*, and *Rhyacoglanis seminiger* sister to *Rhyacoglanis pulcher*. In our molecular genetic analysis, *R. pulcher* was the first species to diverge in the genus, and *R. paranensis* was sister to *R. seminiger* plus an undescribed species from Xingu basin (*R. epiblepsis* and *R. annulatus* not analyzed).

3.2 | Relationships within Batrochoglaninae Shibatta & Silva, new subfamily

LSID: urn:lsid:zoobank.org:pub:EF11973E-91D7-4267-9D29-86457B34706A

Included genera: *Lophiosilurus* Steindachner, 1877; *Cephalosilurus* Haseman, 1911; *Batrochoglanis* Gill, 1858 (type genus); *Microglanis* Eigenmann, 1912.

Diagnosis. Batrochoglaninae is distinguished within Pseudopimelodidae by three morphological synapomorphies: (a) anterior nostril near (vs. distant from) margin of mouth (Shibatta & Vari, 2017: character 15, state 1); (b) vomer absent (vs. present) (Shibatta & Vari, 2017, character 16, state 1); and (c) anterior and posterior margins of pectoral-fin spine with serrae of approximately the same length (vs. anterior serrae shorter than posterior ones) (Shibatta & Vari, 2017: character 27, state 1).

One highly supported clade within Batrochoglaninae includes the monotypic *Lophiosilurus* (endemic to the São Francisco basin) and *Cephalosilurus* with four species distributed in the São Francisco and Orinoco basins and coastal drainages of the Guianas. Based on our results, *Cephalosilurus* is paraphyletic with *Cephalosilurus fowleri* (type species) more closely related to *Lophiosilurus alexandri* than to *Cephalosilurus apurensis* (Figure 2). *Lophiosilurus alexandri* is quite distinct morphologically, and all species in *Cephalosilurus* are more similar to each other than any are to *Lophiosilurus*. The *L. alexandri* phenotype emerges from an ancestral *Cephalosilurus* phenotype, and the close resemblance of *C. fowleri* to other *Cephalosilurus* is not convergent. According to Shibatta and Vari (2017), *Lophiosilurus* and *Cephalosilurus* share four synapomorphies: (a) well-developed unculiferous epidermal structures (vs. little developed; character 2, state 1); (b) seven branched pectoral-fin rays (vs. five, six, eight or more; character 26, state 1); (c) presence of a constrictor muscle of gas bladder (vs. absent; character 36, state 1); and (d) lateral trabeculae on internal T-shaped gas bladder septum (vs. absence of lateral trabeculae; character 37, state 1). Abrahão et al. (2018) also pointed out the reduced *lobus facialis*, comprising less than half length of the lateral line lobe (vs. elongated; state 1). Our results strongly support and suggest *Cephalosilurus* Haseman, 1911 as a junior synonym of *Lophiosilurus* Steindachner, 1877. A study assessing the synonymy of these genera has been conducted by Shibatta et al. (in review), including all species of *Cephalosilurus*.

Our analyses included three out of the six valid species of *Batrochoglanis*: *Batrochoglanis raninus*, *Batrochoglanis melanurus* and specimens of *Batrochoglanis villosus* (from Guamá, Madeira, Xingu, and Negro river basins). *Batrochoglanis raninus* is the sister of a major clade with *B. melanurus* nesting deeply within a paraphyletic *B. villosus* (Figure 3). *Batrochoglanis villosus* is a widely distributed species known from the Orinoco and Amazonas basins as well as coastal drainages of the Guianas, whereas *B. melanurus* is restricted to the upper Paraguay in the La Plata basin (Shibatta & Pavanelli, 2005). In their description of *B. melanurus*, Shibatta and Pavanelli (2005) noted its morphological similarity to *B. villosus*. They also identified *B. villosus* from the upper Tapajós (Amazon basin) which shares a low divide with the upper Paraguay basin. Based on our phylogeny, *B. melanurus* might represents a junior synonym of *B. villosus*; however, the lack of DNA sequence data of *B. villosus* from the type-locality (Potaro river, Guyana) prevents a formal proposal of synonymy.

Microglanis is the most diverse genus of Pseudopimelodidae, with 29 valid species (Tobes et al., 2020) broadly distributed in the Orinoco, Amazon, and La Plata basins as well as Atlantic coastal drainages from Guyana to Uruguay. A couple species occur west of the Andes in Pacific coastal drainages of Ecuador (Tobes et al., 2020). Despite its substantial diversity, no phylogenetic hypothesis has been proposed for the genus. In our topology, *Microglanis* can be divided into four large subclades. The first is represented by an undescribed species from the Orinoco basin. The second group consists of two subclades: species from the Atlantic coastal drainages (*Microglanis cottoides*, *Microglanis* cf. *parahybae*) and the other with two species from La Plata basin *Microglanis garavelloi* (upper Paraná River) and *Microglanis malabarbai* (Uruguay River). Souza-Shibatta et al. (2018) using genetic characters supported a clade composed by the same species, with *M. cottoides* + *M. parahybae* sister to

M. garavelloi + *M. malabarbai*. Alternatively, our results nest *M. parahybae* within a paraphyletic *M. cottoides* (Figure 3).

Microglanis poecilus is the most widely distributed species in the genus (Ruiz & Shibatta, 2011) confirmed to be monophyletic based on our sampling from four distinct Amazonian sub-basins (Arinos, middle Tapajós, Juruá, and Branco). Ruiz and Shibatta (2011) noted that *M. poecilus* shares 11 features with *Microglanis oliveirai*, a species they described from the upper-middle Araguaia basin with drains into the Tocantins River. Our results, however, did not support a close relationship between *M. poecilus* and *M. oliveirai* and placed the latter species as sister *Microglanis sparsus*, a species described from the upper Xingu basin (Ruiz, 2016). Furthermore, our analyses revealed deep splits among lineages of *M. poecilus* suggestive of undescribed taxa.

Finally, our analyses supported a close relationship between *Microglanis leptostriatus*, *M. oliveirai*, and *M. sparsus* in a clade sister to *M. poecilus*. Mori and Shibatta (2006) considered *M. leptostriatus* to be a member of the *M. parahybae* species complex along with *M. garavelloi* and *M. parahybae*. Alcaraz et al. (2008) expanded this group to include *Microglanis pataxo* and *Microglanis carlae*. Our results placed *M. leptostriatus* closer to the Amazonian species *M. sparsus* and *M. oliveirai* than *M. garavelloi* and *M. parahybae* calling into question the cohesiveness of the *M. parahybae* species complex.

4 | CONCLUSIONS

This study represents the most taxon-rich phylogenetic analysis of Pseudopimelodidae to date with representatives of all genera and 36% of the species diversity. Our results support the recognition of two major clades at the subfamilial level, Pseudopimelodinae and Batrochoglaninae. Although our analysis provides strong support for intergeneric relationships, an increased species-level coverage is needed to test the monophyly of *Pseudopimelodus* and to better delimit widely distributed taxa such as *B. villosus*, *M. cottoides*, and *M. poecilus*. The relationships will guide future research aiming to delimit species in well-resolved monophyletic groups as defined herein.

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SUPPORTING INFORMATION

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

Figure S1. Maximum likelihood tree based on the 70% complete matrix (Figure 1).

Figure S2. Maximum likelihood tree based on the 80% complete matrix.

Figure S3. Maximum likelihood tree based on the 90% complete matrix.

Figure S4. Bayesian tree based on the 70% complete matrix.

Figure S5. Bayesian tree based on the 80% complete matrix.

Figure S6. Bayesian tree based on the 90% complete matrix.

Figure S7. Astral tree based on the 70% complete matrix.

Figure S8. Astral tree based on the 80% complete matrix.

Figure S9. Astral tree based on the 90% complete matrix.

Table S1. Sequence reads and assembly statistics for species and specimen used in present study.

Data S1. All matrices are available in Figshare [10.6084/m9.figshare.14182865].

Data S2. All sequences are available at NBCI Sequence Read Archive (SRA) submission: SAMN18849693-SAMN18849744.

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