Original Article

Phylogenomics of Characidae, a hyper-diverse Neotropical freshwater fish lineage, with a phylogenetic classification including four families (Teleostei: Characiformes)

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ABSTRACT

Neotropical tetras of the family Characidae form the largest and most taxonomically complex clade within the order Characiformes. Previous phylogenetic relationships concur on the recognition of four major subclades, whereas knowledge on intergeneric and interspecific relationships remains largely incomplete or nonexistent. We sampled 575 specimens of 494 species and 123 genera classified in Characidae, generated new molecular data of ultraconserved elements (UCEs), and used likelihood and Bayesian analyses. The phylogeny (1348 UCE loci: 538 472 bp) yielded clades with unprecedented resolution at species- and genus-levels, allowing us to propose a new classification of former Characidae into four families: Spintherobolidae, Stevardiidae, Characidae, and Acestrorhamphidae. The family Stevardiidae includes nine subfamilies: Landoninae, Xenurobryconinae, Glandulocaudinae, Argopleurinae, Hemibryconinae, Stevardiinae, Planaltininae, Creagrutinae, and Diapominae. The family Characidae includes five subfamilies: Aphyocharacinae, Cheirodontinae, Exodontinae, Tetragonopterinae, and Characinae. The family Acestrorhamphidae congregates 15 subfamilies: Oxybryconinae, Trochilocharacinae, Stygichthyinae, Megalamphodinae, Stichonodontinae, unnamed subfamily, Stethaprioninae, Pristellinae, Jupiabinae, Tyttobryconinae, Hyphessobryconinae, Thayeriinae, Rhoadsiinae, Grundulinae, and Acestrorhamphinae. The phylogeny resolves intergeneric relationships and supports revalidation of *Myxiops, Megalamphodus, Ramirezella, Holopristis,* and *Astyanacinus*, synonymy of *Aphyodite, Genycharax*, and *Psellogrammus*, and expansion of *Cyanogaster, Makunaima, Deuterodon, Hasemania, Hemigrammus, Bario, Ctenobrycon*, and *Psalidodon*. The phylogeny opens avenues for new systematic reviews and redefinitions of included genera.

Keywords: Neotropics; Ostariophysi; phylogeny; tetras; ultraconserved elements

INTRODUCTION

The delimitation of Characiformes, which includes the Cithariniformes (Distichodontidae and Citharinidae), dates to the middle of the 19th century and extends to recent times

(Müller 1842, Günther 1864, Gill 1896, Regan 1911, Gregory and Conrad 1938, Greenwood *et al.* 1966, Géry 1977, Nelson *et al.* 2016, Betancur-R *et al.* 2017). While the common ancestry of Characiformes and Cithariniformes relative to Gymnotiformes and Siluriformes is supported with seven morphological

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Figure 1. Accumulation curve of the original descriptions of current valid genera of Characidae *s.l.* highlighting the three periods of active descriptions of genera: (i) 1777–1900, (ii) 1900–1955, and (iii) 1955–present.

synapomorphies (Fink and Fink 1981, 1996), the two lineages are not resolved as a clade in phylogenetic studies that range from the earliest single locus analyses in the mid-1990s to phylogenomic analyses in the 21st century (Ortí and Meyer 1996, 1997, Nakatani *et al.* 2011, Betancur-R *et al.* 2013, Chen *et al.* 2013, Chakrabarty *et al.* 2017, Dai *et al.* 2018, Faircloth *et al.* 2020, Simion *et al.* 2020, Melo *et al.* 2022a).

Following recent proposals for the classification of otophysans (Dornburg and Near 2021, Melo et al. 2022a), we consider Characiformes and Cithariniformes as two orders that appear not to share a common ancestry relative to the Gymnotiformes and Siluriformes (Melo et al. 2022a). Characiformes consists of more than 2340 species classified in 287 genera, with 204 new species described over the past 10 years (Fricke et al. 2023). Considerable morphological disparity and patterns of convergent evolution exhibited among the lineages of the species-rich Characiformes has provided challenges to the delimitation of families in the clade (Nelson et al. 2016, Burns and Sidlauskas 2019). Efforts at recognizing suprageneric taxonomic groupings within Characiformes date to the middle of the 19th century and range from 10 to 15 families (Günther 1864, Greenwood et al. 1966, Géry 1977, Vari 1998, Calcagnotto et al. 2005), with a morphological phylogenetic analysis of Characiformes resulting in the delimitation of 18 families of Characiformes (Buckup 1998).

The current family-level classification of Characiformes is the result of a molecular phylogenetic analysis that provided a delimitation of Characidae that represented a monophyletic group and elevated Bryconidae, Acestrorhynchidae, Triportheidae, Chalceidae, and Iguanodectidae from the subfamily rank (Oliveira *et al.* 2011). The conclusions from this early phylogenetic analysis are consistent with the results of more recent phylogenomic analyses and trees inferred from combined molecular and morphological datasets (Arcila *et al.* 2017, Betancur-R. *et al.* 2019, Mirande 2019, Melo *et al.* 2022a, b). With more than 1250 species classified in 141 genera, Characidae *s.l.* are the most species-rich family of Characiformes and of Neotropical freshwater fishes, besides being the third in number of fish species of the world (Fricke *et al.* 2023).

The history of the genus-level classification of Characidae can be summarized in three phases: (i) from 1777 to 1900 with the description of 20 new genera; (ii) from 1900 to 1955 with 72 new genera; and (iii) from 1955 to the present with 51 new genera (Fig. 1). The first period is characterized by relevant descriptions of species/genera (e.g. Charax Scopoli, 1977, Tetragonopterus Cuvier, 1816, Astyanax Baird and Girard, 1854) collected during early explorations such as the Thayer Expedition and by the research activities of European and North American naturalists (Scopoli 1777, Cuvier 1816, Valenciennes in Cuvier and Valenciennes 1850, Baird and Girard 1854, Gill 1858, Günther 1864, Reinhardt 1867, Cope 1870, Steindachner 1876). The second period, marked by the Expedition of the Carnegie Museum to Central and South America (cf. Haseman and Eigenmann 1911), can be recognized by substantial reorganization and classification of 72 new genera that include, for example, Bryconamericus Eigenmann, 1907, Deuterodon Eigenmann, 1907, Glandulocauda Eigenmann, 1911, Hasemania Ellis, 1911, Hyphessobrycon Durbin in Eigenmann, 1908, Knodus Eigenmann, 1911, Moenkhausia Eigenmann, 1903, Phenacogaster Eigenmann, 1907, and Psalidodon Eigenmann, 1911 (Eigenmann 1903, 1907, 1911, 1913, 1914, 1915, Durbin in Eigenmann 1908, Ellis 1911, Myers 1927, 1940, Schultz 1944, Böhlke 1954). The third comprises 51 genera described from 1955 to the present and reflects the extensive research of Géry (1960, 1964a, b, 1965, 1966a, b, 1973) and ichthyologists using Hennigian phylogenetic systematics and detailed taxonomic descriptions (Fink 1976, Weitzman and Vari 1987, Zanata 1997, Malabarba 1998, Castro *et al.* 2003, Menezes *et al.* 2009, Mirande 2010, Vari *et al.* 2016, Terán *et al.* 2020, Frainer *et al.* 2021, Esguícero and Mendonça 2023).

Prior to the application of phylogenetic systematics, species of Characidae were classified into genera based on overall morphological similarities. For example, genera were delimited by external morphological characters that included presence or absence of pseudotympanum and scales covering caudal-fin lobes, development of the laterosensory system, and number, arrangement, and morphology of teeth on jaws (Eigenmann 1917, 1927, Géry 1977, Vari 1998). Molecular phylogenetics and analyses of combined molecular and morphological datasets of Characidae corroborate the extensive non-monophyly of several genera such as Astyanax, Hemigrammus Gill, 1858, and Hyphessobrycon (Javonillo et al. 2010, Oliveira et al. 2011, Mirande 2019). These molecular and combined molecular- and morphology-inferred phylogenies provided the basis for the establishment of a coherent suprageneric classification of Characidae that includes four major clades: (i) Spintherobolinae; (ii) Stevardiinae; (iii) a monophyletic group that includes Aphyocharacinae, Characinae, Cheirodontinae, Exodontinae, and Tetragonopterinae; and (iv) Stethaprioninae that comprises the formerly recognized Stethaprioninae, Rhoadsiinae, and numerous unnamed or weakly supported groups (Malabarba 1998, Javonillo et al. 2010, Mirande 2010, 2019, Oliveira et al. 2011, Thomaz et al. 2015, Betancur-R et al. 2019, Melo et al. 2022a).

With the description of seven genera and 223 species over the past 10 years, there has been a noteworthy pace of discovery in Characidae. The description of new genera and species is reflected in molecular phylogenetic analyses that attempted to reconstruct relationships among the four major lineages of Characidae (Tagliacollo et al. 2012, Thomaz et al. 2015, Melo et al. 2016, Mirande 2019, Terán et al. 2020, Ferreira et al. 2021, Souza et al. 2022). The monophyly of the major characid lineages is consistently supported (Oliveira et al. 2011, Mariguela et al. 2013, Mirande 2019, Melo et al. 2022a) but relationships within and among these lineages remain unresolved or poorly supported. Our knowledge of relationships among genera of Characidae are needed, among others, for the tribes Creagrutini and Diapomini (Thomaz et al. 2015, Ferreira et al. 2021) and Stethaprioninae, which includes Astyanax, Moenkhausia, Deuterodon, Hemigrammus, Hyphessobrycon, Jupiaba Zanata, 1997, and c. 35 other genera (Mariguela et al. 2013, Rossini et al. 2016, Terán et al. 2020, Melo et al. 2022a).

In this study, we follow up on a phylogenomic analysis of Characiformes based on DNA sequences of ultraconserved elements (UCEs) (Melo *et al.* 2022a) with a denser taxon sampling of Characidae *s.l.*. Our new phylogenomic analysis includes 86.7% of the valid genera and 39.4% of the recognized species of the family (accessed in June 2023). The phylogenetic analysis of Characidae is used to investigate the relationships among the four major characid lineages, provide phylogenetic definitions for lineages currently classified in Characidae, discuss morphological characters consistent with clades resolved in the UCE

phylogeny, and provide the basis for a phylogenetic classification of Neotropical tetras. Central to our efforts is the integration of the phylogenomic hypothesis of Characidae into a classification that is based on identification and naming of monophyletic groups.

MATERIALS AND METHODS

Taxon sampling

We sampled 575 specimens of 494 species and 123 genera of Characidae s.l. and outgroups (Supporting Information, Table S1), representing 39.4% of the 1255 species and 86.7% of the genera currently classified in Characidae (Fricke et al. 2023; accessed in June of 2023). Outgroup taxa were selected based on previous family-level molecular phylogenetic analyses of Characiformes (Betancur-R et al. 2019, Melo et al. 2022a, b) and included species of Acestrorhynchidae (Acestrorhynchus Eigenmann and Kennedy, 1903, Gnathocharax Fowler, 1913, Lonchogenys Myers, 1927), Iguanodectidae (Bryconops Kner, 1858, Iguanodectes Cope, 1872), Gasteropelecidae (Carnegiella Eigenmann, 1909, Gasteropelecus Scopoli, 1777), Triportheidae (Agoniates Müller and Troschel, 1845, Triportheus Cope, 1872), and Bryconidae (Brycon Müller and Troschel, 1844, Salminus Agassiz in Spix and Agassiz, 1829). Phylogenies were rooted in one species of Chalceidae (Chalceus Cuvier, 1818). Supporting Information, Table S1 summarizes information on the specimens sampled in this study with museum acronyms following Sabaj (2020, 2022). Specimens were fixed in either 96% ethanol or 10% formalin before being moved to 70% ethanol for long-term preservation.

Phylogenomic data of ultraconserved elements

Total genomic DNA was extracted using the DNeasy tissue kit (Qiagen Inc.) with concentrations varying from 5 to 50 ng/ μ L DNA. Staff from Arbor Biosciences (Ann Arbor, MI) quantified and enriched genomic libraries utilizing the MYbaits Target Enrichment system (MYcroarray) with the Ostariophysans-UCE-2.7Kv1 probe-set containing 6737 baits to capture 2708 nuclear ultraconserved element (UCE) loci (Faircloth *et al.* 2012, 2020). Sequencing was performed on the Illumina platform at Arbor Biosciences with additional details about laboratory procedures available in previous publications for Characiformes (Mateussi *et al.* 2020, Melo *et al.* 2022a, b, Souza *et al.* 2022). The summary of statistics of UCE contigs for each terminal is available in the Supporting Information, Table S2.

We used the PHYLUCE v.1.5.0 (Faircloth 2016) pipeline for analyses of UCE data that included the assembly of raw read sequences to contigs, the identification and separation of UCE loci from contigs, and the building of trimmed alignments of the individual UCE loci. We removed adapter contamination and low-quality bases using Illumiprocessor (Faircloth 2013) and Trimmomatic (Bolger *et al.* 2014), and used VELVET v.1.5.0 (Zerbino and Birney 2008) to assemble fastq reads into fasta contigs. We then searched for the UCE loci using the Ostariophysans-UCE-2.7Kv1 probe-set (Faircloth *et al.* 2020) and the 'phyluce_assembly_match_contigs_to_probes' to remove duplicated or paralog regions. After extracting the UCE loci, we aligned them using the edge-trimming method implemented in MUSCLE (Edgar 2004). We used the 75% complete matrix with loci present in at least 75% of taxa (i.e. loci present in at least 432 terminals), and the 90% complete matrix with loci present in at least 90% of taxa (i.e. loci present in at least 518 terminals). PHYLUCE generated phylip and nexus matrices for downstream phylogenetic analyses of maximum likelihood and Bayesian inference. Data matrices are available in Dryad (Data availability).

Partitions of UCE loci were obtained with PartitionFinder-UCE (Tagliacollo and Lanfear 2018), and the best-fit models were obtained with PartitionFinder (Lanfear et al. 2012). Maximum likelihood (ML) searches were conducted in RAxML v.8.2.11 (Stamatakis 2014) with the GTRGAMMA model for each of the two datasets. RAxML executed five inferences on the original alignments, starting with five randomized trees obtained from parsimony searches. One thousand non-parametric bootstraps were executed using RAxML and the autoMRE function optimizing the MRE-based bootstopping criterion (Pattengale et al. 2009). A posterior set of Bayesian-inferred phylogenies were obtained with ExaBayes v.1.5 (Aberer et al. 2014) using models obtained with PartitionFinder with starting trees inferred using parsimony and Markov chain Monte Carlo (MCMC) run for 10 000 000 generations, with a checkpoint interval of 500, and using AVX implementation for likelihood computations (Aberer et al. 2016). Stationary, convergence of posterior parameter estimates, and trace distributions were inspected with TRACER v.1.7.1 (Rambaut *et al.* 2018).

Species' distribution data and classification

In order to investigate the impact of the geographic distribution across the phylogeny, we categorized each species in five major Neotropical biogeographic zones that encompasses area delimitations of Neotropical freshwater fishes (Reis et al. 2016). The distribution of each species was obtained from the vast literature involving the systematics of subfamilies, genera, and species (e.g. Géry 1977, Lima et al. 2003) and the current knowledge and field experience of the authors. Species occurring in more than one region were properly assigned to multiple regions. The area Amazon-Orinoco-Guianas (first square column; dark green) encompassed characids from these three major basins, including Oyapock, Marowijne, Corantijn, Demerara, Essequibo, Mazaruni, the Orinoco including Caura, Cuyuni, Apure, Guaviare, and Meta, the Amazon basin including Tocantins-Araguaia, Xingu, Tapajós, Madeira-Guaporé, Purus, Juruá, Javari, Ucayali, Napo, Putumayo-Içá, Caquetá-Japurá, Vaupés-Negro, Branco, Uatumã, Trombetas, Jari, and associated drainages and tributaries. The Paraná-Paraguay-Uruguay region (second square column; blue) includes the Uruguay and Iguaçu rivers, the upper Paraná and Paraguay, as well as adjacent rivers draining the lower Río de La Plata in Argentina. The Andean region (third square column; pink) involved piedmont and high altitude rivers of both east and west sides of the Eastern Cordillera, including the Lago Maracaibo, the Cauca-Magdalena system, Pacific versant rivers, and all drainages of Central America and Mexico. The São Francisco-north-east region (fourth square column; orange) includes rivers of central-north-east Brazil, such as the São Francisco, Parnaíba, and coastal rivers of north-eastern Brazil at the north of the São Francisco river mouth. Finally, the Atlantic coastal rivers (fifth

square column; yellow) involve endemics from the Atlantic Rainforest region of eastern Brazil south of the São Francisco, including Jequitinhonha, Mucuri, Doce, Paraíba do Sul, Ribeira de Iguape, Laguna dos Patos, and associated coastal drainages.

Available family-group names of characiforms were obtained from previous nomenclature compilations (Van der Laan *et al.* 2014, Toledo-Piza *et al.* 2024). Clade definitions and phylogenetic classification partially followed the principles of the *PhyloCode* (de Queiroz and Gauthier 1990, 1994). Generic names in section 'Not sampled' indicate instances of tentative placement of particular unsampled genera in the respective clade. These instances involve genera that were previously sampled in molecular phylogenetic analyses (e.g. Thomaz *et al.* 2015, Mirande 2019) and were absent in the present study. Tribelevel rankings were not adopted in this study.

RESULTS

The 75% complete matrix contains 1348 ultraconserved element loci with 538 472 bp, and RAxML analyses results in a ML phylogeny with final score -9,863,085.327660 and 50 bootstrap replicates (Fig. 2). The 90% complete matrix contains 274 UCE loci with 109 324 bp, and RAxML analysis yields a ML phylogeny with final score -1,886,474.911867 and 50 bootstrap replicates (Supporting Information, Fig. S1). In comparison to the ML phylogeny, the Bayesian analyses (75% and 90% complete matrices) produced phylogenies with same phylogenetic positions among subfamilies. The single difference appears in the Bayesian analysis of the 75% complete matrix, with the position of Hemigrammus unilineatus-16881 as sister to the Acestrorhamphidae (support 1.0; Supporting Information, Fig. S2); further investigation on the original data indicates lower average sequencing data for that specimen (contigs 1131, average 1637; total bp 290 113, average 958 084; max length contigs 871, average 1573.66; Supporting Information, Table S2), possibly causing noise in the likelihood analysis. The consistent position of this taxon relative to the second specimen (Hemigrammus unilineatus-82757) in three other analyses confirms the accurate placement in Pristellinae. Minor differences among analyses appear in intergeneric and interspecific relationships in Stygichthyinae, Stethaprioninae, Hyphessobryconinae, Thayeriinae, and Acestrorhamphinae. All figures and tree files are available as Supporting Information (Figs S1–S3).

The phylogenetic analyses based on UCEs indicate that the Neotropical tetras belong to four major lineages, which we recognize at the family level: 1, Spintherobolidae (six species); 2, Stevardiidae (365 species); 3, Characidae (203 species); and 4, Acestrorhamphidae (685 species) (Fig. 2). The reasons for the recognition of the clades at the family level are: (i) the four clades have fully supported nodes (i.e. 100% bootstrap/1.0 Bayesian posterior probability) in our genomic-based phylogenetic analyses; (ii) the four clades are recurrent in several phylogenetic studies using distinct sources of multilocus (Calcagnotto *et al.* 2005; Oliveira *et al.* 2011; Mariguela *et al.* 2013; Thomaz *et al.* 2015; Melo *et al.* 2016), combined multilocus and morphology (Mirande, 2019), and genomic data (Betancur-R *et al.* 2019; Melo *et al.* 2022a; Elfas *et al.* 2023); (iii) the four clades, except Characidae, possess relevant derived features; and (iv)



Oligosarcus

Figure 2. Phylogenetic relationships of the major clades of Spintherobolidae, Stevardiidae, Characidae, and Acestrorhamphidae based on the 75% complete matrix of 1348 ultraconserved elements (575 taxa; 538 472 bp).

the family-level ranking allows the recognition of well-supported and concise subfamilies. The phylogenetic classification presented herein is derived from genomic-based data; thus, our study does not aim to provide morphological support or diagnoses for clades.

DISCUSSION

The development of new sequencing protocols and, more importantly, new sequencing and bioinformatics technology has improved the capacity to analyse massive genetic datasets (Heather and Chain 2016) used to address complex phylogenetic questions in species-rich groups (Youngh and Gillung 2020). Among the most prominent markers in fish phylogenomics are the exon capture sequencing (Betancur-R. *et al.* 2017, 2019, Hughes *et al.* 2018, Varella *et al.* 2023) and the ultraconserved elements (Faircloth *et al.* 2018, Roxo *et al.* 2019, Mateussi *et al.* 2020, Melo *et al.* 2012a, b, Silva *et al.* 2021a). In the present study, using the new UCE probeset developed for ostariophysan fishes (Faircloth *et al.* 2020) we investigated the relationships among Characidae species with a robust resolution as described below.

The name Characoidea has been applied to the clade that includes Ctenoluciidae, Lebiasinidae, Chalceidae, Acestrorhynchidae, Iguanodectidae, Bryconidae, Gasteropelecidae, Triportheidae, and Characidae (Betancur-R et al. 2019). The phylogenetic relationships among the main lineages of Characoidea are mostly congruent through studies with few conflictant regions (Melo et al. 2022a) that limit efforts to propose new subordinal group names in Characiformes. The clade containing Spintherobolidae, Stevardiidae, Acestrorhamphidae, and the revised delimitation of Characidae is supported by two morphological synapomorphies: the absence of the supraorbital and the posterior emergence of the hyoid artery from the anterior ceratohyal (Castro 1984, Malabarba and Weitzman 2003). There is a low probability that these morphological characters are homoplasious as they emerge from developmental truncation at the character level (Mattox et al. 2014). Furthermore, five additional synapomorphies have been reported for this clade (Mirande 2019).

In the past 30 years, the classification of major fish groups has been revised to incorporate advancements in our understanding of these groups and the application of molecular data to construct robust phylogenies (Near and Thacker 2024). Among Siluriformes, Lundberg et al. (1988, 1991) identified three monophyletic groups within the former Pimelodidae, which they initially recognized as subfamilies. Lundberg and Littmann (2003), Bockmann and Guazzelli (2003), and Shibatta (2003) elevated these subfamilies as families Pimelodidae, Heptapteridae, and Pseudopimelodidae. This reclassification allowed further subdivisions of the families into subfamilies and tribes (Silva et al. 2021a, 2021b). Among Cypriniformes, which comprises over 4400 species (Fricke et al. 2023), there was a lack of consensus on the major groupings among families until Tan and Armbruster (2018); cobitoids were previously classified in various families such as algae eaters (Gyrinocheilidae) and suckers (Catostomidae) and, in contrast, the diverse Cyprinoidei, which make up the majority of cypriniforms with over 3000 species, were recognized as Cyprinidae s.l.

and potentially Psilorhynchidae. The extensive work of Tan and Armbruster (2018) changed the Cypriniformes' classification by identifying many families formerly included under Cyprinidae *s.l.* (e.g. Danionidae, Leuciscidae) and proposed new boundaries for Cyprinidae with a more specific group of taxa: the Cyprinidae *s.s.*. In both ostariophysan examples, as well as in other instances in the literature, authors assert that revisions were required since the prior classification restricted the application of the Linnean classification system in representing phylogenetic relationships among natural groups. Below we provide clade descriptions and commentaries for each of the four families and subfamily-level clades.

Spintherobolidae Mirande, 2019, new usage

Type genus: Spintherobolus Eigenmann, 1911.

Included genera: Amazonspinther Bührnheim et al., 2008 and Spintherobolus.

Definition: The least inclusive crown clade that contains *Amazonspinther dalmata* Bührnheim *et al.*, 2008 and *Spintherobolus papilliferus* Eigenmann, 1911. This is a minimumcrown-clade definition. See Figure 3 for a reference phylogeny of Spintherobolidae.

Etymology: From the ancient Greek σπινθηρο (spinθ'3:10 \overline{v}) meaning a spark and βόλος (b' \overline{ovlovz}) meaning a throw with a casting net.

Remarks: We delimit the family Spintherobolidae to include *Amazonspinther* and all species of *Spintherobolus* as the sisterlineage of a clade containing Stevardiidae, Characidae, and Acestrorhamphidae (Figs 2, 3). Spintherobolidae are supported by 15 unambiguous synapomorphies relative to Cheirodontinae (Bührnheim *et al.* 2008), 10 of which are extensively discussed as synapomorphies for *Spintherobolus* (Malabarba 1998; (Weitzman and Malabarba 1998) or a clade containing *A. dalmata* and *Spintherobolus* (Bührnheim *et al.* 2008). The lack of the mesocoracoid was also proposed as a synapomorphy for *Amazonspinther* and *Spintherobolus* (Mirande 2019), thus reinterpreted here as synapomorphic for the Spintherobolidae.

Bührnheim et al. (2008) hypothesized Spintherobolus and Amazonspinther as sister to Cheirodontinae. The clade Spintherobolus and Amazonspinther has not been resolved as closely related to Cheirodontinae, but rather the sistergroup of all other characids (Mariguela et al. 2013, Melo et al. 2022a). Phylogenies inferred from a combined molecular and morphological dataset resolved former Spintherobolinae (Amazonspinther, Atopomesus Myers, 1927, and Spintherobolus) as the sister-group of all characids except former Stethaprioninae (Mirande 2019). Only morphological data were available for Atopomesus and its resolution within Spintherobolinae had low statistical support (Mirande 2019); phylogenetic analysis of the UCE loci resolves Atopomesus with high support in a distinct clade within the Characinae. The phylogeny inferred from the UCE loci offers a compelling hypothesis that Spintherobolus and Amazonspinther form the sister-group of a clade containing Acestrorhamphidae, Stevardiidae, and Characidae (Betancur-R et al. 2019, Melo et al. 2022a; present study).





Figure 3. Phylogeny of Spintherobolidae and Stevardiidae and subfamilies Landoninae, Xenurobryconinae, Glandulocaudinae, Argopleurinae, Hemibryconinae, Stevardiinae, Planaltininae, Creagrutinae, and Diapominae based on 1348 nuclear loci of ultraconserved elements (538 472 bp). Numbers near nodes represent bootstrap support.

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Within Spintherobolidae, the Amazonian *Amazonspinther* is the sister-group of the *Spintherobolus* from the Atlantic coastal rivers and upper Paraná with *S. papilliferus* as sister to all other species, and *S. broccae* Myers, 1925 sister to *S. ankoseion* Weitzman and Malabarba, 1999, and *S. leptoura* Weitzman and Malabarba, 1999 (Fig. 3). The UCE phylogeny and a previous molecular study are congruent with regards to the relationships within *Spintherobolus* (Mattox *et al.* 2023a).

Stevardiidae Gill, 1858, new usage

Type genus: Stervardia Gill, 1858, junior synonym of *Corynopoma* Gill, 1858.

Included subfamilies: Argopleurinae, Creagrutinae, Diapominae, Glandulocaudinae, Hemibryconinae, Landoninae, Planaltininae, and Xenurobryconinae.

Definition: The least inclusive crown clade that contains *Landonia latidens* Eigenmann and Henn, 1914, *Corynopoma riisei* Gill, 1858, and *Xenurobrycon macropus* Myers and Miranda Ribeiro, 1945. This is a minimum-crown-clade definition. See Figure 3 for a reference phylogeny of Stevardiidae.

Etymology: Stervardia Gill, 1858 is a patronym of D. Jackson Steward (1816-1898).

Remarks: Synapomorphies for Stevardiidae include a short frontal fontanel, up to two-thirds the length of the parietal fontanel, ventral margin of anguloarticular crossing perpendicularly to the dentary laterosensory canal, four teeth in the inner premaxillary row, and ectopterygoid expanded laterally to the blade of the lateral ethmoid (Mirande 2019); reversals in all characters are observed in several species (Mirande 2019).

Eigenmann (1914) proposed the subfamily Glandulocaudinae for characids with a gland in caudal fins of mature males (e.g. Corynopoma). Weitzman et al. (2005) delimited Stevardiinae as a lineage distinct from Eigenmann's Glandulocaudinae, and Mirande (2010) on the basis of three synapomorphies merged the two groups under the name Stevardiinae. Malabarba and Weitzman (2003) identified a monophyletic group they named Clade A, which contained the Glandulocaudinae, Stevardiinae (sensu Weitzman et al. 2005), and 18 additional genera considered incertae sedis within Characidae. The monophyly of Clade A has been supported in phylogenetic analyses using morphological (Mirande 2010, Baicere-Silva et al. 2011, Ferreira et al. 2011, Mirande et al. 2011), multilocus (Calcagnotto et al. 2005, Javonillo et al. 2010, Oliveira et al. 2011, Mariguela et al. 2013, Thomaz et al. 2015), combined multilocus and morphology (Mirande 2019, Ferreira et al. 2021), and phylogenomic data (Arcila et al. 2017, Betancur-R. et al. 2019, Melo et al. 2022a). We have elevated Stevardiidae to a family level with nine subfamilies: Landoninae, Xenurobryconinae, Glandulocaudinae, Argopleurinae, Hemibryconinae, Stevardiinae, Planaltininae, Creagrutinae, and Diapominae (Fig. 3).

Landoninae Weitzman and Menezes, 1998, new usage

Type genus: Landonia Eigenmann and Henn, 1914.

Included genera: Eretmobrycon Fink, 1976, Landonia, Markiana Eigenmann, 1903, and Phenacobrycon Eigenmann, 1922.

Definition: The least inclusive crown clade that contains *Landonia latidens, Eretmobrycon emperador* (Eigenmann and Ogle, 1907), and *Markiana nigripinnis* (Perugia, 1891). This is a minimum-crown-clade definition. See Figure 3 for a reference phylogeny of Landoninae.

Etymology: Landonia is a patronym of Hugh McKennan Landon (1867–1947).

Remarks: Roberts (1973) suggested that Iotabrycon Roberts, 1973, Landonia, and Phenacobrycon were a monophyletic group derived from a putative ancestor related to Bryconamericus from the western Andes. Oliveira et al. (2011) identified a monophyletic group including Markiana and Eretmobrycon emperador (formerly Bryconamericus emperador). Thomaz et al. (2015) found the trans-Andean Bryconamericus more related to Markiana than to B. exodon Eigenmann 1907 (type species), and that they should be included in Eretmobrycon in the tribe Eretmobryconini. Ferreira et al. (2021) resolved Landonia inside this clade and renamed the group as Landoniini (= Landonini) based on 19 synapomorphies. Eretmobryconini Thomaz et al., 2015 (Eretmobryconinae; type genus: Eretmobrycon) is a junior synonym of Landonini Weitzman and Menezes, 1998 (Landoninae; type genus: Landonia). Vanegas-Ríos (2018) found that Landonia was the sister-group of Phenacobrycon, but this relationship was not corroborated by Ferreira et al. (2021), who resurrected the monotypic tribe Phenacobryconini proposed by Weitzman and Menezes (1998). Melo et al. (2022a) similarly resolved the clade containing Markiana, Phenacobrycon, and *E. emperador* in a phylogeny inferred from UCE loci.

In the UCE phylogeny, Landoninae are monophyletic and composed of *Markiana, Eretmobrycon, Landonia,* and *Phenacobrycon* (Fig. 3). Our phylogenetic analyses revealed that *Eretmobrycon festae* (Boulenger, 1898) (former *Astyanax festae*) is more closely related to *Phenacobrycon* and *Landonia* than to other *Eretmobrycon* (Fig. 3). The former *Astyanax festae* (Boulenger, 1898) has been hypothesized to be more related to *Markiana* and *Bryconamericus emperador* (Rossini *et al.* 2016) and was recently transferred to *Eretmobrycon* (Terán *et al.* 2020). Additional analyses within the group are necessary to evaluate the present hypothesis that *E. festae* may belong to a distinct genus.

Biogeographically, Landoninae are a group with two lineages: (i) species of *Markiana* occurring in Amazon–Orinoco–Guianas and La Plata [*M. geayi* (Pellegrin, 1909) in Orinoco and *M. nigripinnis* (Perugia, 1891) in the Paraguay and Amazon basins], and (ii) species of *Eretmobrycon*, *Phenacobrycon*, and *Landonia* that diversified in the trans-Andean northern South America and lower Central America (Fig. 3).

Xenurobryconinae Myers and Böhlke, 1956

Type genus: Xenurobrycon Myers and Miranda Ribeiro, 1945.

Included genera: Tyttocharax Fowler, 1913 and *Xenurobrycon*. Not sampled: *Iotabrycon, Ptychocharax* Weitzman *et al.,* 1994, and *Scopaeocharax* Weitzman and Fink, 1985.

Definition: The least inclusive crown clade that contains Xenurobrycon macropus Myers and Miranda Ribeiro, 1945,

Iotabrycon praecox Roberts, 1973, Ptychocharax rhyacophila Weitzman et al., 1994, Scopaeocharax rhinodus (Böhlke 1958), and Tyttocharax madeirae Fowler, 1913. This is a minimumcrown-clade definition. See Figure 3 for a reference phylogeny of Xenurobryconinae. Although Iotabrycon praecox, Ptychocharax rhyacophila, and Scopaeocharax rhinodus are not included in the reference phylogeny, they resolve as a monophyletic group with Tyttocharax tambopatensis and Xenurobrycon macropus in a phylogenetic analysis of a dataset of mtDNA, nuclear genes, and morphology (Ferreira et al. 2011:fig. 1).

Etymology: From the ancient Greek $\xi \epsilon v \circ \varsigma (z'i:novz)$ meaning strange or unusual, $o \dot{v} \rho \alpha ('u: z'\alpha:)$ meaning tail, and $\beta \rho \dot{v} \kappa \omega (b z'v k a v)$ meaning to bite.

Remarks: Myers and Böhlke (1956) erected the tribe Xenurobryconini to include Xenurobrycon and Tyttocharax based on the similarity of their caudal fin morphology. The tribe Xenurobryconini was expanded to include Argopleura Eigenmann, 1913, Iotabrycon, and Scopaeocharax (Weitzman and Fink 1985), and later Chrysobrycon Weitzman and Menezes, 1998 and Ptychocharax (Weitzman and Menezes 1998). Thomaz et al. (2015) considered Argopleura as incertae sedis and transferred Chrysobrycon to their Stevardiini. Mirande (2019) corroborated the monophyly of Xenurobryconini (sensu Thomaz et al. 2015), and tentatively included Cyanogaster Mattox et al., 2013, in this clade supported by four synapomorphies. Our phylogenetic analysis of the UCE loci indicates that Cyanogaster is placed closer to species of Aphyocharacinae. Ferreira et al. (2021) included Iotabrycon, Ptychocharax, Scopaeocharax, Tyttocharax, and Xenurobrycon in Xenurobryconini based on four morphological synapomorphies. In other phylogenomic analyses, Scopaeocharax was resolved as the sister-lineage of Cyanocharax Malabarba and Weitzman, 2003 or Diapoma Cope, 1894 (Arcila et al. 2017, Betancur-R. et al. 2019). Although UCE data for Iotabrycon, Ptychocharax, and Scopaeocharax are not yet available, they are included in Xenurobryconinae along with Tyttocharax and Xenurobrycon based on phylogenetic analyses of a combined mtDNA, nuclear genes, and morphology dataset (Ferreira et al. 2021).

Glandulocaudinae Eigenmann, 1914

Type genus: Glandulocauda Eigenmann, 1911.

Included genera: Glandulocauda, Lophiobrycon Castro et al., 2003, and Mimagoniates Regan, 1907.

Definition: The least inclusive crown clade that contains *Glandulocauda melanopleura* (Ellis 1911) and *Lophiobrycon weitzmani* Castro *et al.*, 2003. This is a minimum-crown-clade definition. See Figure 3 for a reference phylogeny of Glandulocaudinae.

Etymology: From Latin *glandulae* (gl'ænduːl_iei) meaning glands of the throat or swollen tonsils and *cauda* (k'ɔːdə) meaning the tail of animals.

Remarks: Menezes and Weitzman (2009) reviewed the systematics of the Glandulocaudinae, providing an overview of the long taxonomic history and persistent nomenclatural issues for taxa in the clade. In previous classifications, the clade has been treated as the family Glandulocaudidae (Fernández-Yépez and Anton 1966), the subfamily Glandulocaudinae (e.g. Menezes and Weitzman 2009), and the tribe Glandulocaudini (e.g. Eigenmann 1914, Myers and Böhlke 1956, Menezes and Weitzman 1990, Mirande 2010). The group's composition among previous classifications varied until Weitzman *et al.* (2005) restricted Glandulocaudinae to *Glandulocauda*, *Lophiobrycon*, and *Mimagoniates*.

Several phylogenetic analyses using molecular data or combinations of molecular and morphological datasets resolved Glandulocauda, Lophiobrycon, and Mimagoniates as a monophyletic group, with Mimagoniates as the sister-lineage of a clade containing Lophiobrycon and Glandulocauda (Oliveira et al. 2011, Thomaz et al. 2015, Mirande 2019, Ferreira et al. 2021). Alternative hypotheses based on analyses of morphological characters resolved Lophiobrycon as the sisterlineage of a clade containing *Glandulocauda* and *Mimagoniates* (Castro et al. 2003, Menezes and Weitzman 2009). Ferreira et al. (2021) identified five morphological synapomorphies for Glandulocaudinae. Phylogenetic analysis of mtDNA sequences resolves Glandulocauda as paraphyletic with G. melanopleura (Ellis, 1911) and L. weitzmani Castro et al., 2003 as sister-taxa, and G. caerulea Menezes and Weitzman, 2009 resolved as the sister-lineage of Mimagoniates (Camelier et al. 2018). The phylogeny inferred from the UCE loci is consistent with previous studies in resolving Glandulocaudinae as monophyletic and Glandulocauda as paraphyletic (Fig. 3). The UCE phylogeny indicates that Glandulocaudinae represents a La Plata-derived lineage, and that Mimagoniates diversified into the Atlantic coastal rivers (Fig. 3).

Argopleurinae Melo and Oliveira, new subfamily

ZooBank: urn:lsid:zoobank.org:act:D266860E-A816-4B4D-84C3-AC7BB9F88CAC.

Type genus: Argopleura Eigenmann, 1913.

Included genus: Argopleura.

Definition: The least inclusive crown clade that contains Argopleura chocoensis (Eigenmann, 1913), Argopleura conventus (Eigenmann, 1913), Argopleura diquensis (Eigenmann, 1913), and Argopleura magdalenensis (Eigenmann, 1913). This is a minimum-crown-clade definition. See Figure 3 for a reference phylogeny of Argopleurinae. Although Argopleura conventus and Argopleura diquensis are not sampled in the reference phylogeny, it is assumed that the four species of Argopleura form a monophyletic group (Weitzman and Fink 1985).

Etymology: From the ancient Greek ἀργός ('dːɹgoʊz) meaning shinning or glistening and πλευρά (pl'oːɹə) meaning rib or side of the body.

Remarks: Weitzman and Menezes (1998) placed *Argopleura* in Xenurobryconini but recognized that the group was based on limited and ambiguous data. According to Weitzman *et al.* (2005), a plesiomorphic pouch scale observed in *Argopleura* comprises what appears to be a terminal lateral-line tube, and thus it looks superficially like a scale derived from the lateral-line

scale series. The authors suggested that new studies should be conducted to better understand this character. Thomaz *et al.* (2015) and Ferreira *et al.* (2021) resolved *Argopleura* as a deepbranching lineage not closely related to other stevardiine genera and classified it as *incertae sedis* in Stevardiinae. Mirande (2019) placed *Argopleura* within Stevardiini but did not discuss its relationships with other genera. Our UCE inferred phylogeny resolves *Argopleura* as the sister-lineage of all Stevardiidae excluding Landoninae, Xenurobryconinae, and Glandulocaudinae (Fig. 3); thus we formally describe the new subfamily, Argopleurinae, endemic to the Andean region (Fig. 3).

Hemibryconinae Géry, 1966, new usage

Type genus: Hemibrycon Günther, 1864.

Included genera: Acrobrycon Eigenmann and Pearson in Pearson, 1924 and *Hemibrycon*.

Definition: The least inclusive crown clade that contains *Acrobrycon ipanquianus* (Cope, 1877), *Hemibrycon polyodon* (Günther, 1864), and *Hemibrycon caucanus* (Eigenmann, 1913). This is a minimum-crown-clade definition. See Figure 3 for a reference phylogeny of Hemibryconinae. Although *Hemibrycon polyodon* is not included in the reference phylogeny, the species resolves with other species of *Hemibrycon* in a molecular phylogeny (Thomaz *et al.* 2015) and species in the genus are thought to represent a monophyletic group (Weitzman and Fink 1985).

Etymology: From the ancient Greek ήμί- (h'ɛmi) a prefix meaning half and βρύκω (bɹ'uːkoʊ) meaning bite or βρύχω (bɹ'uːkoʊ) meaning gnash.

Remarks: Géry (1966a) delimited Hemibryconini to include Boehlkea Géry, 1966, Bryconacidnus Myers, 1929, Bryconamericus, Ceratobranchia Eigenmann, 1914, Coptobrycon Géry, 1966, Hemibrycon, Knodus, Microgenys Eigenmann, 1913, Nematobrycon Eigenmann, 1911, Piabarchus Myers, 1928, Rhinobrycon Myers, 1944, and Rhinopetitia Géry, 1964. Thomaz et al. (2015) resolved Hemibryconini to include Acrobrycon, Hemibrycon, and tentatively Boehlkea (not analysed there). Ferreira et al. (2021) resolved Acrobrycon and Hemibrycon as a clade supported with five morphological synapomorphies. Phylogenetic analyses of the UCE loci resolve Acrobrycon ipanquianus (Cope, 1877) as the sister-lineage of Hemibrycon (Fig. 3); the two specimens of Boehlkea are placed closer to Bryconamericus macarenae Román-Valencia et al., 2010, Phallobrycon Menezes et al., 2009, and Knodus cf. delta Géry, 1972, in the subfamily Diapominae (Fig. 3). Hemibryconinae are primarily an Andean lineage, although some species of Hemibrycon occur in the Amazon and Orinoco basins (Fig. 3).

Stevardiinae Gill, 1858, new usage

Type genus: Stevardia Gill, 1858.

Included genera: Chrysobrycon, Corynopoma, Gephyrocharax Eigenmann, 1912, Pseudocorynopoma Perugia, 1891, and Pterobrycon Eigenmann, 1913. Not sampled: Hysteronotus Eigenmann, 1911 and Varicharax Vanegas-Ríos et al., 2020. Definition: The least inclusive crown clade that contains Chrysobrycon hesperus (Böhlke, 1958), Corynopoma riisei Gill, 1858, Hysteronotus megalostomus Eigenmann, 1911, and Varicharax nigrolineatus Vanegas-Ríos et al., 2020. This is a minimum-crown-clade definition. See Figure 3 for a reference phylogeny of Stevardiinae. Although not included in the reference phylogeny, Hysteronotus megalostomus resolves in a clade with species of Pseudocorynopoma and Varicharax nigrolineatus is placed as the sister-lineage of all other species of Stevardiinae in phylogenetic analyses of combined molecular and morphological characters (Vanegas-Ríos et al. 2020, Ferreira et al. 2021).

Etymology: Stervardia Gill, 1858 is a patronym of D. Jackson Steward (1816–1898).

Remarks: Weitzman and Menezes (1998) proposed a rearrangement in the Glandulocaudinae and defined the tribe Corynopomini with Corynopoma, Gephyrocharax, and Pterobrycon, and the tribe Hysteronotini with Hysteronotus and Pseudocorynopoma. Thomaz et al. (2015) included Corynopomini, Hysteronotini, and Chrysobrycon in what they delimited as Stevardiini, a result corroborated by Ferreira et al. (2021) who identified three morphological synapomorphies supporting the clade. The phylogenies inferred from the UCE loci resolve Stevardiinae as a monophyletic group that includes the subclades Corynopomini (Corynopoma, Gephyrocharax, and *Pterobrycon*) and Hysteronotini (Chrysobrycon, Pseudocorynopoma, and tentatively Hysteronotus) (Fig. 3). The UCE phylogeny also suggests Gephyrocharax is paraphyletic with G. valencia Eigenmann, 1920 more closely related to Corynopoma riisei Gill, 1858 than to G. venezuelae Schultz, 1944, and G. machadoi Ferreira et al., 2018 and Pseudocorynopoma *stanleyi* Malabarba *et al.*, 2020 are sister-species (Fig. 3).

Planaltininae Oliveira and Souza, new subfamily

ZooBank: urn:lsid:zoobank.org:act:06E06366-6662-4FB0-AF63-6CD306320A2B.

Type genus: Planaltina Böhlke, 1954.

Included genera: Lepidocharax Ferreira et al., 2011 and Planaltina.

Definition: The least inclusive crown clade that contains *Planaltina myersi* Böhlke, 1954 and *Lepidocharax diamantina* Ferreira *et al.*, 2011. This is a minimum-crown-clade definition. See Figure 3 for a reference phylogeny of Planaltininae.

Etymology: Planaltina, Goiás, Brazil is the type locality of *Planaltina myersi*.

Remarks: Previous authors proposed that *Planaltina* is more closely related to *Acrobrycon* and *Diapoma* and is a sublineage of the Diapomini (Weitzman and Menezes 1998, Thomaz *et al.* 2015). Alternatively, Mirande (2019) proposed Creagrutini as containing *Carlastyanax* Géry, 1972, *Creagrutus* Günther, 1864, *Microgenys, Lepidocharax*, and *Planaltina*. Ferreira *et al.* (2021) placed *Lepidocharax* and *Planaltina* in Diapomini as the sistergroup of the remaining genera and identified 11 morphological synapomorphies for the clade. The UCE phylogeny resolves

Planaltina and *Lepidocharax* as a monophyletic group and the sister-lineage of a clade containing Creagrutinae and Diapominae (Fig. 3); thus, we describe a new subfamily Planaltininae that contains *Lepidocharax* and *Planaltina*. Species of Planaltininae are endemic to the Brazilian Shield in upland river systems of the Paraná, São Francisco, Paraguaçu, and Tocantins (Fig. 3).

Creagrutinae Miles, 1943, new usage

Type genus Creagrutus Günther, 1864.

Included genera: Caiapobrycon Malabarba and Vari, 2000, *Creagrutus*, and *Microgenys*. Not sampled: *Carlastyanax*.

Definition: The least inclusive crown clade that contains *Creagrutus muelleri* (Günther 1859), *Caiapobrycon tucurui* Malabarba and Vari, 2000, and *Microgenys minuta* Eigenmann, 1913. This is a minimum-crown-clade definition. See Figure 3 for a reference phylogeny of Creagrutinae. Although not included in the reference phylogeny, *Creagrutus muelleri* resolves in a clade with other species of *Creagrutus* in a phylogenetic analysis of morphological characters (Vari and Harlod 2001).

Etymology: From the ancient Greek κρεάγρευτος (kıˈiːɡɹuːtˈɑːs) meaning tearing off flesh.

Remarks: Mirande *et al.* (2013) and Thomaz *et al.* (2015) resolved a clade containing *Creagrutus* and *Carlastyanax*. Mirande (2019) later expanded Creagrutini to include *Planaltina, Lepidocharax*, and *Microgenys* with two subclades: one with *L. burnsi* Ferreira *et al.*, 2011 and *P. britskii* Menezes *et al.*, 2003 (see Planaltininae), and the second containing *Microgenys*, *Carlastyanax*, and *Creagrutus*. Ferreira *et al.* (2021) delimited Creagrutini to include *Carlastyanax*, *Creagrutus*, and *Microgenys* that was supported with 12 morphological synapomorphies. Our UCE phylogeny resolves *Microgenys* as the sister-lineage of a paraphyletic *Creagrutus* (Fig. 3). *Caiapobrycon tucurui* is nested within *Creagrutus* (Fig. 3). We delimit Creagrutinae to include the genera *Caiapobrycon, Creagrutus, Microgenys*, and *Carlastyanax*.

Diapominae Eigenmann, 1909, new usage

Type genus: Diapoma Cope, 1894.

Included genera: Attonitus Vari and Ortega, 2000, Aulixidens Böhlke, 1952, Boehlkea, Bryconamericus, Ceratobranchia, Diapoma, Knodus, Phallobrycon, Piabarchus, Piabina Reinhardt, 1867, and Rhinopetitia. Not sampled: Bryconacidnus, Hypobrycon, Monotocheirodon Eigenmann and Pearson, 1924, Nantis Mirande et al., 2004, Odontostoechus Gomes, 1947, Othonocheirodus Myers, 1927, and Rhinobrycon.

Definition: The least inclusive crown clade that contains *Diapoma speculiferum* Cope 1894, *Diapoma alburnum* (Hensel, 1870), and *Knodus breviceps* (Eigenmann, 1908). This is a minimum-crown-clade definition. See Figure 3 for a reference phylogeny of Diapominae. Although *Diapoma speculiferum* is not included in the reference phylogeny it resolves with other species of *Diapoma* in phylogenies inferred from molecular and

combined molecular and morphological datasets (Thomaz *et al.* 2015, Ferreira *et al.* 2021).

Etymology: From the ancient Greek $\delta_{l\dot{\alpha}}(d'aI_{\bar{a}})$ meaning through and $\pi \tilde{\omega} \mu \alpha (p' \tilde{ov} m_{\bar{a}})$ meaning lid or cover.

Remarks: Weitzman and Menezes (1998) identified a clade containing Diapoma, Acrobrycon, and Planaltina. Thomaz et al. (2015) proposed a delimitation of Diapomini that included Attonitus, Bryconamericus, Bryconacidnus, Ceratobranchia, Cyanocharax, Diapoma, Hypobrycon, Knodus, Nantis, Odontostoechus, Piabina, Piabarchus, Rhinobrycon, and tentatively Lepidocharax and Planaltina. Ferreira et al. (2021) resolved a monophyletic Diapomini supported by five morphological synapomorphies and two subclades: one containing Bryconadenos Weitzman et al., 2005, Knodus, Phallobrycon, and Rhinobrycon, and a second containing Attonitus, Ceratobranchia, Bryconacidnus, Bryconamericus, Diapoma, Monotocheirodon, Nantis, Odontostoechus, Piabina, and Rhinopetitia.

The UCE phylogeny resolves two monophyletic groups: the first containing a paraphyletic *Bryconamericus*, *Diapoma*, a paraphyletic *Piabarchus*, and *Piabina*, and the second containing *Attonitus*, *Aulixidens*, *Boehlkea*, *Bryconamericus macarenae*, *Ceratobranchia*, a paraphyletic *Knodus*, *Phallobrycon*, and *Rhinopetitia* (Fig. 3). Given the disparities in clade composition between UCE phylogeny and that of Ferreira *et al.* (2021), we consider a deeper discussion of these relationships premature at this time.

Bryconadenos was treated as a synonym of Knodus (Thomaz et al. 2015). Although the type species of Knodus, K. meridae Eigenmann, 1911, was not sampled in the UCE phylogeny, Bryconadenos tanaothoros Weitzman et al., 2005 is nested within Knodus, supporting Thomaz et al.'s hypothesis that Bryconadenos is a junior synonym of Knodus (Thomaz et al. 2015).

Diapominae are the most species-rich clade of Stevardiidae, containing two of the family's largest genera: *Bryconamericus* (54 species) and *Knodus* (39 species) (Fricke *et al.* 2023), indicating that numerous taxonomic issues at the specieslevel remain unresolved (García-Melo *et al.* 2019, Malabarba *et al.* 2021). Following Ferreira *et al.* (2021) and Thomaz *et al.* (2015), some genera not sampled in UCE phylogeny were provisionally included in Diapominae: *Bryconacidnus, Hypobrycon, Monotocheirodon, Nantis, Odontostoechus, Othonocheirodus,* and *Rhinobrycon.* The UCE phylogeny indicates the diversification of *Bryconamericus, Diapoma, Piabarchus,* and *Piabina* may be associated with the expansion from Paraguay basin to the upper Paraná, Uruguay, and São Francisco basins (Fig. 3).

Characidae Latreille, 1825, new usage

Type genus: Charax Scopoli, 1777.

Included subfamilies: Aphyocharacinae, Characinae, Cheirodontinae, Exodontinae, and Tetragonopterinae.

Definition: The least inclusive crown clade that contains *Charax gibbosus* (Linnaeus, 1758), *Aphyocharax pusillus* Günter, 1868, *Cheirodon pisciculus* Girard, 1855, *Exodon paradoxus* Müller and Troschel, 1844, and *Tetragonopterus argenteus* Cuvier 1816. This is a minimum-crown-clade definition. See Figure 4 for a reference phylogeny of Characidae.

Etymology: From the ancient Greek $\chi \dot{\alpha} \rho \alpha \xi$ (k' α :luæks) as a name for species of Sparidae that exhibit teeth on the oral jaws (Thompson 1947: 284–5).

Remarks: There are no known morphological synapomorphies for Characidae; however, most species in the clade have a pseudotympanum, a hiatus of the hypaxial muscle along the anterior portion of the gas bladder (Malabarba 1998; Mattox and Toledo-Piza 2012). The pseudotympanum exhibits different shapes, muscles, and rib delimitation among the Aphyocharacinae, Characinae, Cheirodontinae, Hyphessobrycon (cf. Carvalho 2011), and some species of Tetragonopterinae (Malabarba 1998, Mattox and Toledo-Piza 2012). A pseudotympanum is also present in members of Alestidae, Crenuchidae, Cynodontidae, and Serrasalmidae (Zanata and Vari 2005; Mattox and Toledo-Piza 2012, Zanata and Camelier 2014, 2015) and may represent a plesiomorphic condition in Characiformes as it is present in cithariniforms (Vari 1979, Mattox and Toledo-Piza 2012), siluriforms (Shibatta and Vari 2017, Slobodian et al. 2017, 2021), gymnotiforms (Dutra et al. 2015), and cypriniforms (e.g. Britz et al. 2021). However, additional investigations are needed to refine our understanding of this character across Characiformes and Ostariophysi.

Several authors have hypothesized a close relationship between Cheirodontinae and Aphyocharacinae based on morphological similarities (Eigenmann 1917, Géry 1977, Malabarba 1998). Alternatively, Mirande (2010) resolved Cheirodontinae as the sister-group of Aphyoditeinae and this clade as the sistergroup of Aphyocharacinae. Molecular phylogenetic studies consistently resolve Cheirodontinae and Aphyocharacinae as a monophyletic group (Calcagnotto *et al.* 2005, Javonillo *et al.* 2010, Oliveira *et al.* 2011, Tagliacollo *et al.* 2012, Melo *et al.* 2016).

In a pre-cladistic study, Géry (1964c) hypothesized a close relationship between Characinae and Exodontinae by proposing the tribe Exodontidi, which included *Exodon*, *Roeboexodon*, and *Roeboides* Günther, 1864. Molecular phylogenies support a close relationship between the Characinae and Exodontinae (Javonillo *et al.* 2010, Oliveira *et al.* 2011, Melo *et al.* 2016), and phylogenomic studies resolve Exodontinae as the sister-lineage of a clade containing Tetragonopterinae and Characinae (Fig. 4; Betancur-R *et al.* 2019, Melo *et al.* 2022a, Souza *et al.* 2022).

Aphyocharacinae Eigenmann, 1909, new usage

Type genus: Aphyocharax Günther, 1868.

Included genera: Aphyocharax, Cyanogaster, Leptagoniates Boulenger, 1887, Paragoniates Steindachner, 1876, Phenagoniates Eigenmann and Wilson in Eigenmann et al., 1914, Prionobrama Fowler, 1913, Xenagoniates Myers, 1942. Not sampled: Amazonichthys Esguícero and Mendonça, 2023, and Aphyocharacidium.

Definition: The least inclusive crown clade that contains *Aphyocharax pusillus* Günther, 1868 and *Cyanogaster noctivaga* Mattox *et al.*, 2013. This is a minimum-crown-clade definition. See Figure 4 for a reference phylogeny of Aphyocharacinae. Species of *Amazonichthys* and *Aphyocharacidium* were not sampled in this study.

Etymology: From the ancient Greek ἀφύη (𝔅fī'æ), which is a name used by ancient authors for anchovies, smelts, silversides, and the goby *Aphia minuta* (Risso 1810) and χάραξ (k'α⊥ıæks) as a name for species of *Sparidae* that exhibit teeth on the oral jaws (Thompson 1947: 21–2, 284–5).

Remarks: Recent taxonomic treatments of Characidae included eight genera in the Aphyocharacinae: Paragoniates, Phenagoniates, Xenagoniates, Inpaichthys, Leptagoniates (not analysed), Rachoviscus Myers, 1926 (not analysed), Aphyocharax, and Prionobrama (Mirande 2009, 2010). Phylogenetic studies using molecular data or combined morphological and molecular characters demonstrate that Rachoviscus and Inpaichthys are not closely related to Aphyocharacinae (Oliveira et al. 2011), resolves Aphyocharacidium (latter identified as Hemigrammus cf. geisleri Zarske and Géry, 2007) within Aphyocharacinae (Tagliacollo et al. 2012), and resulted in a delimitation of Aphyocharacinae that includes Aphyocharacidium, Aphyocharax, Prionobrama, Paragoniates, Phenagoniates, Leptagoniates, and Xenagoniates supported by two dorsal-fin rays articulating with the first dorsal pterygiophore (Tagliacollo et al. 2012, Vari et al. 2016). More recently, the composition of Aphyocharacinae was expanded to include Axelrodia lindeae Géry, 1973 and 12 synapomorphies were identified for the clade (Mirande 2019); A. lindeae has been transferred to the newly described Amazonichthys (Esguícero and Mendonça 2023).

The phylogeny inferred from the UCE loci resolved Aphyocharax and Prionobrama as sister-lineages and a clade containing Paragoniates, Phenagoniates, Leptagoniates, and Xenagoniates (Fig. 4). A result not presented in other phylogenetic studies is the resolution of a clade in Aphyocharacinae that contains Cyanogaster noctivaga Mattox et al., 2013, four undescribed species of Cyanogaster (Leticia, Tapajós, Negro, and Apure), and a specimen previously identified as Hemigrammus geisleri (Fig. 4). Cyanogaster noctivaga was described as a miniature characid belonging to the Stevardiinae based on the presence of ii + 8 dorsal-fin rays and four teeth in the inner premaxillary series (Mattox et al. 2013). Phylogenetic analysis of morphological characters resolves Cyanogaster in the Stevardiinae (Mirande 2019). In the phylogenies inferred from the UCE loci, Cyanogaster was consistently resolved as the sister-lineage of all other species of Aphyocharacinae (Fig. 4). Considering that the type species of Hemigrammus (H. unilineatus Gill, 1858) is phylogenetically placed in the Pristellinae, we transfer Hemigrammus geisleri to the genus Cyanogaster as Cyanogaster geisleri, new combination (Fig. 4; Table 1). Aphyocharacidium remains unsampled in phylogenomic studies and thus with uncertain position and here tentatively included in Aphyocharacinae. Species of Aphyocharacinae are primarily distributed in Amazon-Orinoco-Guianas; Cyanogaster geisleri and Prionobrama paraguayensis (Eigenmann 1914) extend to the Paraguay basin of La Plata, and Phenagoniates to the trans-Andean region (Fig. 4).

Cheirodontinae Eigenmann 1915, new usage

Type genus: Cheirodon Girard, 1855.

Included genera: Acinocheirodon Malabarba and Weitzman, 1999, Aphyocheirodon Eigenmann, 1915, Cheirodon, Cheirodontops,



Figure 4. Phylogeny of Characidae and subfamilies Aphyocharacinae, Cheirodontinae, Exodontinae, Tetragonopterinae, and Characinae based on 1348 nuclear loci of ultraconserved elements (538 472 bp). Numbers near nodes represent bootstrap support.

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Table 1. Nomenclature	e changes at species-lev	rel proposed in this study.
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Subfamily	Names prior to this study	New combination
Aphyocharacinae	Hemigrammus geisleri	 Cyanogaster geisleri (Zarske and Géry, 2007)
Stygichthyinae	Deuterodon aphos	Myxiops aphos Zanata and Akama, 2004
	Deuterodon pelecus	Myxiops pelecus (Bertaco and Lucena, 2006)
Megalamphodinae	Hyphessobrycon bentosi	Megalamphodus bentosi (Durbin, 1908)
	Hyphessobrycon copelandi	Megalamphodus copelandi (Durbin, 1908)
	Hyphessobrycon epicharis	Megalamphodus epicharis (Weitzman and Palmer, 1997)
	Hyphessobrycon eques	Megalamphodus eques (Steindachner, 1882)
	Hyphessobrycon erythrostigma	Megalamphodus erythrostigmus (Fowler, 1943)
	Hyphessobrycon haraldschultzi	Megalamphodus haraldschultzi (Travassos, 1960)
	Hyphessobrycon khardinae	Megalamphodus khardinae (Zarske, 2008)
	Hyphessobrycon megalopterus	Megalamphodus megalopterus Eigenmann, 1915
	Hyphessobrycon micropterus	Megalamphodus micropterus Eigenmann, 1915
	Hyphessobrycon rosaceus	Megalamphodus rosaceus (Durbin, 1909)
	Hyphessobrycon socolofi	Megalamphodus socolofi (Weitzman, 1977)
	Hyphessobrycon sweglesi	Megalamphodus sweglesi Géry, 1961
	Moenkhausia pittieri	Makunaima pittieri (Eigenmann, 1920)
Stichonodontinae	Hyphessobrycon diastatos	Hasemania diastata (Dagosta, Marinho and Camelier, 2014)
	Hyphessobrycon negodagua	Hasemania negodagua (Lima and Gerhard, 2001)
	Jupiaba zonata	Moenkhausia zonata (Eigenmann, 1908)
Pristellinae	Aphyodite grammica	Hemigrammus grammicus (Eigenmann, 1912)
	Aphyodite apiaka	Hemigrammus apiaka (Esguícero and Castro, 2017)
	Aphyodite tupebas	Hemigrammus tupebas (Esguícero and Castro, 2017)
	Moenkhausia collettii	Hemigrammus collettii (Steindachner, 1882)
	Moenkhausia eigenmanni	Hemigrammus eigenmanni (Géry, 1964)
	Moenkhausia melogramma	Hemigrammus melogrammus (Eigenmann, 1908)
Thayeriinae	Hemigrammus aguaruna	Holopristis aguaruna (Lima, Correa and Ota, 2016)
	Hemigrammus guyanensis	Holopristis guyanensis (Géry, 1959)
	Hemigrammus haraldi	Holopristis haraldi (Géry, 1961)
	Hemigrammus neptunus	Holopristis neptunus (Zarske and Géry, 2002)
	Hemigrammus newboldi	Ramirezella newboldi Fernández-Yépez, 1949
	Hemigrammus ocellifer	Holopristis ocellifer (Steindachner, 1882)
	Hemigrammus pulcher	Holopristis pulcher (Ladiges, 1938)
	Hemigrammus skolioplatus	Bario skolioplatus (Bertaco and Carvalho, 2005)
	Moenkhausia australis	Bario australis (Eigenmann, 1908)
	Moenkhausia cosmops	Bario cosmops (Lima, Britski and Machado, 2007)
	Moenkhausia forestii	Bario forestii (Benine, Mariguela and Oliveira, 2009)
	Moenkhausia oligolepis	Bario oligolepis (Günther, 1864)
	Moenkhausia pyrophthalma	Ramirezella pyrophthalma (Costa, 1994)
	Moenkhausia sanctaefilomenae	Bario sanctaefilomenae (Steindachner, 1907)
	Moenkhausia uirapuru	Bario uirapuru (Ohara and Lima, 2015)
Grundulinae	Astyanax moorii	Astyanacinus moorii (Boulenger, 1892)
Acestrorhamphinae	Andromakhe saguazu	Psalidodon saguazu (Casciotta, Almirón and Azpelicueta, 2003)
	Astyanax alleni	Psalidodon alleni (Eigenmann and McAtee, 1907)
	Astyanax biotae	Psalidodon biotae (Castro and Vari, 2004)
	Astyanax cremnobates	Psalidodon cremnobates (Bertaco and Malabarba, 2001)
	Astyanax dissimilis	Psalidodon dissimilis (Garavello and Sampaio, 2010)
	Astyanax goyanensis	Psalidodon goyanensis (Miranda Ribeiro, 1944)
	Astyanax henseli	Psalidodon henseli (Melo and Buckup, 2006)
	Astyanax laticeps	Psalidodon laticeps (Cope, 1894)
	Astyanax magdalenae	Ctenobrycon magdalenae (Eigenmann and Heinn, 1916)
	Astyanax minor	Psalidodon minor (Garavello and Sampaio, 2010)

Subfamily	Names prior to this study	New combination
	Astyanax togoi	Psalidodon togoi (Miquelarena and López, 2006)
	Astyanax varzeae	Psalidodon varzeae (Abilhoa and Duboc, 2007)
	Astyanax vermilion	Psalidodon vermilion (Zanata and Camelier, 2009)
	Genycharax tarpon	Astyanax tarpon (Eigenmann, 1912)
	Hasemania kalunga	Psalidodon kalunga (Bertaco and Carvalho, 2010)
	Hasemania uberaba	Psalidodon uberaba (Serra and Langeani, 2015)
	Hyphessobrycon balbus	Psalidodon balbus (Myers, 1927)
	Hyphessobrycon hamatus	Psalidodon hamatus (Bertaco and Malabarba, 2005)
	Hyphessobrycon uaiso	Psalidodon uaiso (Carvalho and Langeani, 2013)
	Moenkhausia pirauba	Astyanax pirauba (Zanata, Birindelli and Moreira, 2010)
	Psellogrammus kennedyi	Ctenobrycon kennedyi (Eigenmann, 1903)

Table 1. Continued

Heterocheirodon Malabarba, 1998, Kolpotocheirodon Malabarba and Weitzman, 2000, Macropsobrycon Eigenmann, 1915 (in part), Nanocheirodon Malabarba, 1998, Odontostilbe Cope, 1870, Prodontocharax, Protocheirodon Vari et al., 2016, Pseudocheirodon Meek and Hildebrand, 1916, Saccoderma Schultz, 1944, and Serrapinnus Malabarba, 1998. Not sampled: Compsura Eigenmann, 1915 and Ctenocheirodon Malabarba and Jerep, 2012.

Definition: The least inclusive crown clade that contains *Cheirodon pisciculus* Girard 1855 and *Protocheirodon pi* (Vari 1978). This is a minimum-crown-clade definition. See Figure 4 for a reference phylogeny of Cheirodontinae.

Etymology: From the ancient Greek χειρός (k'allouz) meaning hand and $\delta\delta\omega v$ ('oudu:n) meaning tooth.

Remarks: Cheirodontinae are consistently supported as a monophyletic group in molecular (Ortí and Meyer 1997, Calcagnotto et al. 2005, Mirande 2009, 2010, Javonillo et al. 2010, Mariguela et al. 2013) and morphological studies (Malabarba 1998, Mirande 2019). A proposal to include the miniature Amazonspinther dalmata in Cheirodontinae (Bührnheim et al. 2008) is countered by molecular phylogenetic studies that resolved Amazonspinther and Spintherobolus as the sister-lineage to a clade that contains all other species of Characidae, Stevardiidae, and Acestrorhamphidae (Oliveira et al. 2011, Mariguela et al. 2013). Molecular phylogenetic analysis led to the description of Protocheirodon (Vari et al. 2016), which is consistently resolved as the sister-lineage of all other species of Cheirodontinae (Fig. 4; Vari et al. 2016, Melo et al. 2022a). The phylogeny inferred from the UCE loci includes 14 of the 16 extant genera of Cheirodontinae (Fig. 4). The inclusion of Compsura and Ctenocheirodon in Cheirodontinae is based on previous morphological and molecular studies (Malabarba 1998, Malabarba and Jerep 2012, Mariguela *et al.* 2013).

Exodontinae Fowler, 1958, new usage

Type genus: Exodon Müller and Troschel, 1845.

Included genera: Bryconexodon Géry, 1980, Exodon, Roeboexodon.

Definition: The least inclusive crown clade that contains *Exodon paradoxus* Müller and Troschel, 1844 and *Bryconexodon juruenae* Géry, 1980. This is a minimum-crown-clade definition. See Figure 4 for a reference phylogeny of Exodontinae.

Etymology: From the ancient Greek $\xi \omega$ ($\varepsilon g z' o \overline{v}$) meaning on the outside and $\delta \delta \omega v$ ($o \overline{v} d \alpha : n$) meaning tooth.

Remarks: The tribe Exodonidi was first characterized by 'the presence of external denticles on outer surface of jaws, clavicle not notched to receive pectoral base, and short anal fin with less than 30 rays' (Fowler 1958). Phylogenetic analyses of molecular and morphological characters resolve a clade containing three lepidophagous characid genera Bryconexodon, Exodon, and Roeboexodon that is delimited here as Exodontinae (Mirande 2009, 2010, Mattox and Toledo-Piza 2012, Melo et al. 2022a). Within Exodontinae, all three possible relationships among the three genera are resolved: Roeboexodon as the sisterlineage of all other exodontines (Mirande 2010), Exodon as the sister to all other exodontines (Mattox and Toledo-Piza 2012), and Bryconexodon the sister-lineage of the clade containing Roeboexodon and Exodon (Fig. 4; Melo et al. 2022a). Exodontinae are supported by 12 morphological synapomorphies, some of which are associated with reinforcement of the anterior portion of the head and are probably associated with their peculiar way of plucking scales (Mattox and Toledo-Piza 2012). Species of Exodontinae are distributed in the Amazon-Orinoco-Guianas region (Fig. 4).

Tetragonopterinae Gill, 1858

Type genus: Tetragonopterus Cuvier, 1816. Included genus: *Tetragonopterus*.

Definition: The least inclusive crown clade that contains *Tetragonopterus argenteus* Cuvier, 1816 and *Tetragonopterus georgiae* (Géry, 1965). This is a minimum-crown-clade definition. See Figure 4 for a reference phylogeny of Tetragonopterinae.

Etymology: From the ancient Greek τετρά- (t'ετ.ə) meaning four, γωνία (g'oʊniə) meaning angle, and πτερόν (t'ε.ia:n) meaning fin or wing.

Remarks: The initial description of Tetragonopterinae dates to the 19th century and traditionally included many species of Characidae (Gill 1858, Géry 1977). The composition changed with the publication of the Checklist of the Freshwater Fishes of South and Central America (Reis et al. 2003), where Tetragonopterinae was limited to the genus Tetragonopterus (Reis 2003). The molecular studies in the early 21st century have resulted in recognized species' diversity in Tetragonopterus increasing from two to 13 species (Melo et al. 2011, Silva et al. 2013, 2016, Urbanski et al. 2018). The monophyly of Tetragonopterus is supported in molecular phylogenies and morphological studies (Melo et al. 2016, 2022, Mirande 2019), and relaxed clock analyses indicate the lineage diversified in the Miocene (Melo et al. 2016). The relationships among species of Tetragonopterus in the UCE phylogeny differ from those inferred from Sanger-sequenced datasets (Fig. 4), specifically the resolution of *T. argenteus* as the sisterspecies of a clade containing T. araguaiensis Silva et al., 2013 and T. ommatus Silva et al., 2016 (Fig. 4). Tetragonopterinae and Exodontinae exhibit a similar biogeographic pattern with many species distributed on the Brazilian Shield; T. argenteus is the only species distributed in the La Plata basin (Fig. 4).

Characinae Latreille, 1825, new usage

Type genus: Charax Scopoli, 1777.

Included genera: Acanthocharax Eigenmann, 1912, Acestrocephalus Eigenmann, 1910, Atopomesus, Charax, Cynopotamus Valenciennes, 1850, Galeocharax Fowler, 1910, Phenacogaster, and Roeboides. Not sampled: Microschemobrycon.

Definition: The least inclusive crown clade that contains *Charax* gibbosus (Linnaeus, 1758), *Atopomesus pachyodus* Myers, 1927, *Phenacogaster pectinata* (Cope, 1870), and *Acestrocephalus anomalus* (Steindachner, 1880). This is a minimum-crown-clade definition. See Figure 4 for a reference phylogeny of Characinae.

Etymology: From the ancient Greek $\chi \dot{\alpha} \rho \alpha \xi$ (k' α :luæks) as a name for species of Sparidae that exhibit teeth on the oral jaws (Thompson 1947: 284–5).

Remarks: A group that includes *Charax*, the type genus of Characiformes, and small to medium-sized predators such as *Acanthocharax*, *Acestrocephalus*, *Cynopotamus*, *Galeocharax*, and *Roeboides* have been treated as closely related prior to the application of Hennigian phylogenetic systematics (Howes 1976, Géry 1977). Phylogenetic analysis of morphological characters led to a delimitation of Characinae that included *Phenacogaster*, *Priocharax* Weitzman and Vari, 1987, and six genera of heterocharacins (Lucena 1998) currently classified in Acestrorhynchidae (Oliveira *et al.* 2011). Subsequent studies identified a number of morphological synapomorphies, removed the heterocharacins, and added *Microschemobrycon* to the Characinae (Mirande 2009, 2010, 2019, Mattox and Toledo-Piza 2012).

Phylogenomic analysis of UCE loci results in the resolution of four major lineages of Characinae delimited as tribes (Souza *et al.* 2022): Phenacogasterini (*Phenacogaster*), Acanthocharacini (*Acanthocharax*), Cynopotamini (*Acestrocephalus, Cynopotamus,* and *Galeocharax*), and Characini (*Charax* and *Roeboides*). The UCE inferred phylogeny presented here is congruent with trees presented by Souza *et al.* (2022) and includes *Atopomesus* as the sister-lineage of all other species of Characinae (Fig. 4). Previous morphological phylogenetic studies resolved *Atopomesus* in the Spintherobolinae (Mirande 2019). To investigate this novel phylogenetic hypothesis, specimens from the sequenced lot of *Atopomesus* (LBP 23871) were prepared for muscle and skeleton observation, revealing that *Atopomesus* possesses four Characinae synapomorphies, i.e. characters 3, 7, 8, and 10 of Mattox and Toledo-Piza (2012). *Microschemobrycon* was not sampled in the UCE inferred phylogeny but is treated here as *incertae sedis* in Characinae following the results from combined multilocus and morphological phylogenetics (Mirande 2019).

Acestrorhamphidae Eigenmann, 1907

Type genus: Acestrorhamphus Eigenmann and Kennedy, 1903, junior synonym of *Oligosarcus* Günther, 1864.

Included subfamilies: Acestrorhamphinae, Grundulinae, Hyphessobryconinae, Jupiabinae, Megalamphodinae, Oxybryconinae, Pristellinae, Rhoadsiinae, Stethaprioninae, Stichonodontinae, Stygichthyinae, Thayeriinae, Trochilocharacinae, Tyttobryconinae, and an unnamed subfamily.

Definition: The least inclusive crown clade that contains Oligosarcus argenteus Günther, 1864, Grundulus bogotensis (Humboldt, 1821), Rhoadsia altipinna Fowler, 1911, Thayeria obliqua Eigenmann, 1908, Hyphessobrycon compressus (Meek, 1904), Tyttobrycon xeruini Géry, 1973, Jupiaba poranga Zanata, 1997, Pristella maxillaris (Ulrey, 1894), Stethaprion erythrops Cope, 1870, Stichonodon insignis (Steindachner, 1876), Megalamphodus megalopterus Eigenmann, 1915, Stygichthys typhlops Brittan and Böhlke, 1965, Trochilocharax ornatus Zarske, 2010, and Oxybrycon parvulus Géry, 1964. This is a minimumcrown-clade definition. See Figures 5–7 for a reference phylogeny of Acestrorhamphidae.

Etymology: From the ancient Greek ἄκεστρα (' α :kɛstɹə) meaning a darning needle and ῥάμφος (ι' æmfoυz) meaning curved beak.

Remarks: The presence of a very large metacentric pair of chromosomes, at least two times bigger than the second chromosome pair, is a putative synapomorphy for Acestrorhamphidae (Sánchez-Romero et al. 2015). Studying Rhoadsia altipinna, Sánchez-Romero *et al.* (2015) discovered 2n = 50 chromosomes with the first pair being very large metacentric chromosomes that are at least twice as large as the second pair. The authors concluded, based on all available cytogenetic information for characids, that this large pair 1 is present in all karyotyped Clade C species but not in any other karyotyped characid species. The large metacentric pair is present in more than 100 species of Acestrorhamphidae and absent in more than 50 species of Stevardiidae and Characidae s.s. (Sánchez-Romero et al. 2015). We hypothesize that this large first chromosome pair represents a derived condition and is, therefore, synapomorphic for Acestrorhamphidae.

Three additional synapomorphies of Acestrorhamphidae include: interrupted lateral line, three or fewer maxillary teeth, and three or four unbranched rays articulating with first dorsal fin pterygiophore (Mirande 2019). Additionally, the majority of species of Acestrorhamphidae have two rows of premaxillary teeth with typically five teeth in the inner row, nine branched dorsal-fin rays, and anterior branch of laterosensory canal of sixth infraorbital absent, but recognized that 'the huge diversity of this clade precludes any diagnosis based on exclusive characters, but the combination of these three characters with the listed synapomorphies should be useful to recognize a species of this subfamily' (Mirande 2019).

Phylogenetic studies using Sanger-sequenced mitochondrial and nuclear genes (Javonillo *et al.* 2010, Oliveira *et al.* 2011, Mariguela *et al.* 2013, Melo *et al.* 2016), total evidence analyses (Mirande 2019), and analysis of phylogenomic datasets (Arcila *et al.* 2017, Betancur-R *et al.* 2019, Melo *et al.* 2022a; present study) resolve Acestrorhamphidae as a monophyletic group. Acestrorhamphidae has been labelled as 'clade C' or 'Stethaprioninae' in previous phylogenetic studies (Javonillo *et al.* 2010, Oliveira *et al.* 2011, Mirande 2019). The name Stethaprioninae was proposed by Eigenmann (1907) in a paper published in December of that year, while Eigenmann *et al.* (1907) published the name Acestrorhamphinae in July of 1907 (Van der Laan *et al.* 2014). Thus, we recognize Acestrorhamphidae as a valid family-group name, with Acestrorhamphus Eigenmann and Kennedy (1903) (= Oligosarcus) as the type genus.

Given the species-richness and the phylogenetic relationships presented in Figures 5–7, we classify species of Acestrorhamphidae among 15 subfamilies. Several genera, including *Astyanax*, *Hemigrammus*, *Hyphessobrycon*, *Jupiaba*, and *Moenkhausia*, have long been resolved as polyphyletic (Oliveira *et al.* 2011, Mirande 2019, Melo *et al.* 2022a), a result corroborated in the UCE phylogeny (Figs 5–7). Future revisionary work on the taxonomy of Acestrorhamphidae will require the study of a higher number of species to establish monophyletic genera, which is beyond the scope of this study.

Oxybryconinae Melo, Mattox & Oliveira, new subfamily

ZooBank: urn:lsid:zoobank.org:act:1F86C7A9-015C-4CC6-9132-9C11CFD4E80E.

Type genus: Oxybrycon Géry, 1964.

Included genus: Oxybrycon.

Etymology: From the ancient Greek ὀξύς (h'eikeis) meaning sharp and βρύκω (bu'ukau) meaning to bite.

Remarks: The genus and species *Oxybrycon parvulus* were described by Géry (1964b), who compared it with *Leptobrycon* Eigenmann, 1915 and *Macropsobrycon*. *Oxybrycon* was subsequently included in the informal group Aphyoditeina (Géry 1973) that was elevated as the subfamily Aphyoditeinae (Mirande 2010). Lima *et al.* (2018: 101) summarized the main morphological features of *Oxybrycon* as: 'small adult body size; elongate body shape; large dentary; distinctly upturned mouth; teeth conical, tiny; two tooth rows on the dentary; maxilla

toothed; small pseudotympanum present; (...) anal fin very short, with 10–13 branched rays; lateral line not complete, with 2–3 pored scales (...)'. *Oxybrycon parvulus* is considered a miniature species (*sensu* Weitzman and Vari 1988).

In the UCE inferred phylogeny, *Oxybrycon* is resolved as the sister-lineage of all remaining Acestrorhamphidae (Fig. 5), requiring the recognition of a new subfamily, Oxybryconinae. In the maximum likelihood inferred phylogeny, *Oxybrycon parvulus* is on a relatively long branch (Supporting Information, Figs S1–S3), as is the case with other miniature species included in the UCE phylogenomic analyses (e.g. *Trochilocharax*).

Trochilocharacinae Zarske, 2010, new usage

Included genus: Trochilocharax.

Type genus: Trochilocharax Zarske, 2010.

Etymology: From the ancient Greek τροχιλία (t₁οῦk' Iliə) meaning a pulley and χάραξ (k'α: J.aæks) as a name for species of *Sparidae* that exhibit teeth on the oral jaws (Thompson 1947: 284–5).

Remarks: The genus and species Trochilocharax ornatus were described based on aquarium specimens from Peru (Zarske 2010). Trochilocharax ornatus is a very distinctive characid due to its small size (maximum reported length: 17 mm standard lenght), absence of body scales (except for a pouch scale in the caudal fin of males), and highly pronounced sexual dimorphism, which includes the presence of numerous extraoral conical teeth on the premaxillary and dentary in males (Zarske 2010). Morphological comparisons between Trochilocharax and several genera of Stevardiinae (Tyttocharax, Argopleura, Xenurobrycon, Iotabrycon, Scopaeocharax, Ptychocharax, and *Chrysobrycon*) led to the classification of *Trochilocharax ornatus* as the only species in the tribe Trochilocharacini within Stevardiinae (Zarske 2010). Among characiforms, the presence of a pouch scale is unique to some genera of Stevardiidae, and the presence of extraoral conical teeth in mature males is unique to species of Tyttocharax. The UCE phylogeny demonstrates that *Trochilocharax* is a deeply branching monotypic lineage that is resolved as the sister-group of a clade that contains Stygichthyinae, Megalamphodinae, Stichonodontinae, an unnamed subfamily, Stethaprioninae, Pristellinae, Jupiabinae, Tyttobryconinae, Hyphessobryconinae, Thayeriinae, Rhoadsiinae, Grundulinae, and Acestrorhamphinae (Figs 5–7). Based on the resolution of the UCE phylogeny, we elevate Trochilocharacini to the subfamily-level Trochilocharacinae to include Trochilocharax (Fig. 5). Trochilocharax ornatus and *Oxybrycon parvulus* are both endemic to the Amazon basin (Fig. 5), suggesting that Amazonia might have been the location of the initial diversification of the species and lineages that comprise Acestrorhamphidae.

Stygichthyinae Géry, 1972, new usage

Type genus: Stygichthys Brittan and Böhlke, 1965.

Included genera: Astyanax (in part), Coptobrycon, Deuterodon, Myxiops Zanata and Akama, 2004, and Stygichthys.



Figure 5. Phylogeny of Acestrorhamphidae and subfamilies Oxybryconinae, Trochilocharacinae, Stygichthyinae, Megalamphodinae, and Stichonodontinae based on 1348 nuclear loci of ultraconserved elements (538 472 bp). Numbers near nodes represent bootstrap support.



Figure 6. Phylogeny of Acestrorhamphidae and subfamilies Stethaprioninae, Pristellinae, Jupiabinae, Tyttobryconinae, and Hyphessobryconinae based on 1348 nuclear loci of ultraconserved elements (538 472 bp). Numbers near nodes represent bootstrap support.



Figure 7. Phylogeny of Acestrorhamphidae and subfamilies Thayeriinae, Rhoadsiinae, Grundulinae, and Acestrorhamphinae based on 1348 nuclear loci of ultraconserved elements (538 472 bp). Numbers near nodes represent bootstrap support.

Definition: The least inclusive crown clade that contains *Stygichthys typhlops, Astyanax mutator* Eigenmann, 1909, and *Deuterodon iguape* Eigenmann, 1907. This is a minimum-crown-clade definition. See Figure 5 for a reference phylogeny of Stygichthyinae.

Etymology: The River Styx is the main river in the Underworld of ancient Greek mythology.

Remarks: Phylogenetic analysis of the UCE dataset resolves Stygichthyinae as monophyletic and the sister-lineage of all other species of Acestrorhamphidae, except for *Trochilocharax ornatus* and *Oxybrycon parvulus* (Fig. 5). Monophyly of Stygichthyinae was supported in previous phylogenomic studies, but with more limited taxon sampling (Betancur-R *et al.* 2019, Melo *et al.* 2022a).

Within Stygichthyinae, the UCE inferred phylogeny includes a clade with three species provisionally classified as *Astyanax* that comprise a new and unnamed genus: *Astyanax* sp. Kuribrong that is probably an undescribed species with a very similar pattern as exhibited in *A. wappi* Valenciennes in Cuvier and Valenciennes, 1850, and *Astyanax mutator* Eigenmann 1909 that, contrary to a previous hypothesis, is not resolved in *Deuterodon* (Terán *et al.* 2020). *Hyphessobrycon eos* Durbin, 1909 is probably an unnamed genus. The Brazilian blind characid *Stygichthys typhlops* and *Coptobrycon bilineatus* (Ellis, 1911) are both deeply branching monotypic lineages in Stygichthyinae. Based on morphological characters, *Coptobrycon* was suggested to be related to *Grundulus* Valenciennes in Cuvier and Valenciennes, 1846 (Langeani and Serra 2010), but the lineages are distantly related in the UCE phylogeny (Figs 5, 7).

The two species of *Myxiops* [*Myxiops aphos* Zanata and Akama, 2004 and Myxiops pelecus (Bertaco and Lucena, 2006), new combination (former Astyanax pelecus); Table 1] are resolved as a monophyletic group and the sister-lineage of *Deuterodon*. The genus Myxiops was described based on an exclusive combination of morphological characteristics (Zanata and Akama 2004). Analysis of morphological characters resulted in phylogenies where species of Myxiops were nested in Deuterodon (Terán et al. 2020). Given the relationships inferred from the UCE loci, we revalidate Myxiops (Fig. 5; Table 1). Similarly, Terán et al. (2020) found *M. aphos* and *M. pelecus* as belonging to a monophyletic clade reinforcing the new combination *Myxiops pelecus*. Eigenmann (1907) described *Deuterodon* distinguishing it from other characids by the number and position of premaxillary teeth. Our results corroborate the expansion of Deuterodon to include several species traditionally classified in Astyanax (Terán et al. 2020). All species of Deuterodon are found in the Atlantic rainforest zone, mainly in coastal rivers flowing directly into the Atlantic Ocean (Fig. 5).

Megalamphodinae Carvalho, Lima & Melo, new subfamily

ZooBank: urn:lsid:zoobank.org:act:5366C168-9D5A-4C10-83BC-1CC92D99A05A.

Type genus: Megalamphodus Eigenmann, 1915.

Included genera: Axelrodia, Brittanichthys Géry, 1965, Hemigrammus (in part), Makunaima Terán et al., 2020, Megalamphodus, Paracheirodon Géry, 1960, and Petitella Géry and Boutière, 1964.

Definition: The least inclusive crown clade that contains *Megalamphodus megalopterus* and *Hemigrammus stictus* (Durbin, 1909). This is a minimum-crown-clade definition. See Figure 5 for a reference phylogeny of Megalamphodinae.

Etymology: From the ancient Greek μεγαλάμφοδος $(m_1 \varepsilon g_3)$ lemf \overrightarrow{ovdovz}) meaning with spacious ways.

Remarks: Megalamphodinae are presented as a new subfamily that includes three major clades: a lineage comprising Axelrodia stigmatias Fowler, 1913 (type species of the genus), Petitella georgiae Géry and Boutière, 1964 (type species of the genus), P. bleheri Géry and Mahnert, 1986, Hemigrammus stictus (Durbin, 1909), Brittanichthys axelrodi Géry, 1965, three species of Paracheirodon, species of Makunaima, and species of Megalamphodus (Fig. 5). Hemigrammus stictus is a new and undescribed genus from Amazon-Orinoco-Guianas (Melo et al. in prep.). The genus Makunaima was described to include the species M. guaporensis (Eigenmann, 1911), M. guianensis (Eigenmann, 1909), and M. multidens (Eigenmann, 1908) (Terán et al. 2020). The UCE phylogeny supports Makunaima as monophyletic and includes two additional species, Makunaima pittieri (Eigenmann, 1920) new combination, and probably an undescribed species from the Tapajós (Fig. 5; Table 1).

Megalamphodus was described by Eigenmann (1915) and classified in Cheirodontinae, based on the presence of a single tooth row in the premaxilla. Species subsequently added to Megalamphodus include M. uruguayensis Fowler, 1943, M. roseus Géry, 1960, and M. sweglesi Géry, 1961. Géry (1977) considered Megalamphodus as belonging to the 'Pristella-group', together with Pristella Eigenmann, 1908. However, Weitzman and Palmer (1997) noticed that large specimens of Megalamphodus megalopterus, the type species of Megalamphodus, possess two premaxillary tooth rows, and considered Megalamphodus a junior synonym of Hyphessobrycon.

The present phylogeny supports part of the monophyletic group of rosy tetras (sensu Weitzman and Palmer 1997); thus, we revalidate *Megalamphodus* to accommodate these species (Table 1), namely: M. bentosi (Durbin, 1908) (former Hyphessobrycon bentosi), M. copelandi (Durbin in Eigenmann, 1908) (former Hyphessobrycon copelandi), M. epicharis (Weitzman and Palmer, 1997) (former *Hyphessobrycon epicharis*), *M. eques* (Steindachner, 1882) (former Hyphessobrycon eques), M. erythrostigma (Fowler, 1943) (former Hyphessobrycon erythrostigma), M. haraldschultzi (Travassos, 1960) (former Hyphessobrycon haraldschultzi), M. khardinae (Zarske, 2008) (former Hyphessobrycon khardinae), *M. megalopterus* (former *Hyphessobrycon megalopterus*, type species), M. micropterus Eigenmann, 1915 (former Hyphessobrycon micropterus), M. socolofi (Weitzman, 1977) (former Hyphessobrycon socolofi), M. sweglesi (former Hyphessobrycon sweglesi), and two possibly new species: Megalamphodus cf. rosaceus and Megalamphodus sp. Leticia (Fig. 5; Table 1).

Species of *Megalamphodus* have been included in molecular and morphological phylogenetic analyses and the resolution of *M. megalopterus* in the 'rosy tetra clade' justifies the resurrection of *Megalamphodus* as a valid genus (Javonillo *et al.* 2010, Oliveira *et al.* 2011, Mirande 2019). The relationships among lineages of Megalamphodinae have been investigated with morphological and phylogenomic datasets (Terán *et al.* 2020, Melo *et al.* 2022a). A feature shared by the majority of species of Megalamphodinae is the presence of red, reddish, or reddish brown pigmentation over most or entire bodies. *Megalamphodus* can be diagnosed by the presence of a conspicuous black blotch on the dorsal fin. Most species of Megalamphodinae are distributed in cis-Andean northern South America (Fig. 5), and many are popular in the ornamental fish trade as, for example, *Axelrodia stigmatias*, *M. bentosi*, *M. eques*, *M. erythrostigma*, *M. sweglesi*, *Paracheirodon*, and *Petitella*.

Stichonodontinae Eigenmann, 1910, new usage

Type genus: Stichonodon Eigenmann, 1903.

Included genera: Hasemania, Hemigrammus (in part), Hyphessobrycon (in part), Moenkhausia (in part), Nematocharax Weitzman, Menezes and Britski, 1986, and Stichonodon.

Definition: The least inclusive crown clade that contains *Stichonodon insignis, Moenkhausia xinguensis* (Steindachner, 1882), and *Hyphessobrycon stegemanni* Géry, 1961. This is a minimum-crown-clade definition. See Figure 5 for a reference phylogeny of Stichonodontinae.

Etymology: From the ancient Greek $\sigma \tau (\chi \circ \varsigma (st'i:kovz) meaning a row or line of soldiers or a line of poetry and <math>\delta \delta \omega v$ ($\delta v (st'ovda:n)$ meaning tooth.

Remarks: The phylogeny inferred from the UCE loci resolves Stichonodontinae as monophyletic (Fig. 5), reflecting previous analysis of molecular characters (Mariguela et al. 2013, Betancur-R et al. 2019, Melo et al. 2022a). Moenkhausia is paraphyletic with one clade containing M. britskii Azevedo-Santos and Benine, 2016, M. grandisquamis (Müller and Troschel, 1845), M. pankilopteryx Bertaco and Lucinda, 2006, M. surinamensis Géry, 1965, M. xinguensis (Steindachner, 1882) (type species of Moenkhausia), and M. restricta Soares and Benine, 2019, whereas the other clade includes M. abyss Oliveira and Marinho, 2016, M. costae (Steindachner, 1907), M. dichroura (Kner, 1858), M. heikoi Géry and Zarske, 2004, M. intermedia Eigenmann, 1908, M. ischyognatha Petrolli and Benine, 2015, M. lata Eigenmann, 1908, M. sthenosthoma Petrolli and Benine, 2015, and Stichonodon insignis (type and only species of the genus). Moenkhausia lepidura (Kner, 1858), M. nigromarginata Costa, 1994, and Nematocharax venustus Weitzman et al., 1986 (type species of the genus) are successive branching lineages leading to a clade containing Hasemania, species currently classified with Hemigrammus and Moenkhausia, Hemigrammus sp. Leticia, Hyphessobrycon stegemanni Géry, 1961, and Hyphessobrycon sp. Araguaia (Fig. 5).

Similar to several characid genera, *Moenkhausia* is traditionally characterized by a combination of characters that include five multicuspid teeth in the inner premaxillary series, caudal fin partially covered by scales, and complete lateral line (Eigenmann 1917). *Hasemania* is diagnosed by the absence of the adipose fin (Ellis 1911). *Stichonodon* differs from other characids by the keel-shaped ventral area, two series of teeth in the premaxilla, and dentary in a single series of teeth (Eigenmann and Myers 1929). *Nematocharax* is diagnosed by a combination of elongate branched rays of the dorsal, pelvic, and anal fins, two rows of premaxillary teeth in adults, and an almost complete row of teeth along the free ventral maxillary border (Weitzman *et al.* 1986). However, all these characters are polymorphic in these lineages, requiring the proposal of new diagnoses based on shared derived features among species within these monophyletic groups. Stichonodontinae probably originated in the Amazon–Orinoco–Guianas with multiple transitions to La Plata and upland rivers of the São Francisco and Atlantic coastal drainages (Fig. 5).

Unnamed subfamily

Included genera: Hemigrammus (in part), Jupiaba (in part).

Definition: The least inclusive crown clade that contains *Jupiaba acanthogaster* (Eigenmann, 1911) and *Jupiaba scologaster* (Weitzman and Vari, 1986). This is a minimum-crown-clade definition. See Figure 6 for a reference phylogeny of the clade.

Remarks: Analysis of the UCE loci resolves a monophyletic group composed of Jupiaba acanthogaster, J. scologaster, Hemigrammus ora Zarske et al., 2006, and a new species tentatively identified as Jupiaba cf. essequibensis (Eigenmann, 1909) (Fig. 6). Species classified as Jupiaba and Hemigrammus are consistently resolved among several characid lineages (Oliveira et al. 2011, Mirande 2019, Melo et al. 2022a). The unnamed clade resolved in the UCE phylogeny does not include the type species of those genera Jupiaba poranga or Hemigrammus unilineatus (Gill 1858). We understand that smaller named clades are preferable for the sake of classification rather than sinking species in a large subfamily. In addition, this structure retains the existing family-group designations Stethaprioninae and Pristellinae. The type species of Jupiaba and Hemigrammus are not placed inside the clade, which thus requires the description of a new genus before designating the subfamily.

Stethaprioninae Eigenmann, 1907, new usage

Type genus: Stethaprion Cope, 1870.

Included genera: Brachychalcinus Boulenger, 1892, Ectrepopterus Fowler, 1943, Moenkhausia (in part), Orthospinus Reis, 1989, Poptella Eigenmann, 1908, and Stethaprion.

Definition: The least inclusive crown clade that contains *Stethaprion erythrops* and *Moenkhausia dasalmas* Bertaco *et al.,* **2011.** This is a minimum-crown-clade definition. See Figure 6 for a reference phylogeny of Stethaprioninae.

Etymology: From the ancient Greek στῆθος (st'i:θοῦz) meaning breast and πρίων (pɹ'aiən) meaning a saw.

Remarks: When first described, the subfamily Stethaprioninae included *Stethaprion, Fowlerina* Eigenmann, 1907 (= *Poptella*), and *Brachychalcinus* (Eigenmann, 1907). A taxonomic revision of Stethaprioninae added *Orthospinus franciscensis* (Eigenmann, 1914) to the subfamily and identified the presence of a bony spine

directed anteriorly, preceding the first dorsal-fin ray as a synapomorphy for the group (Reis 1989). Within Acestrorhamphidae, a predorsal spine is unique to Stethaprioninae; however, the trait is present in other lineages of Characiformes (as expanded pterygiophore or lepidotrichia e.g. Curimatidae, Prochilodontidae, and Serrasalmidae) (Reis 1989, Vari 1992, Castro and Vari 2004, Mirande 2010).

In the UCE phylogeny, *Moenkhausia dasalmas* is resolved as the sister-species of all other lineages of Stethaprioninae (Fig. 6). *Moenkhausia dasalmas* was described based on the presence of three unbranched and nine branched dorsal-fin rays (Bertaco *et al.* 2011). A more detailed study of the tiny first unbranched ray under the skin of *M. dasalmas* may be useful to establish its relationship with the anteriormost spine in the dorsal fin of the remaining Stethaprioninae. *Moenkhausia* does not resolve as a monophyletic group in the UCE phylogeny, indicating that *M. dasalmas* is probably a new and unnamed genus (Fig. 6).

Previous phylogenies inferred from multilocus DNA sequence and combined molecular and morphological datasets resolved Stethaprioninae as paraphyletic because *Gymnocorymbus* Eigenmann, 1908 (Pristellinae) was placed as the sister-lineage of a clade of Stethaprioninae containing *Brachychalcinus*, *Orthospinus, Poptella*, and *Stethaprion* (Oliveira *et al.* 2011, Benine *et al.* 2015, Mirande 2019). The UCE inferred phylogeny differs from previous phylogenetic analyses and taxonomic delimitations of Stethaprioninae in resolving both *Moenkhausia dasalmas* and *Ectrepopterus uruguayensis* (Fowler, 1943) as closely related to a clade containing *Stethaprion, Poptella*, *Brachychalcinus*, and *Orthospinus* (Fig. 6; Reis 1989, Oliveira *et al.* 2011, Benine *et al.* 2015).

Ectrepopterus was revalidated as distinct from *Hyphessobrycon* (*sensu* Eigenmann, 1918) due to the presence of numerous teeth on maxilla (Malabarba *et al.* 2012), a trait that is absent in all other species of Stethaprioninae (*sensu* Reis 1989) but present in several other species of the Acestrorhamphidae. Analysis of combined molecular and morphological datasets resulted in phylogenies grouping *E. uruguayensis, Hyphessobrycon moniliger* Moreira *et al.*, 2002, three species of *Jupiaba*, and other lineages of Stethaprioninae (Mirande 2019), suggesting future work may discover additional morphological traits consistent with the monophyly of Stethaprioninae. The phylogeny and geographic distribution of Stethaprioninae indicate that La Plata and the Brazilian Shield had an important role in the diversification of the clade (Fig. 6).

Pristellinae Géry and Boutière, 1964, new usage

Type genus: Pristella Eigenmann, 1908.

Included genera: Gymnocorymbus, Moenkhausia (in part), Hemigrammus (in part), and Pristella.

Definition: The least inclusive crown clade that contains *Pristella maxillaris* and *Gymnocorymbus thayeri* Eigenmann, 1908. This is a minimum-crown-clade definition. See Figure 6 for a reference phylogeny of Pristellinae.

Etymology: From the ancient Greek πρίστις (pu'Istiz) a name used by ancient Mediterranean authors for the largetooth saw-fish, *Pristis pristis* (Thompson 1947: 219).

Remarks: The delimitation of Pristellinae presented here includes *Hemigrammus unilineatus*, the type species of the genus, and was partially resolved in phylogenetic analyses as the '*Hemigrammus* clade' (Mirande 2009, 2010, 2019). The clade was characterized by homoplastic morphological characters: a dorsal bony process in the rhinosphenoid (Mirande 2009) and incomplete lateral line (Mirande 2010).

Within Pristellinae *Gymnocorymbus* is the sister-lineage of all other species in the clade (Fig. 6). In previous phylogenetic studies, *Gymnocorymbus* was resolved as closely related to other genera with a very deep body such as *Brachychalcinus*, *Orthospinus*, *Poptella*, *Stethaprion*, and *Stichonodon* (Javonillo *et al.* 2010, Mirande 2010, 2019, Oliveira *et al.* 2011, Benine *et al.* 2015). The phylogeny inferred from UCE loci strongly resolves *Gymnocorymbus* with other lineages of Pristellinae.

Lima *et al.* (2021) obtained a clade containing *Pristella* and *Bryconella pallidifrons* (Fowler 1946) as the sister-lineage of a clade comprising many of the species included in Pristellinae. In the phylogeny inferred from the UCE loci, *Pristella* and *H. erythrozonus* Durbin, 1909 are sister-lineages and they form the sister-group of species currently classified as *Moenkhausia* and *Hemigrammus* (Fig. 6).

In the UCE phylogeny, *Aphyodite grammica* Eigenmann, 1912 is sister to Hemigrammus microstomus Durbin, 1918 and nested in a clade of species currently classified as *Hemigrammus* (Fig. 6). Morphological phylogenetic analyses resolve Aphyodite as closely related to Atopomesus, Aphyocharacidium, Axelrodia, Leptobrycon, Microschemobrycon, Oxybrycon, Parecbasis, and Tyttobrycon Géry, 1973 (Mirande 2010, Esguícero and Castro 2016). However, molecular (Oliveira et al. 2011, Mariguela et al. 2013, Britzke et al. 2018, Melo et al. 2022a) or combined molecular and morphological hypotheses (Mirande 2019) resolve Aphyodite more closely related to species classified in Pristellinae, including the type species Hemigrammus unilineatus. As the resolution of *Aphyodite* being well supported in the phylogeny inferred from UCE loci and corroborated in other studies, we classify Aphyodite grammica as a species of Hemigrammus (Table 1). A recent taxonomic revision of *Aphvodite* resulted in the description of two species: Aphyodite apiaka Esguícero and Castro, 2017 and A. tupebas Esguícero and Castro, 2017. In addition to Aphyodite grammica, we classify A. apiaka and A. tupebas as species of Hemigrammus, resulting in the new combinations Hemigrammus grammicus, Hemigrammus apiaka, and Hemigrammus tupebas (Table 1). Considering this new composition of Hemigrammus, the three species previously classified in Aphyodite are the only species of Hemigrammus possessing a single row of premaxillary teeth.

Although there are no known morphological synapomorphies for Pristellinae, all species in the clade lack a caudal spot and many species have a broad stripe across the eye and a dark stripe along the anal-fin base. These features were used to define the *Hemigrammus lunatus* Durbin, 1918 species-group (Ota *et al.* 2014, 2019). It was suggested these shared colour patterns provided evidence for a clade containing *H. barrigonae* Eigenmann and Henn, 1914, *H. changae* Ota *et al.*, 2019, *H. lunatus*, *H. machadoi* Ota *et al.*, 2014, and *H. ulreyi* (Boulenger, 1895), possibly related to *Moenkhausia collettii* (Steindachner, 1882).

The UCE phylogeny corroborates phylogenies inferred from mitochondrial and nuclear loci in resolving a close relationship

between Hemigrammus ulreyi and Moenkhausia collettii (Britzke et al. 2018). In addition, the UCE phylogeny resolves the Hemigrammus lunatus species-group as monophyletic (Fig. 6), but more inclusive than previously (Ota et al. 2014, 2019) (Fig. 6). Following the phylogenetic relationships resulting from analysis of the UCE loci (Fig. 6), we are proposing the generic reassignment of Moenkhausia collettii, M. eigenmanni Géry, 1964, M. melogramma Eigenmann, 1908 (present study), and M. copei and M. flava (based on Britzke et al., 2018) to Hemigrammus, under the new combinations Hemigrammus collettii, Hemigrammus copei, Hemigrammus eigenmanni, Hemigrammus flavus, and Hemigrammus melogrammus (Fig. 6; Table 1). Moenkhausia conspicua Soares and Bührnheim, 2016 and M. venerei Petrolli et al., 2016 have not been sampled in any molecular phylogenetic analysis, but exhibit a broad stripe across the eye and a dark stripe along the anal-fin base and are probably closely related to species in the Hemigrammus lunatus species-group; however, pending their inclusion in a phylogenetic analysis we avoid the transfer of these species to Hemigrammus at this time. Within the Hemigrammus lunatus species-group, H. eigenmanni lacks the dark stripe across the eye but has a dark stripe of variable intensity along the anal-fin base. This feature is also shared by H. unilineatus (with less intensity), H. grammicus, and H. microstomus, possibly supporting the close relationship of these species to the H. lunatus species-group.

As pointed out by previous authors (Mirande 2010, Britzke et al. 2018, Soares et al. 2020, Marinho et al. 2021), the relationships resolved in the UCE phylogeny highlight the weakness of the degree of lateral line perforation as a diagnostic character to distinguish Hemigrammus and Moenkhausia, which can be attributed to the paedomorphic condition retained during a truncated development (Marinho et al. 2021). The phylogenetic relationships within Pristellinae (Fig. 6) suggest that pigmentation patterns are more consistent with clades resolved in the phylogeny than is the degree of development of the laterosensory system or caudal-fin squamation. Biogeographically, species of Pristellinae are mostly distributed in Amazon-Orinoco-Guianas; some species of Pristella and Hemigrammus are distributed in the São Francisco basin; Gymnocorymbus ternetzi and H. ulreyi are distributed in the La Plata, and H. lunatus is distributed in both Amazon and La Plata basins (Fig. 6).

Jupiabinae Benine and Ota, new subfamily

ZooBank: urn:lsid:zoobank.org:act:A5287E4A-6D3A-4454-B72C-D80AB1AF072C.

Type genus: Jupiaba Zanata, 1997.

Included genus: Jupiaba (in part).

Etymology: From the Tupí *ju* meaning thorn and *piaba* meaning small fish.

Remarks: Jupiaba was described to include 21 species traditionally classified in *Astyanax* or *Deuterodon*, based on six synapomorphies related to the structures of the pelvic girdle and adjacent musculature (Zanata 1997). The monophyly of *Jupiaba* has never been supported in phylogenetic studies (Oliveira *et* al. 2011, Mirande 2019, Melo et al. 2022a), which is reflected in substantial differences in the distribution of teeth and the pelvicfin bone morphology (Zanata 1997, Zanata and Lima 2005). The phylogenetic analysis of UCE loci resolves a monophyletic group containing Jupiaba abramoides (Eigenmann, 1909), J. anteroides (Géry, 1965), J. anterior (Eigenmann, 1908), and J. poranga (type species) that are classified in a newly erected subfamily Jupiabinae (Fig. 6), partially corroborating previous phylogenetic analyses (Terán et al. 2020). The current delimitation of *Jupiaba* is polyphyletic in the UCE phylogeny (Fig. 6), with species resolving in Hyphessobryconinae [J. apenima, J. asymmetrica, J. iasy Netto-Ferreira et al., 2009, J. keithi, J. ocellata (Géry, Planquette and Le Bail, 1996), J. pirana Zanata, 1997, J. polylepis (Günther, 1864), and J. zonata (Eigenmann, 1908)] and in an unnamed clade with Hemigrammus ora (J. acanthogaster, J. cf. essequibensis, and J. scologaster).

Tyttobryconinae Mattox and Melo, new subfamily

ZooBank: urn:lsid:zoobank.org:act:E42BE820-B9A4-4F64-A020-9DB10D7AFBF3.

Type genus: Tyttobrycon Géry, 1973.

Included genera: Hyphessobrycon (in part), Priocharax, Tucanoichthys Géry and Römer, 1997, and Tyttobrycon.

Definition: The least inclusive crown clade that contains *Tyttobrycon xeruini* and *Priocharax ariel* Weitzman and Vari, 1987. This is a minimum-crown-clade definition. See Figure 6 for a reference phylogeny of Tyttobryconinae.

Etymology: From the ancient Greek τυτθός (t' Λ tθ \widetilde{ovz}) meaning small or young and βρύκω (ba'ʊkaʊ) meaning to bite.

Remarks: The subfamily Tyttobryconinae is delimited here to include four genera (Fig. 6): the miniatures Tyttobrycon, Tucanoichthys, Priocharax, and the non-miniature Hyphessobrycon boulengeri (Eigenmann, 1907). Traditionally Tyttobrycon was classified along with other miniatures in the Aphyoditeinagroup (Géry 1973) that was subsequently classified as the Aphyoditeinae (Mirande 2010). In an earlier phylogenomic analysis of UCE loci, Tyttobrycon xeruini and the miniature Tucanoichthys tucano Géry and Römer, 1997 were resolved as sister-species (Melo et al. 2022a). In the phylogeny inferred from UCE loci, two of the six species of Tyttobrycon, T. hamatus Géry, 1973 and T. xeruini, resolve as a clade and are the sisterlineages of the only non-miniature species of Tyttobryconinae, the Hyphessobrycon boulengeri (Fig. 6). The clade comprising Tyttobrycon and H. boulengeri is sister to a clade of exclusively miniature species: Tucanoichthys tucano and species of Priocharax (Fig. 6). There are no known morphological synapomorphies for the clade we delimit here as Tyttobryconinae.

Four of the seven valid species of *Priocharax* were included in the phylogenetic analysis of the UCE loci and resolved as a monophyletic group (Fig. 6). This is the first attempt to include *Priocharax* in a broad molecular phylogeny, as examination of voucher specimens of the samples of *Priocharax* in previous studies revealed an instance of misidentification (see: Souza *et al.* 2022). When *Priocharax* was described, it was hypothesized as closely related to lineages classified here as Characinae (Weitzman and Vari, 1987). The morphological reductions in *Priocharax*, interpreted as developmental truncations, have made it difficult to use morphological characters to resolve the phylogenetic relationships of the lineage among Characiformes (Mattox and Toledo-Piza 2012, Mattox *et al.* 2016).

Priocharax and the enigmatic Tucanoichthys tucano resolve as sister-lineages in the UCE phylogeny (Fig. 6). A detailed anatomical study revealed many similarities between the skeletons of T. tucano and Priocharax (Mattox and Conway 2021). Many of the skeletal similarities are developmental truncations common to other miniature characid lineages, such as reduction in laterosensory system, reduced squamation, reduced number of fin rays, and specific bones that are absent or exhibit truncated development. Clearly any potential morphological synapomorphies among miniature characid lineages require a cautious interpretation due to the potential for convergent or parallel loss or reduction of traits (Weitzman and Fink 1983). There are two striking morphological characters that may represent reductive morphological synapomorphies for the clade containing Priocharax and Tucanoichthys: absence of the claustrum in the Weberian apparatus and the shape of the opercle that is developed ventrally but leaves a gap dorsally exposing part of the branchial chamber (Mattox et al. 2016, Mattox and Conway 2021). The claustrum is absent in all species of *Priocharax* with the exception of a rudimentary claustrum present in P. nanus Toledo-Piza et al., 2014 and P. toledopizae Mattox et al., 2023 (Toledo-Piza et al. 2014, Mattox et al. 2023). Tucanoichthys and *Priocharax* also share a peculiar shape of the maxilla, with a long series of strictly conical teeth extending to the distal tip of the bone (Géry and Römer 1997, Mattox and Conway 2021), which is uncommon among small characids. It is interesting to note the relatively long branches of all miniature species throughout the phylogeny inferred from the UCE loci (Supporting Information, Figs S1-S3), something noted above for other miniature taxa (e.g. Oxybrycon, Trochilocharax). Species of Tyttobryconinae occur in Amazonia, with the exception of Hyphessobrycon *boulengeri* that is distributed in Atlantic coastal rivers (Fig. 6).

Hyphessobryconinae Lima, Carvalho & Faria, new subfamily

ZooBank: urn:lsid:zoobank.org:act:B7A1E353-CC55-4480-842E-CFA88155FA94.

Type genus: Hyphessobrycon Durbin in Eigenmann, 1908.

Included genera: Dinotopterygium Frainer et al., 2021, Erythrocharax Netto-Ferreira et al., 2013, Hemigrammus (in part), Hyphessobrycon (in part), Jupiaba (in part), Macropsobrycon (in part), Moenkhausia (in part), Parecbasis, and Phycocharax Ohara et al., 2017.

Definition: The least inclusive crown clade that contains *Hyphessobrycon agulha* Fowler, 1913 and *Jupiaba polylepis* (Günther, 1864). This is a minimum-crown-clade definition. See Figure 6 for a reference phylogeny of Hyphessobryconinae.

Etymology: From the ancient Greek ὑφήσσων (h'uːfɑːsˌoʊn) meaning of lesser stature and βρύκω (bɹˈʊkaʊ) meaning to bite.

Remarks: The new subfamily Hyphessobryconinae is delimited as containing many species and genera that have long been challenged in the systematics and taxonomy of Characiformes (Fig. 6). A clade comprising eight species currently classified in *Jupiaba* and *Hyphessobrycon moniliger* is the sister-lineage of all other species of Hyphessobryconinae (Fig. 6). Within Hyphessobryconinae there is a clade that includes several species with large bony hooks on the anal fin of males: *Parecbasis cyclolepis* Eigenmann, 1914, eight species of *Hyphessobrycon*, one species of *Macropsobrycon*, three species of *Moenkhausia*, and three species of *Hemigrammus* (Fig. 6). A close phylogenetic affinity of species sharing large bony hooks on the anal fins of males had been suggested for the *Hyphessobrycon panamensis* group (Ota *et al.* 2020), *H. bayleyi* Lima *et al.*, 2022, *H. diancistrus*, and *H. otrynus* (Lima *et al.* 2022).

Hyphessobrycon compressus is the type species of the genus and in the UCE phylogeny resolves in a monophyletic group that also contains H. columbianus Zarske and Géry, 2002, H. ecuadorensis (Eigenmann, 1915), H. panamensis Durbin, 1908, and Hyphessobrycon sp. Dagua (Fig. 6). This monophyletic trans-Andean lineage was supported in other phylogenetic studies that included H. bussingi Ota et al., 2020, H. columbianus, H. compressus, H. condotensis Regan, 1913, H. ecuadoriensis Eigenmann and Henn, 1914, H. panamensis, H. savagei Bussing, 1967, and H. tortuguerae Böhlke, 1958 (Melo et al. 2022a, Elías et al. 2023), which differs from the hypothesis based on morphology of a close relationship with cis-Andean species of the rosy tetra clade (Weitzman and Palmer 1997, Carvalho and Malabarba 2015). Pending additional taxonomic and phylogenetic research, we refrain from proposing changes in the generic classification and nomenclature for Moenkhausia gracilima, Moenkhausia mikia, Hemigrammus levis, Macropsobrycon xinguensis, Moenkhausia ceros, and Hemigrammus hyanuary.

The specimen identified as Hyphessobrycon sp. Dagua (15715) from Río Dagua in south-western Colombia in the UCE phylogeny has the morphological features of Astyanax daguae Eigenmann, 1913, such as complete lateral line and absence of scales over caudal-fin lobes (Eigenmann 1913). The species was recently analysed based on a single mitochondrial gene and transferred to *Tetragonopterus* (Terán *et al.*, 2020). Due to the phylogenetic position of the specimen relatively close to *Hyphessobrycon compressus* (Fig. 6), and the presence of a second species Hyphessobrycon daguae (Eigenmann, 1922) in that river, we use the provisional name Hyphessobrycon sp. Dagua, with an indication that future research will evaluate the status of both species. This also reveals that the species should not be placed in the genus *Tetragonopterus* (Tetragonopterinae) within Characidae (Fig. 3). The genus *Macropsobrycon* requires additional taxonomic research because Macropsobrycon xinguensis phylogenetically resolved as a lineage of Hyphessobryconinae, but the type species of the genus Macropsobrycon uruguayanae is placed in Cheirodontinae (Characidae) in the UCE phylogeny (Figs 3, 6).

Erythrocharax, Dinotopterygium, and *Phycocharax* are speciesdepauperate genera described over the past 10 years that are nested in a clade of Hyphessobryconinae that includes several species of *Hyphessobrycon* (Fig. 6; Netto-Ferreira *et al.* 2013, Ohara *et al.* 2017, Frainer *et al.* 2021). Species in this clade are predominantly from the Brazilian Shield and possess up to seven cusps, with *Hyphessobrycon psittacus* Dagosta *et al.*, 2016 being the exception with five cusps. Some species have a higher number of cusps, such as *Erythrocharax altipinnis* with up to eight cusps, and *H. juruna* Faria *et al.*, 2018, *P. rasbora* Ohara *et al.*, 2017, and *Dinotopterygium diodon* Frainer *et al.*, 2021 with up to nine cusps.

Dinotopterygium has a unique combination of 10 synapomorphies, including modifications in anal-fin morphology leading to the anal-fin base strongly convex in males, and suggesting a close relationship with *Erythrocharax* and *Phycocharax* (Frainer et al. 2021). Phycocharax rasbora has a unique combination of characters: presence of a single row of relatively compressed premaxillary teeth, large teeth with four to nine cusps on premaxilla and dentary, absence of pseudotympanum, incomplete lateral line, sexually dimorphic males with distal margin of anal fin approximately straight, and presence of a nearly triangular and horizontally elongated blotch from the posterior half of the body to caudal peduncle (Ohara et al. 2017). Phylogenetic analysis of morphological characters resolved a clade containing Phycocharax, Paracheirodon axelrodi (Schultz, 1956), Hyphessobrycon elachys Weitzman, 1985, H. loweae Costa and Géry, 1994, and H. vanzolinii Lima and Flausino Junior, 2016 (Ohara et al. 2017). The relationships resolved in the UCE phylogeny corroborate the phylogenetic affinities of relationship between Phycocharax and H. loweae, but are not consistent with a close phylogenetic relationship with P. axelrodi. Hyphessobrycon elachys and H. vanzolinii were not included in phylogenetic analyses of the UCE loci.

The phylogeny resolves a clade containing 14 species of *Hyphessobrycon*, *Hemigrammus* cf. *bellottii* (Steindachner, 1882), Hemigrammus rubrostriatus Zarske, 2015, and Hemigrammus sp. Leticia (Fig. 6). Species in this clade have teeth with up to five cusps; the presence of a longitudinal black stripe typically starting posteriorly to the humeral blotch (when humeral blotch is present) and typically darker on the caudal peduncle region. The black stripe presents interspecific variation, ranging from weakly marked and diffuse (e.g. Hyphessobrycon amapaensis Zarske and Géry, 1998 and Hemigrammus bellottii) to very dark and broad stripe (e.g. *Hyphessobrycon peruvianus* Ladiges, 1938), and in some cases more than one pattern may occur on the same species (e.g. Hyphessobrycon agulha). The known species of the group share a thin iridescent stripe above the black stripe and humeral blotch. Our phylogeny indicates that live coloration patterns might support monophyletic assemblages within the Hyphessobryconinae, opening new avenues for studies within these clades.

Many of the species in this clade were previously classified in the *Hyphessobrycon agulha* and *Hyphessobrycon heterorhabdus* (Ulrey 1894) species-groups (Géry 1977, Lima *et al.* 2014, Faria *et al.* 2020a, b). The *Hyphessobrycon agulha* species group is defined by the presence of 'a broad, relatively diffuse lateral stripe (typically more discernible ventrally, posterior to the midbody), and a humeral blotch that may or may not coalesce with the stripe (although a humeral blotch is absent in *H. loretoensis* Ladiges, 1938 and *H. mutabilis* Costa and Géry, 1994)' (Ohara and Lima 2015) and in its most recent proposition is composed of *Hyphessobrycon agulha, Hyphessobrycon clavatus* Zarske, 2015, *Hyphessobrycon eschwartzae* García-Alzate *et al.*, 2013, Hyphessobrycon herbertaxelrodi Géry, 1961, Hyphessobrycon klausanni García-Alzate et al., 2017, Hyphessobrycon loretoensis, Hyphessobrycon lucenorum Ohara and Lima, 2015, Hyphessobrycon margitae Zarske, 2016, Hyphessobrycon metae Eigenmann and Henn, 1914, Hyphessobrycon mutabilis, Hyphessobrycon peruvianus, Hyphessobrycon wadai Marinho et al., 2016, and Hyphessobrycon zoe Faria et al., 2020 (Faria et al. 2020a). The Hyphessobrycon heterorhabdus species group is currently defined by a tricolor longitudinal pattern along midbody, i.e. dorsal red stripe, middle iridescent stripe and ventral longitudinal black pattern composed by a single humeral blotch, a midlateral black stripe continuous with humeral blotch and increasingly blurred towards caudal peduncle (Faria et al. 2020b); the group includes Hyphessobrycon amapaensis, Hyphessobrycon cantoi Faria et al., 2021, Hyphessobrycon heterorhabdus, Hyphessobrycon ericae Moreira and Lima, 2017, Hyphessobrycon montagi Lima et al., 2014, Hyphessobrycon sateremawe Faria et al., 2020, and Hyphessobrycon wosiackii Moreira and Lima, 2017 (Faria et al. 2021). The phylogeny inferred from the UCE loci resolves both the Hyphessobrycon agulha and H. heterorhabdus species-groups as non-monophyletic (Fig. 6).

Thayeriinae Ota, Reia & Benine, new subfamily

ZooBank: urn:lsid:zoobank.org:act:56486412-0A9F-42B8 BBE2-50E138915341.

Type genus: Thayeria Eigenmann, 1908.

Included genera: Bario Myers, 1940, Bryconamericus (in part), Bryconella Géry, 1965, Inpaichthys, Hollandichthys Eigenmann, 1910, Holopristis Eigenmann, 1903, Hemigrammus (in part), Hyphessobrycon (in part), Parapristella Géry, 1964, Rachoviscus, Ramirezella Fernández-Yépez, 1949, and Thayeria.

Definition: The least inclusive crown clade that contains *Thayeria obliqua*, *Holopristis ocellifer* (Steindachner, 1882), and *Inpaichthys kerri* Géry and Junk, 1977. This is a minimum-crown-clade definition. See Figure 7 for a reference phylogeny of Thayeriinae.

Etymology: A patronym for Nathaniel Thayer (1808–1883).

Remarks: The phylogeny inferred from the UCE loci resolves a clade of three species that includes *Inpaichthys kerri*, *Bryconamericus orinocoense* Román-Valencia, 2003, and *Hyphessobrycon* sp. Jari as the sister-lineage of all other species of Thayeriinae (Fig. 7). A DNA barcoding study did not resolve *B. orinocoense* with a clade containing *Bryconamericus* or other species of Stevardiidae (García-Melo *et al.* 2019). The undescribed species identified here as *Hyphessobrycon* sp. Jari has the morphological characteristics consistent with the genus *Hyphessobrycon* (Eigenmann 1917) but is distantly related to *H. compressus*. This clade must be investigated further in order to understand the species composition, as many species may be absent from the present study.

There is an interesting clade in Thayeriinae that contains species distributed in Atlantic coastal rivers (Fig. 7). *Hyphessobrycon flammeus* Myers, 1924 and *H. griemi* Hoedeman, 1957 are similar morphologically and found in coastal rivers in the Atlantic rainforest from Rio de Janeiro to Santa Catarina, Brazil (Weitzman *et al.* 1988). *Hollandichthys multifasciatus* (Eigenmann and Norris, 1900) is resolved as the sister-species of *Rachoviscus crassiceps* Myers, 1926 and *R. graciliceps* Weitzman and Cruz, 1981 (Fig. 7), corroborating results from previous phylogenetic analyses (Quagio-Grassioto *et al.* 2012, Betancur-R *et al.* 2019, Mirande 2019, Melo *et al.* 2022a). Several phenotypic traits are consistent with a close phylogenetic relationship between *Hollandichthys* and *Rachoviscus* that includes a unique type of spermiogenesis, presence of a long and spiralling mitochondria in the midpiece of the spermatozoa in both genera, and presence of a ventral body cavity between pelvic and anal fins that houses internally the anus and the urogenital opening in both males and females (Bertaco and Malabarba 2013).

Ramirezella newboldi Fernández-Yépez, 1949 and R. pyrophthalma (Costa, 1994) (former Hemigrammus newboldi and Moenkhausia pyrophthalma) form a monophyletic group resolved as the sister-lineage of Thayeria (Fig. 7). Ramirezella newboldi was described as a new species and new monotypic genus, initially diagnosed by the presence of scales covering the basal portion of caudal fin, incomplete lateral-line, and short maxilla (Fernández-Yépez 1949). The species was subsequently transferred to Hemigrammus (Taphorn 1992), which also highlighted a similar colour pattern shared with Moenkhausia cotinho Eigenmann, 1908. Recently, Ramirezella newboldi was redescribed and diagnosed from comparisons to M. cotinho (Mathubara and Toledo-Piza 2020). Moenkhausia pyrophthalma was described by Costa (1994), who hypothesized a close relationship with M. oligolepis (Günther, 1864), M. sanctaefilomenae (Steindachner, 1907) (herein classified as a species of Bario; Table 1), and M. cotinho based on a reticulate colour pattern, a relationship not supported in the UCE phylogeny (Fig. 7). Considering that the clade Hemigrammus newboldi and Moenkhausia pyrophthalma is phylogenetically distant from both *M. xinguensis* (type species of *Moenkhausia*) and H. unilineatus (type species of Hemigrammus), we revalidate Ramirezella Fernández-Yépez, 1949 to include Ramirezella newboldi new combination, and Ramirezella pyrophthalma new combination (Table 1). Ramirezella and Bario possess a reticulate colour pattern, but according to the phylogeny, this feature seems to have evolved independently in these two lineages (Fig. 7). Moenkhausia cotinho was not included in the UCE phylogenomic dataset, but ongoing research is investigating the phylogenetic placement of this species (L. Reia, unpublished data).

Thayeria is unique among characids in that the lower caudalfin lobe is longer than the upper caudal-fin lobe, there is a dark stripe across the lower caudal-fin lobe that is continuous with a longitudinal stripe, and the body is directed slightly upwards when swimming (Moreira and Lima 2017). Previous molecular phylogenetic analyses resolved *T. boehlkei* Weitzman, 1957 and *T. ifati* Géry, 1959 as a monophyletic group sister to *Moenkhausia sanctaefilomenae* (Javonillo *et al.* 2010). Morphological phylogenetic analysis resolved *T. boehlkei* and *T. obliqua* Eigenmann, 1908 as monophyletic based on four synapomorphies, and as the sister-group of *Hemigrammus* (Mirande 2010). An expanded morphological dataset of Mirande (2010) resulted in phylogenies where a monophyletic *Thayeria* was the sister-lineage of a clade containing *Petitella bleheri* (Géry and Mahnert, 1986) and *Petitella georgiae* (Ohara *et al.* 2017). The resolution of *Thayeria* in Thayeriinae reflects results from a previous phylogenomic study of UCE loci (Melo *et al.* 2022a).

Ramirezella and *Thayeria* form a clade sister to a more inclusive group with *Bario*, some species assigned to *Hemigrammus*, *Parapristella*, and *Bryconella* (fourth to seventh lineages; Fig. 7). With the exception of *Bryconella* and a few *Bario* species, which have green to blue eyes when alive, the majority of taxa belonging to this lineage present the upper margin of the eye red in live specimens (Ohara and Lima 2015).

Bario and several species of Moenkhausia and Hemigrammus skolioplatus Bertaco and Carvalho, 2005 are resolved as a clade of Thayeriinae (Fig. 7). The genus Bario was described by Myers (1940) after a complex taxonomic history involving Tetragonopterus lineatus Steindachner, 1891 (Steindachner 1891). Eigenmann (1893) observed that T. lineatus was preoccupied by a species described by Perugia and replaced it with T. steindachneri Eigenmann, 1893. Eigenmann (1917) transferred this species to the monotypic genus Entomolepis. Myers (1940) described Bario to replace Entomolepis, since that name was preoccupied in Crustacea (Entomolepis Brady). Molecular and morphological phylogenetic studies have shown a close relationship between *B. steindachneri* and species of *Moenkhausia*: M. oligolepis, M. sanctaefilomenae, M. forestii Benine et al., 2009, and *M. australis* Eigenmann, 1908 (Mirande 2009, 2010, 2019, Mariguela et al. 2013, Melo et al. 2022a). These species comprise the Moenkhausia oligolepis/M. sanctaefilomenae complex (Costa 1994, Lima et al. 2007, Ohara and Lima 2015). The group was defined by a colour pattern characterized by a higher concentration of dark chromatophores in the distal margins of the scales, a vertically elongate humeral blotch, and a conspicuous dark blotch on the caudal peduncle preceded by a lighter area (Costa 1994). Two subgroups in the species complex were proposed based on the degree of flattening in the pre- and post-pelvic region: laterally compressed in *M. australis*, *M. forestii*, *M. oligolepis*, M. sanctaefilomenae, and Bario steindachneri, and ventrally flattened in M. cosmops Lima et al., 2007, M. uirapuru Ohara and Lima, 2015, M. diktyota Lima and Toledo-Piza, 2001, and M. lineomaculata Dagosta et al., 2015 (Reia et al. 2019).

The genus *Bario* is expanded to include all the eight species analysed here of the *M. oligolepis/M. sanctaefilomenae* complex (Fig. 7; Table 1). The phylogeny inferred from the UCE loci provides some corroboration for the species groups delimited in Reia *et al.* (2019), and the UCE phylogeny resolves *Bario skolioplatus* as the sister-lineage of a clade containing *Bario uirapuru* and *Bario cosmops* that was proposed in a previous taxonomic revision (Ohara and Lima 2015).

One of the clades resolved in the UCE phylogeny is the *Hemigrammus ocellifer* group that includes *H. aguaruna* Lima et al., 2016, *H. falsus* Meinken, 1959, *H. haraldi* Géry, 1961, *H. guyanensis* Géry, 1959, *H. luelingi* Géry, 1964, *H. neptunus* Zarske and Géry, 2002, *H. ocellifer*, *H. pulcher* Ladiges, 1938, and *H. yinyang* Lima and Sousa, 2009 (Fig. 7; Lima and Sousa 2009, Lima et al. 2016). Species in this clade possess two humeral blotches, a dark blotch on the caudal peduncle, a red upper eye margin in life, and a single medium-sized hook per anal-fin ray that are arranged in a row along the last unbranched

and seven anteriormost branched anal-fin rays in adult males (Lima and Sousa 2009). *Holopristis* was described to include *Tetragonopterus ocellifer* (Eigenmann, 1903), later synonymized in *Hemigrammus* (Géry 1959). Considering the morphological and phylogenomic support for monophyly of this group (Fig. 7; Lima and Sousa 2009, Lima *et al.* 2016), we revalidate the genus *Holopristis* to accommodate *Holopristis aguaruna*, *H. falsus*, *H. guyanensis*, *H. haraldi*, *H. luelingi*, *H. neptunus*, *H. ocellifer*, *H. pulcher*, and *H. yinyang*. Three species of *Holopristis* were not sampled in the UCE phylogeny: *H. falsus*, *H. luelingi*, and *H. yinyang*.

Species of Parapristella are resolved as a monophyletic group in Thayeriinae (Fig. 7). Parapristella was described to include P. georgiae Géry, 1964 and Pristella aubynei Eigenmann, 1909 (Géry 1964a). In the UCE phylogeny, Parapristella is resolved as the sister-lineage of a clade containing Bryconella and Hemigrammus vorderwinkleri Géry, 1963 (Fig. 7). Bryconella is a monotypic genus described to allocate Cheirodon pallidifrons Fowler, 1946 (Géry 1965). Although future studies may suggest that H. vorderwinkleri should be moved to Bryconella, we avoid this transference until further detailed studies are conducted into the taxonomy and phylogeny of species of Thayeriinae. The subfamily contains several clades associated with distinct biogeographic regions. The clade has predominance across the Amazon-Orinoco-Guianas with Bario reaching the La Plata and São Francisco, and the clade with Hyphessobrycon flammeus, H. griemi, Hollandichthys, and Rachoviscus distributed in the Atlantic coastal rivers of eastern Brazil (Fig. 7).

Rhoadsiinae Fowler, 1911

Type genus: Rhoadsia Fowler, 1911.

Included genera: Carlana Strand, 1928, Nematobrycon, Parastremma Eigenmann, 1912, Pseudochalceus Kner, 1863, and Rhoadsia.

Definition: The least inclusive crown clade that contains *Rhoadsia altipinna* Fowler, 1911 and *Nematobrycon palmeri* Eigenmann 1911. This is a minimum-crown-clade definition. See Figure 7 for a reference phylogeny of Rhoadsiinae.

Etymology: A patronym for Samuel N. Rhoads (1862–1952).

Remarks: The phylogeny inferred from the UCE loci resolves a clade we delimit as the subfamily Rhoadsiinae that includes *Nematobrycon, Pseudochalceus, Rhoadsia, Parastremma,* and *Carlana* (Fig. 7). Rhoadsiinae was elevated to classify species of *Rhoadsia* and *Parastremma,* and the monotypic *Carlana eigenmanni* (Meek, 1912) (Cardoso 2003). Species of Rhoadsiinae have a single tooth series in the premaxilla when juveniles and two series when adults, except for *C. eigenmanni,* which maintains only the inner tooth series, and the outer teeth series of the premaxilla is composed of two conical teeth and the inner series consists of five multicuspid teeth (Cardoso 2003). Previous molecular phylogenetic analyses resolve *Carlana eigenmanni* and *Nematobrycon* as sister-lineages (Oliveira *et al.* 2011). Phylogenetic analysis of a combined molecular and morphological dataset resolves a clade containing *Bario, Carlana,*

Hollandichthys, Inpaichthys, Nematobrycon, Pseudochalceus, Rachoviscus, Rhoadsia, and Thayeria that is supported by two non-exclusive synapomorphies (Mirande 2019).

Within Rhoadsiinae the UCE phylogeny shows successive branching lineages of *Nematobrycon*, the two species of *Pseudochalceus*, and a clade containing *Rhoadsia*, *Parastremma*, and *Carlana* (Fig. 7). *Nematobrycon* contains two species endemic to the Atrato and San Juan rivers of north-western Colombia, whereas *Pseudochalceus* includes four species distributed in the Pacific versant rivers of Ecuador and Colombia (Géry 1977). All species of Rhoadsiinae are distributed in the western Andes and Central America (Fig. 7). In addition, species in this clade share an incomplete lateral line, very elongated dorsal-fin rays that may reach the caudal fin in adult males resulting in a pronounced sexual dimorphism, two teeth rows in the premaxilla (except *Carlana*), and 10–15 unicuspid to tricuspid teeth on the maxillary.

Grundulinae Fowler, 1958, new usage

Type genus: Grundulus Valenciennes, 1846.

Included genera: Astyanacinus Eigenmann, 1907 and Grundulus.

Definition: The least inclusive crown clade that contains *Grundulus bogotensis* and *Astyanacinus moorii* (Boulenger, 1892). This is a minimum-crown-clade definition. See Figure 7 for a reference phylogeny of Grundulinae.

Etymology: From the Middle English *grundel* in reference to several species of fishes.

Remarks: Grundulus was described for Poecilia bogotensis Humboldt, 1821 (Valenciennes in Cuvier and Valenciennes, 1846) and includes three species endemic to lakes in the northern Andes of South America (Román-Valencia et al. 2005). Morphological phylogenetic analysis resolved Grundulus as monophyletic, supported with 11 synapomorphies (Román-Valencia et al. 2010), and G. quitoensis Román-Valencia et al., 2005 is the sister-species of a clade including G. cochae Román-Valencia et al, 2003 and G. bogotensis. Alternative phylogenetic studies using morphology resolved Grundulus and Coptobrycon from eastern Brazil as sister-lineages classified in the subfamily Gymnocharacinae (Mirande 2009, 2010). Phylogenetic analysis of combined morphological and molecular data resolved Grundulus as closely related to Coptobrycon, Stygichthys, some species of Hyphessobrycon, Phycocharax, Myxiops, Probolodus, Deuterodon, and a species of Astyanax, which were classified in the tribe Grundulini Fowler, 1958 (Mirande 2019). This delimitation of Grundulini has not been supported in molecular phylogenetic analyses (Figs 3-7; Oliveira et al. 2011, Melo et al. 2022a).

Astyanacinus was described by Eigenmann (1907: 769) and differentiated from Astyanax by possessing a 'lengthened upper jaw' (Géry 1977: 415). Astyanacinus was synonymized with Astyanax based on the phylogenetic resolution of Astyanacinus moorii (Boulenger, 1892) as nested within Astyanax, a result supported by two morphological synapomorphies (Terán *et al.* 2020). A phylogenomic study resolved Grundulus and Rhoadsia as sister-lineages and *Astyanacinus* as the sister-lineage of a clade containing *Psellogrammus* Eigenmann, 1908, *Ctenobrycon* Eigenmann, 1908, *Oligosarcus*, and *Astyanax* (Betancur *et al.* 2019). An earlier phylogenomic study using UCE loci reflects results presented in Figure 7, with the resolution of a clade containing *Grundulus* and *Astyanacinus* that is the sister-lineage of a clade containing Rhoadsiinae, *Psellogrammus*, *Ctenobrycon*, *Oligosarcus*, and *Astyanax* (Melo *et al.* 2022a).

The phylogenetic analysis of UCE loci supports the monophyly of Grundulinae, which are the sister-lineage of a species-rich clade that we delimit as the subfamily Acestrorhamphinae (Fig. 7). Based on the UCE phylogeny, we recognize the subfamily Grundulinae and revalidate *Astyanacinus* as a monotypic genus (Fig. 7; Table 1). A taxonomic revision delimited the *Astyanax orthodus* species group that included *Astyanacinus moori* (Ruiz-C. *et al.* 2018), indicating the presence of additional species currently classified as *Astyanax* that may be more closely related to *Astyanacinus*. Grundulinae exhibit a geographically disjunct distribution with *Grundulus* in the Andes and *Astyanacinus* in the La Plata basin (Fig. 7).

Acestrorhamphinae Eigenmann 1907, new usage

Type genus: Acestrorhamphus Eigenmann and Kennedy 1903, junior synonym of *Oligosarcus* Günther 1864.

Included genera: Andromakhe Terán et al., 2020, Astyanax (in part), Ctenobrycon, Hyphessobrycon (in part), Oligosarcus, and Psalidodon (in part).

Definition: The least inclusive crown clade that contains *Oligosarcus argenteus, Ctenobrycon oliverai* Benine *et al.,* 2010 and *Psalidodon fasciatus* (Cuvier, 1819). This is a minimum-crown-clade definition. See Figure 7 for a reference phylogeny of Acestrorhamphinae.

Etymology: From the ancient Greek ἄκεστρα (' α :kɛst.Jə) meaning a darning needle and ῥάμφος (J'æmfouz) meaning curved beak.

Remarks: The subfamily Acestrorhamphinae is resolved as monophyletic in the UCE phylogeny and comprises four major lineages (Fig. 7): *Ctenobrycon, Astyanax,* a clade containing *Hyphessobrycon* and *Oligosarcus,* and *Psalidodon.* There are modifications to the taxonomy for each of these lineages that are outlined below.

Ctenobrycon includes four species C. spilurus (Valenciennes, 1850), C. oliverai, and two species transferred here: Ctenobrycon kennedyi (Eigenmann, 1903) (former Psellogrammus kennedyi) and C. magdalenae (Eigenmann and Henn, 1916) (former Astyanax magdalenae) (Fig. 7). The taxonomic history starts with the description of Ctenobrycon with Tetragonopterus hauxwellianus Cope, 1870 as the type species based on the presence of ctenoid (= spinoid) scales in the pre-ventral region (Eigenmann 1908). The monotypic genus Psellogrammus, with Hemigrammus kennedyi Eigenmann, 1903 as type species, was described in the same study (Eigenmann 1908). Tetragonopterus spilurus Valenciennes, 1848 was transferred to Ctenobrycon (Eigenmann 1910). A close relationship between Psellogrammus and Ctenobrycon was suggested based on shared

characteristics such as elongated anal fin, ctenoid scales, high body depth, maxilla not extending to the orbit, and absence of scales on the caudal fin (Eigenmann 1927). The hypothesized relationship between Psellogrammus and Ctenobrycon in precladistic taxonomic studies was corroborated by molecular and combined molecular and morphological phylogenetic studies (Oliveira et al. 2011, Betancur-R et al. 2019, Mirande 2019, Melo et al. 2022a). A phylogenetic analysis identified a 'Ctenobrycon clade' supported by three morphological synapomorphies that included Ctenobrycon, Psellogrammus, Astyanax magdalenae, A. stilbe (Cope, 1870), and A. atratoensis Eigenmann, 1907 (Terán et al. 2020). In light of the present phylogenetic evidence and morphological similarities (Oliveira et al. 2011, Betancur-R et al. 2019, Mirande 2019, Terán et al. 2020, Melo et al. 2022a), we transfer all species in the 'Ctenobrycon clade' to Ctenobrycon, resulting in the new combinations Ctenobrycon magdalenae and Ctenobrycon kennedyi (Table 1).

Astyanax as defined by Terán et al. (2020: 9) resolves as a lineage of Acestrorhamphinae in the UCE phylogeny (Fig. 7). In addition, Moenkhausia pirauba Zanata et al., 2010 and Genycharax tarpon Eigenmann, 1912 resolve within Astyanax, thus resulting in Astyanax pirauba and Astyanax tarpon, new combinations (Fig. 7; Table 1). The clade Astyanax is supported by two morphological synapomorphies, but A. tarpon and A. pirauba were not included in the morphological analysis (Terán et al. 2020). This clade also contains A. metae Eigenmann, 1914 and A. venezuelae Schultz, 1944 from the Orinoco, and a clade with widespread species such as A. bimaculatus (Linnaeus, 1758) and A. lacustris (Lütken, 1875) (Fig. 7).

A monophyletic *Oligosarcus* is resolved as the sister-lineage of a clade containing two species of *Hyphessobrycon*: *H. bifasciatus* Ellis, 1911 and *H. igneus* Miquelarena *et al.*, 1980 in the UCE phylogeny (Fig. 7), corroborating results from phylogenetic analyses of morphological and combined molecular and morphological datasets (Ribeiro and Menezes 2015, Mirande 2019, Terán *et al.* 2020). The UCE phylogeny results show *Hyphessobrycon bifasciatus* and *H. igneus* as the sister-lineage of *Oligosarcus* (Fig. 7). The two *Hyphessobrycon* species need reallocation to a different genus considering the morphological evidence supporting *Oligosarcus* (Ribeiro and Menezes 2015). Because the purpose of this study is not to describe new genera or species, we currently consider that the best decision is maintaining it in *Hyphessobrycon* until a further generic description and reallocation are published.

In the phylogeny inferred from the UCE loci, a monophyletic *Psalidodon (sensu* Terán *et al.* 2020) is resolved as a sister-lineage to the clade containing *Hyphessobrycon* and *Oligosarcus* (Fig. 7). *Psalidodon* includes species previously classified in the genera *Astyanax, Hasemania, Hyphessobrycon,* and *Moenkhausia* (Fig. 7). Terán *et al.* (2020) transferred many species of *Astyanax* to the genus *Psalidodon,* a clade supported with two morphological synapomorphies, and found monophyly of *Andromakhe saguazu* (Casciotta *et al.,* 2003) is resolved inside *Psalidodon* in our phylogeny (Fig. 7). However, we treat *Andromakhe* as valid as the type species of the genus, *A. latens* (Mirande *et al.,* 2004), was not included in our UCE dataset. However, considering the phylogenetic position of *A. saguazu,* we transfer this species to

Psalidodon, as *Psalidodon saguazu*, new combination (Table 1). Other species are herein transferred to Psalidodon under the new combinations Psalidodon alleni (Eigenmann and McAtee, 1907), Psalidodon balbus (Myers, 1927), Psalidodon biotae (Castro and Vari, 2004), Psalidodon cremnobates (Bertaco and Malabarba, 2001), Psalidodon dissimilis (Garavello and Sampaio, 2010), Psalidodon goyacensis (Eigenmann, 1908), Psalidodon hamatus (Bertaco and Malabarba, 2005), Psalidodon henseli (de Melo and Buckup, 2006), Psalidodon kalunga (Bertaco and Carvalho, 2010), Psalidodon laticeps (Cope, 1894), Psalidodon minor (Garavello and Sampaio, 2010), Psalidodon scabripinnis (Jenyns, 1842), Psalidodon serratus (Garavello and Sampaio, 2010), Psalidodon togoi (Miquelarena and López, 2006), Psalidodon varzeae (Abilhoa and Duboc, 2007), Psalidodon vermilion (Zanata and Camelier, 2009), Psalidodon uaiso (Carvalho and Langeani, 2013), and Psalidodon uberaba (Serra and Langeani, 2015) (Fig. 7; Table 1). Some of these species were originally assigned to other genera based on morphological features, such as the lack of an adipose fin (e.g. Hasemania kalunga and H. uberaba) or incomplete lateral line (e.g. Hyphessobrycon balbus and *H. uaiso*). However, based on the resolution of these species in the UCE phylogeny (Fig. 7), we hypothesize that these features are homoplastic.

CONCLUSION

This study represents the largest phylogeny of Neotropical tetras of the families Acestrorhamphidae, Characidae, Spintherobolidae, and Stevardiidae to date in terms of taxa and characters. The incorporation of a large taxon sampling allowed us to identify a number of monophyletic units that merit intrafamilial classification. This study also contains a significantly larger number of characters than any other Characidae phylogeny. The two recent phylogenomic studies of Characiformes included 91 species or 7% (Betancur-R et al. 2019), 154 species or 12% (Melo et al. 2022a), whereas our study includes 494 species or 39.4% of all Characidae s.l.. Considering our new family-level configuration, we sampled approximately 83% of Spintherobolidae, 20% of Stevardiidae, 47% of Characidae, and 46% of Acestrorhamphidae. This dataset is also novel in the number of nuclear genomic regions and characters (1348 loci; 538 472 bp) compared to previous multilocus phylogenetic studies explicitly focused on Characidae (Javonillo et al. 2010, Oliveira et al. 2011, Thomaz et al. 2015). These factors, in conjunction with the precision of species' identification, render this database relevant for supporting our taxonomic decisions involving synonyms, new combinations, revalidations of genera and subfamilies, and the proposition of new family-group names (Figs 2–7; Table 1).

While not definitive, we emphasize some prominent synapomorphies that provide support for these four clades at family level (Fig. 2). In addition to the morphological characteristics described in the literature, such as the absence of the mesocoracoid bone in Spintherobolidae and the presence of four premaxillary teeth and eight branched dorsal-fin rays in Stevardiidae (Bührnheim *et al.* 2008, Thomaz *et al.* 2015, Mirande 2019), the largest metacentric chromosome pair may represent a synapomorphy for Acestrorhamphidae. Continuous morphological and genetic investigation might test the current family- and subfamily-level hypotheses presented here.

Some genera were not sampled here and were considered members of proposed monophyletic groups when previous data were available. Examples include *Iotabrycon*, *Ptychocharax*, and *Carlastyanax* in Stevardiidae (Fig. 3) and *Aphyocharacidium*, *Compsura*, *Ctenocheirodon*, and *Microschemobrycon* in Characidae (Fig. 4). Some others have never been included in phylogenetic studies and the available data are insufficient for any proposal, thus remaining *incertae sedis*. This is the case of *Dectobrycon* Zarske and Géry 2006, *Leptobrycon*, *Mixobrycon* Eigenmann, 1915, *Oligobrycon* Eigenmann, 1915, *Schultzites* Géry, 1964, *Scissor* Günther, 1864, *Serrabrycon* Vari, 1986, and *Thrissobrycon* Böhlke, 1953. *Gymnocharacinus* Steindachner, 1903 was included in previous phylogenetic studies but no agreement of its placement exists (Mirande 2019, Terán *et al.* 2020), and thus it is also considered as *incertae sedis* in Acestrorhamphidae.

This study proposes a classification that divides the traditional Characidae into four families according to the phylogenetic structure (Spintherobolidae (Acestrorhamphidae (Characidae Stevardiidae))) (Figs 2–7). One important factor leading to the decision of a new classification is the unavailability of monophyletic suprageneric entities in the former Stethaprioninae (sensu Mirande 2019). Before this study, this clade comprised 670 species and a few proposed tribes (e.g. Gymnocharacini, Rhoadsiini, and Stethaprionini); this study proposes the family Acestrorhamphidae with 14 subfamilies fully supported by our phylogenomic dataset (Figs 5–7). Another reason is the recurrence of monophyly for these four major clades in more than a decade of relevant characid phylogenetics using distinct datasets, providing a solid understanding of their composition by ichthyologists (Oliveira et al. 2011, Tagliacollo et al. 2012, Mariguela et al. 2013, Thomaz et al. 2015, Melo et al. 2016, 2022a, b, Betancur-R et al. 2019, Mirande 2019). Finally, our proposal provides multiple opportunities for systematic investigations in smaller and monophyletic units especially within subfamilies of Acestrorhamphidae.

SUPPLEMENTARY DATA

Supplementary data are available at *Zoological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY

The data underlying this article are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.bzkh189jw. Additional data is available in the online supplementary material.

REFERENCES

- Aberer AJ, Kobert K, Stamatakis AE. Massively parallel Bayesian tree inference for the whole-genome era. *Molecular Biology and Evolution* 2014;31:2553–6.
- Alfaro ME, Faircloth BC, Harrington RC et al. Explosive diversification of marine fishes at the Cretaceous–Palaeogene boundary. Nature Ecology and Evolution 2018;2:688–96.
- Aberer AJ, Stamatakis A, Ronquist F. An efficient independence sampler for updating branches in Bayesian Markov chain Monte Carlo sampling of phylogenetic trees. *Systematic Biology* 2016;65: 161–76.
- Arcila D, Ortí G, Vari R et al. Genome-wide interrogation advances resolution of recalcitrant groups in the tree of life. Nature Ecology and Evolution 2017;1:1–10.
- Baicere-Silva CM, Ferreira KM, Malabarba LR et al. Spermatic characteristics and sperm evolution on the subfamily Stevardiinae (Ostariophysi: Characiformes: Characidae). Neotropical Ichthyology 2011;9:377–92. https://doi.org/10.1590/s1679-62252011005000014
- Baird SF, Girard CF. Descriptions of new species of fishes collected in Texas, New Mexico and Sonora, by Mr. John H. Clark, on the U.S. and Mexican Boundary Survey, and in Texas by Capt. Stewart Van Vliet, U.S.A. Proceedings of the Academy of Natural Sciences of Philadelphia 1854;7:24–9.
- Benine RC, Melo BF, Castro RMC et al. Taxonomic revision and molecular phylogeny of Gymnocorymbus Eigenmann, 1908 (Teleostei, Characiformes, Characidae). Zootaxa 2015;3956:1–28. https://doi. org/10.11646/zootaxa.3956.1.1

- Bertaco VA, Malabarba LR. A new species of the characid genus Hollandichthys Eigenmann from coastal rivers of southern Brazil (Teleostei: Characiformes) with a discussion on the diagnosis of the genus. Neotropical Ichthyology 2013;11:767–78. https://doi. org/10.1590/s1679-62252013000400004
- Bertaco VA, Jerep FC, Carvalho FR. New species of *Moenkhausia* Eigenmann (Ostariophysi: Characidae) from the upper rio Tocantins basin in Central Brazil. *Neotropical Ichthyology* 2011;9:57–63. https:// doi.org/10.1590/s1679-62252011000100003
- Betancur R R, Broughton RE, Wiley EO *et al*. The tree of life and a new classification of bony fishes. *PLOS Currents: Tree of Life* 2013;1–45. https://doi.org/10.1371/ecurrents.tol.53ba26640df0ccaee75bb165 c8c26288
- Betancur-R R, Wiley EO, Arratia G et al. Phylogenetic classification of bony fishes. BMC Evolutionary Biology 2017;17:1–40.
- Betancur-R R, Arcila D, Vari RP et al. Phylogenomic incongruence, hypothesis testing, and taxonomic sampling: the monophyly of characiform fishes. Evolution 2019;73:329–45. https://doi. org/10.1111/evo.13649
- Bockmann FA, Guazzelli GM. Heptapteridae (Heptapterids). In: Reis RE, Kullander SO, Ferraris CJ (eds), Check List of the Freshwater Fishes of South and Central America. Porto Alegre: Edipucrs, 2003, 406–31.
- Böhlke JE. Studies on fishes of the family Characidae. No. 7. A new genus and species of glandulocaudine characids from Central Brazil. *Stanford Ichthyological Bulletin* 1954;**4**:265–74.
- Bolger AM, Lohse M, Usadel B. Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* 2014;**30**:2114–20. https:// doi.org/10.1093/bioinformatics/btu170
- Britz R, Conway KW, Rüber L. The emerging vertebrate model species for neurophysiological studies is *Danionella cerebrum*, new species (Teleostei: Cyprinidae). *Scientific Reports* 2021;11:18942. https:// doi.org/10.1038/s41598-021-97600-0
- Britzke R, Troy WP, Oliveira C et al. Description of a new species of Moenkhausia (Characiformes: Characidae) from the upper Paraguay basin, Central Brazil, with comments on its phylogenetic relationships. Neotropical Ichthyology 2018;16:e170086.
- Buckup PA. Relationships of the Characidiinae and phylogeny of characiform fishes (Teleostei: Ostariophysi). In: Malabarba LR, Reis RE, Vari RP et al. (eds), Phylogeny and Classification of the Neotropical Fishes. Porto Alegre: Edipucrs, 1998, 123–44.
- Bührnheim CM, Carvalho TP, Malabarba LR et al. A new genus and species of characid fish from the Amazon basin—the recognition of a relictual lineage of characid fishes (Ostariophysi: Cheirodontinae: Cheirodontini). Neotropical Ichthyology 2008;6:663–78. https://doi. org/10.1590/s1679-62252008000400016
- Burns MD, Sidlauskas BL. Ancient and contingent body shape diversification in a hyperdiverse continental fish radiation. *Evolution* 2019;73:569–87. https://doi.org/10.1111/evo.13658
- Calcagnotto D, Schaefer SA, DeSalle R. Relationships among characiform fishes inferred from analysis of nuclear and mitochondrial gene sequences. *Molecular Phylogenetics and Evolution* 2005;**36**:135–53. https://doi.org/10.1016/j.ympev.2005.01.004
- Camelier P, Menezes NA, Costa-Silva GJ et al. Molecular phylogeny and biogeographic history of the Neotropical tribe Glandulocaudini (Characiformes: Characidae: Stevardiinae). Neotropical Ichthyology 2018;16:e170157.
- Cardoso AR. Subfamily Rhoadsiinae (Characins, tetras). In: Reis RE, Kullander SO, Ferraris CJ Jr (eds), *Check List of the Freshwater Fishes* of South and Central America. Porto Alegre: Edipucrs, 2003, 213–14.
- Carvalho FR. Sistemática de Hyhessobrycon Durbin, 1908 (Ostariophysi: Characidae). Unpublished Ph.D. Dissertation, Universidade Federal do Rio Grande do Sul, 2011.
- Carvalho FR, Malabarba LR. Redescription and osteology of Hyphessobrycon compressus (Meek) (Teleostei: Characidae), type species of the genus. Neotropical Ichthyology 2015;13:513–40. https:// doi.org/10.1590/1982-0224-20140173
- Castro RMC. Osteologia e relações filogenéticas de Engraulisoma taeniatum Castro, 1981 (Ostariophysi, Characiformes, Characidae). Unpublished Master dissertation, Universidade de São Paulo, 1984.

- Castro RMC, Vari RP. Detritivores of the South American fish family Prochilodontidae (Teleostei: Ostariophysi: Characiformes): a phylogenetic and revisionary study. *Smithsonian Contributions to Zoology* 2004;**622**:1–189. https://doi.org/10.5479/si.00810282.622
- Castro RMC, Ribeiro AC, Benine RC *et al. Lophiobrycon weitzmani*, a new genus and species of glandulocaudine fish (Characiformes: Characidae) from the rio Grande drainage, upper rio Paraná system, southeastern Brazil. *Neotropical Ichthyology* 2003;1:11–9. https://doi. org/10.1590/s1679-62252003000100002
- Chakrabarty P, Faircloth BC, Alda F *et al.* Phylogenomic systematics of ostariophysan fishes: ultraconserved elements support the surprising nonmonophyly of Characiformes. *Systematic Biology* 2017;**66**:881–95. https://doi.org/10.1093/sysbio/syx038
- Chen W-J, Lavoué S, Mayden RL. Evolutionary origin and early biogeography of otophysan fishes (Ostariophysi: Teleostei). *Evolution* 2013;67:2218–39. https://doi.org/10.1111/evo.12104
- Cope ED. Contribution to the ichthyology of the Marañon. *Proceedings of the American Philosophical Society* 1870;11:559–70.
- Costa WJEM. Description of two new species of the genus *Moenkhausia* (Characiformes: Characidae) from the central Brazil. *Zoologischer Anzeiger* 1994;**232**:21–9.
- Cuvier G. Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annelids, 1st edn. Paris: A. Belin, 1816.
- Cuvier G, Valenciennes A. Histoire naturelle des poissons. Tome dix-huitième. Suite du livre dix-huitième. Cyprinoïdes. Livre dix-neuvième. Des Ésoces ou Lucioïdes. Paris and Strasbourg: Ch. Pitois, and V. Levrault, 1846.
- Cuvier G, Valenciennes A. Histoire naturelle des poissons. Tome vingtdeuxième. Suite du livre vingt-deuxième. Suite de la famille des Salmonoïdes. Paris: Libraire de la Société Géologique de France, 1850.
- Dai W, Zou M, Yang L et al. Phylogenomic perspective on the relationships and evolutionary history of the major Otocephalan lineages. *Scientific Reports* 2018;8:1–12.
- Dornburg A, Near TJ. The emerging phylogenetic perspective on the evolution of actinopterygian fishes. Annual Review of Ecology, Evolution, and Systematics 2021;52:427–52. https://doi.org/10.1146/annurev-ecolsys-122120-122554
- Dutra GM, Jerep FC, Vari RP *et al.* The pseudotympanum in the Gymnotiformes (Teleostei, Ostariophysi, Otophysi): homology and evolution of a previously unexplored system in neotropical electric fishes. *Zoological Journal of the Linnean Society* 2015;**174**:114–29. https://doi.org/10.1111/zoj.12221
- Edgar RC. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 2004;**32**:1792–7. https://doi.org/10.1093/nar/gkh340
- Eigenmann CH. Catalogue of the fresh-water fishes of Central America and southern Mexico. A. Fishes collected by Frederick C. Hartt. *Proceedings of the United States National Museum* 1893;16:53-60. https://doi.org/10.5479/si.00963801.925.53
- Eigenmann CH. New genera of South American fresh-water fishes, and new names for some old genera. *Washington: Smithsonian Institution* 1903;**45**:1862–972.
- Eigenmann CH. Fowler's 'Heterognathus Fishes' with a note on the Stethaprioninae. *American Naturalist* 1907;**41**:767–72. https://doi. org/10.1086/278878
- Eigenmann CH. Preliminary descriptions of new genera and species of tetragonopterid characins. (Zoölogical Results of the Thayer Brazilian expedition.). Bulletin of the Museum of Comparative Zoology 1908;52:91–106.
- Eigenmann CH. Reports on the expedition to British Guiana of the Indiana University and the Carnegie Museum, 1908. Report no. 1. Some new genera and species of fishes from British Guiana. *Annals of the Carnegie Museum* 1909;**6**:4–54. https://doi.org/10.5962/p.331035
- Eigenmann CH. Catalogue of the fresh-water fishes of tropical and south temperate America. In: Reports of the Princeton University expeditions to Patagonia 1896–99. *Zoology. Fishes Patagonia* 1910;**3**:375–511.
- Eigenmann CH. New characins in the collection of the Carnegie Museum. Annals of the Carnegie Museum 1911;8:164–81. https://doi. org/10.5962/p.14707

- Eigenmann CH. Some results from an ichthyological reconnaissance of Colombia, South America. Part I. Indiana University Studies 1912; 16:1–27.
- Eigenmann CH. Some results from an ichthyological reconnaissance of Colombia, South America. Part II. Indiana University Studies 1913;18:1–32.
- Eigenmann CH. Some results from studies of South American fishes. IV. New genera and species of South American fishes. *Indiana University Studies* 1914;**20**:44–8.
- Eigenmann CH. The Cheirodontinae, a subfamily of minute characid fishes of South America. *Memoirs of the Carnegie Museum* 1915;7:1– 99. https://doi.org/10.5962/p.34482
- Eigenmann CH. The American Characidae [Part 1]. Memoirs of the Museum of Comparative Zoology 1917;43:1–102.
- Eigenmann CH. The American Characidae. Memoirs of the Museum of Comparative Zoology 1927;43:311–428.
- Eigenmann CH, Henn AW. On new species of fishes from Colombia, Ecuador, and Brazil. *Indiana University Studies* 1914;2:231–4.
- Eigenmann CH, Henn AW. Description of three new species of characid fishes. Annals of the Carnegie Museum 1916;10:87–90. https://doi. org/10.5962/p.78059
- Eigenmann CH, Myers GS. The American Characidae. Memoirs of the Museum of Comparative Zoology, Harvard 1929;43:511-46.
- Eigenmann CH, McAtee WL, Ward DP. On further collections of fishes from Paraguay. Annals of the Carnegie Museum 1907;4:110–57.
- Elías DJ, McMahan CD, Alda F et al. Phylogenomics of trans-Andean tetras of the genus Hyphessobrycon Durbin 1908 (Stethaprioninae: Characidae) and colonization patterns of Middle America. PLoS One 2023;18:e0279924. https://doi.org/10.1371/journal.pone.0279924
- Ellis MD. On the species of Hasemania, Hyphessobrycon, and Hemigrammus collected by J. D. Haseman for the Carnegie Museum. Annals of the Carnegie Museum 1911;8:148-63. https://doi.org/10.5962/p.14706
- Esguícero ALH, Castro RMC. Taxonomic revision of the genus Atopomesus Myers, 1927 (Characiformes: Characidae), with comments on its phylogenetic relationships. Vertebrate Zoology 2016;66:241–9. https://doi.org/10.3897/vz.66.e31562
- Esguícero ALH, Castro RMC. Taxonomic revision of the genus *Aphyodite*, with description of two new species (Teleostei: Characidae). *Copeia* 2017;**105**:753–64. https://doi.org/10.1643/ci-16-481
- Esguícero ALH, Mendonça MB. A new genus and two new species of tetras (Characiformes, Characidae), with a redescription and generic reassignment of Axelrodia lindeae Géry. Ichthyology and Herpetology 2023;111:426–47.
- Faircloth BC. Illumiprocessor: A Trimmomatic Wrapper for Parallel Adapter and Quality Trimming. 2013. https://doi.org/10.6079/J9ILL. Date accessed 1 June 2023.
- Faircloth BC. PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics* 2016;**32**:786–8. https://doi. org/10.1093/bioinformatics/btv646
- Faircloth BC, McCormack JE, Crawford NG et al. Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. Systematic Biology 2012;61:717–26. https://doi. org/10.1093/sysbio/sys004
- Faircloth BC, Sorenson L, Santini F et al. A phylogenomic perspective on the radiation of ray-finned fishes based upon targeted sequencing of ultraconserved elements (UCEs). PLoS One 2013;8:e65923. https:// doi.org/10.1371/journal.pone.0065923
- Faircloth BC, Alda F, Hoekzema K et al. A target enrichment bait set for studying relationships among ostariophysan fishes. Copeia 2020;108:47–60. https://doi.org/10.1643/cg-18-139
- Faria TC, Lima FCT, Wosiacki WB. A New Hyphessobrycon (Characiformes: Characidae) from the Guiana Shield in Northern Brazil. Copeia 2020a;108:369–75. https://doi.org/10.1643/ci-19-311
- Faria TC, Bastos DA, Zuanon J et al. A new Hyphessobrycon (Characiformes: Characidae) of the Hyphessobrycon heterorhabdus species-group from the Central Amazon basin, Brazil. Zootaxa 2020b;**4859**:275–84.
- Faria TC, Guimarães KLA, Rodrigues LRR et al. A new Hyphessobrycon (Characiformes: Characidae) of the Hyphessobrycon heterorhabdus

species-group from the lower Amazon basin, Brazil. *Neotropical Ichthyology* 2021;**19**:e200102.

- Fernández-Vépez A. Ramirezella newboldi nuevo género y especie de pez Tetragonopteridae colectado en Venezuela. Evencias 1949;6:1–3.
- Fernández-Yépez A, Antón JR. Estudio (analisis) ictiológico 'Las Majaguas' hoyas de los ríos 'Cojedes-Sarare'. Republica de Venezuela: Portuguesa, Direccion de Obras Hidraulicas, Ministerio de Obras Publicas, 1966.
- Ferreira KM, Menezes NA, Quagio-Grassioto I. A new genus and two new species of Stevardiinae (Characiformes: Characidae) with a hypothesis on their relationships based on morphological and histological data. *Neotropical Ichthyology* 2011;9:281–98. https://doi. org/10.1590/s1679-62252011000200005
- Ferreira KM, Mirande JM, Quagio-Grassiotto I et al. Testing the phylogenetic hypotheses of Stevardiinae Gill, 1858 in light of new phenotypic data (Teleostei: Characidae). Journal of Zoological Systematics and Evolutionary Research 2021;59:1–26.
- Fink WLA. New genus and species of characid fish from the Bayano River Basin, Panamá (Pisces: Cypriniformes). *Proceedings of the Biological Society of Washington* 1976;**88**:331–44.
- Fink SV, Fink WL. Interrelationships of Ostariophysan fishes (Teleostei). Zoological Journal of the Linnean Society 1981;72:297–353. https:// doi.org/10.1111/j.1096-3642.1981.tb01575.x
- Fink SV, Fink WL. Interrelationships of Ostariophysan fishes (Teleostei). In: Stiassny MLJ, Parenti LP, Johnson GD (eds), *Interrelationship of Fishes*. New York: Academic Press, 1996, 209–49.
- Fowler HW. Description of a new South American characin (*Cheirodon pallidifrons* new species). *The Fish Culturist* 1946;**26**:1–2.
- Fowler HW. Some new taxonomic names of fishlike vertebrates. *Notulae Naturae* (*Philadelphia*) 1958;**310**:1–16.
- Frainer G, Carvalho FR, Bertaco VA et al. Museum specimens reveal a rare new characid fish genus, helping to refine the interrelationships of the Probolodini (Characidae: Stethaprioninae). Systematics and Biodiversity 2021;19:1135–48. https://doi.org/10.1080/14772000. 2021.1986167
- Fricke R, Eschmeyer WN, Van der Laan R (eds), Eschmeyer's Catalog of Fishes: Genera, Species, References, 2023. http://researcharchive. calacademy.org/research/ichthyology/catalog/fishcatmain.asp. (June 2023, date last accessed).
- García-Melo JE, Oliveira C, Costa Silva GJ *et al.* Species delimitation of Neotropical Characins (Stevardiinae): Implications for taxonomy of complex groups. *PLoS One* 2019;**14**:e0216786.
- Géry J. Contributions a l'étude des Poissons Characoïdes (Ostariophysi) (IV) Nouvelles espèces de Guyane française du genre *Hemigrammus* (Tetragonopterinae) avec une liste critique des formes recensées. *Bulletin Mensuel de la Société Linnéenne de Lyon* 1959;**28**:248–60. https://doi.org/10.3406/linly.1959.8088
- Géry J. Contributions to the study of the characoid fishes, N°. 6. New Cheirodontinae from French Guiana. Senckenbergiana Biologica 1960;**41**:15-39.
- Géry J. Three new tetras from the upper Rio Negro near Tapurucuara. *Tropical Fish Hobbyist* 1963;**12**:9–15,57–59,62–63.
- Géry J. Preliminary description of seven new species and two new genera of characoid fishes from the Upper Rio Meta in Colombia. *Tropical Fish Hobbyist* 1964a;**12**:25–32,41–48.
- Géry J. Poissons characoïdes de l'Amazonie péruvienne. *Beitrage zur Neotropischen Fauna* 1964b;**4**:1–44. https://doi. org/10.1080/01650526409360375
- Géry J. Poissons characoïdes nouveaux ou non signalés de l'Ilha do Bananal, Brésil. Vie et Milieu 1964c; Suppl. **17**:447–71, Pls. 1–4.
- Géry J. Poissons characoïdes sud-américains du Senckenberg Muséum, II. Characidae et Crenuchidae de l'Igarapé Préto (Haute Amazonie). *Senckenbergiana Biologica* 1965;**46**:11–45.
- Géry J. A review of certain Tetragonopterinae (Characoidei), with the description of two new genera. *Ichthyologica, the Aquarium Journal* 1966a;**3**:211–36.
- Géry J. Hoplocharax goethei, a new genus and species of South American characoid fishes, with a review of the sub-tribe Heterocharacini. Ichthyologica, the Aquarium Journal 1966b;**38**:281–96.

- Géry J. Contribution à L'étude des poissons Characoïdes de l'Équateur. Avec une révision du genre *Pseudochalceus* et la description d'une nouveaux genre endémique du rio Cauca en Colombie. *Acta Humboldtiana, Series Geologica, Paleontologica et Biologica* 1972;**2**:1–110.
- Géry J. New and little-known Aphyoditeina (Pisces, Characoidei) from the Amazon Basin. *Studies on the Neotropical Fauna* 1973;**8**:81–137.
- Géry J. Characoids of the World. Neptune City, NJ: T.F.H. Publications, 1977.
- Géry J, Junk WJ. Inpaichthys kerri n. g. n. sp., um novo peixe caracídeo do alto no Aripuanã, Mato Grosso, Brasil. Acta Amazonica 1977;7:417– 23. https://doi.org/10.1590/1809-43921977073417
- Géry J, Römer U. Tucanoichthys tucano gen. n. sp. n., a new miniature characid fish (Teleostei: Characiformes: Characidae) from the Rio Uaupes basin in Brazil. aqua, Journal of Ichthyology and Aquatic Biology 1997;2:65–72.
- Gill TN. Synopsis of the fresh water fishes of the western portion of the island of Trinidad, W. I. Annals of the Lyceum of Natural History of New York 1858;6:363–430. https://doi.org/10.1111/j.1749-6632.1858. tb00373.x
- Gill TN. The differential characters of characinoid and erythrinoid fishes. Proceedings of the United States National Museum 1896;18:205–9. https://doi.org/10.5479/si.00963801.18-1056.205
- Greenwood PH, Rosen DE, Weitzman SH et al. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bulletin of the American Museum of Natural History 1966;131:341–455.
- Gregory WK, Conrad GM. The phylogeny of the characin fishes. Zoologica: Scientific Contributions of the New York Zoological Society 1938;23:319–60. https://doi.org/10.5962/p.203667
- Günther A. Catalogue of the Fishes in the British Museum. Catalogue of the Physostomi, Containing the Families Siluridae, Characinidae, Haplochitonidae, Sternoptychidae, Scopelidae, Stomiatidae in the Collection of the British Museum. London: Order of Trustees, 1864.
- Harrington RC, Faircloth BC, Eytan RI *et al*. Phylogenomic analysis of carangimorph fishes reveals flatfish asymmetry arose in a blink of the evolutionary eye. *BMC Evolutionary Biology* 2016;**16**:1–14.
- Haseman JD, Eigenmann CH. A brief report upon the expedition of the Carnegie Museum to Central South America. *Annals of the Carnegie Museum* 1911;7:187–314.
- Heather JM, Chain B. The sequence of sequencers: the history of sequencing DNA. *Genomics* 2016;**107**:1–8. https://doi. org/10.1016/j.ygeno.2015.11.003
- Howes GJ. The cranial musculature and taxonomy of characoid fishes of the tribes Cynodontini and Characoni. Bulletin of the British Museum of Natural History (Zoology) 1976;23:203–48.
- Hughes LC, Ortí G, Huang Y et al. Comprehensive phylogeny of rayfinned fishes (Actinopterygii) based on transcriptomic and genomic data. Proceedings of the National Academy of Sciences of the United States of America 2018;115:6249–54. https://doi.org/10.1073/ pnas.1719358115
- Javonillo R, Malabarba LR, Weitzman SH et al. Relationships among major lineages of characid fishes (Teleostei: Ostariophysi: Characiformes), based on molecular sequence data. Molecular Phylogenetics and Evolution 2010;54:498–511. https://doi. org/10.1016/j.ympev.2009.08.026
- Lanfear R, Calcott B, Ho SYW et al. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 2012;29:1695–701. https://doi.org/10.1093/molbev/mss020
- Langeani F, Serra JP. Coptobrycon bilineatus (Ellis, 1911) (Characiformes: Characidae): redescription and comments on its phylogenetic relationships. Neotropical Ichthyology 2010;8:727–36. https://doi. org/10.1590/s1679-62252010000400004
- Lima FCT, Sousa LM. A new species of *Hemigrammus* from the upper rio Negro basin, Brazil, with comments on the presence and arrangement of anal-fin hooks in *Hemigrammus* and related genera (Ostariophysi: Characiformes: Characidae). aqua, International Journal of Ichthyology 2009;15:153–68.
- Lima FCT, Malabarba LR, Buckup PA *et al.* 2003. Genera incertae sedis in Characidae. In: Reis RE, Kullander SO, Ferraris CJ Jr. (eds), *Check*

List of the Freshwater Fishes of Southand Central America. Porto Alegre: Edipucrs, 2003, 106–69.

- Lima FCT, Britski HA, Machado FA. A new *Moenkhausia* (Characiformes: Characidae) from central Brazil, with comments on the area relationship between the upper rio Tapajós and upper rio Paraguai systems. *aqua, International Journal of Ichthyology* 2007;**13**:45–54.
- Lima FCT, Coutinho DP, Wosiacki WB. A new *Hyphessobrycon* (Ostariophysi: Characiformes: Characidae) from the middle Amazon basin, Brazil. *Zootaxa* 2014;**3872**:167–79. https://doi.org/10.11646/zootaxa.3872.2.3
- Lima FCT, Correa V, Ota RP. A new species of *Hemigrammus* Gill 1858 (Characiformes: Characidae) from the western Amazon basin in Peru and Colombia. *aqua, International Journal of Ichthyology* 2016;**22**:123–32.
- Lima FCT, Van der Sleen P, Moreira C. Subfamily Aphyoditeinaeaphyoditeine tetras. In: Van der Sleen P, Albert JS (eds), *Field guide to the fishes of the Amazon, Orinoco and Guianas*. New Jersey: Princeton University Press, 2018, 97–100.
- Lima FCT, Caires RA, Conde-Saldaña CC et al. A new miniature Pristella (Actinopterygii: Characiformes: Characidae) with reversed sexual dimorphism from the rio Tocantins and rio São Francisco basins, Brazil. Canadian Journal of Zoology 2021;**99**:339–48. https://doi. org/10.1139/cjz-2020-0241
- Lima FCT, Bastos DA, Rapp Py-Daniel LH *et al*. A new sexually dimorphic *Hyphessobrycon* from the western Amazon basin (Characiformes: Characidae). *Zootaxa* 2022;**5116**:253–66.
- Lucena CAS. Relações filogenéticas e definição do gênero *Roeboides*, Günther (Ostariophysi; Characiformes; Characidae). *Comunicações do Museu de Ciências e Tecnologia da PUCRS* 1998;**11**:19–59.
- Lundberg JG, Linares OJ, Antonio ME et al. Phractocephalus hemiliopterus (Pimelodidae, Siluriformes) from the Upper Miocene Urumaco formation, Venezuela: a further case of evolutionary stasis and local extinction among South American fishes. *Journal of Vertebrate Paleontology* 1988;8:131–8. https://doi.org/10.1080/02724634.19 88.10011693
- Lundberg JG, Mago-Leccia F, Nass P. Exallodontus aguanai, a new genus and species of Pimelodidae (Pisces: Siluriformes) from deep river channels of South America, and delimitation of the subfamily Pimelodinae. Proceedings of the Biological Society of Washington 1991;104:840–69.
- Lundberg JG, Littmann M. Family Pimelodidae. In: Reis RE, Kullander SO, Ferraris CJ Jr (eds), *Check List of the Freshwater Fishes of South and Central America*. Porto Alegre: Edipucrs, 2003, 432–46.
- Malabarba LR. Monophyly of the Cheirodontinae, characters and major clades (Ostariophysi: Characidae). In: Malabarba LR, Reis RE, Vari RP *et al.* (eds), *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre: EDIPUCRS, 1998, 193–233.
- Malabarba LR, Jerep FC. A new genus and species of Cheirodontine fish from South America (Teleostei: Characidae). *Copeia* 2012;**2012**:243–50. https://doi.org/10.1643/ci-11-143
- Malabarba LR, Weitzman SH. Description of a new genus with six new species from Southern Brazil, Uruguay and Argentina, with discussion of a putative characid clade (Teleostei: Characiformes: Characidae). *Comunicações do Museu de Ciências e Tecnologia da PUCRS* 2003;**16**:67–151.
- Malabarba LR, Bertaco VA, Carvalho FR *et al.* Revalidation of the genus *Ectrepopterus* Fowler (Teleostei: Characiformes), with the redescription of its type species, *E. uruguayensis. Zootaxa* 2012;**3204**:47–60.
- Malabarba LR, Chuctaya J, Hirschmann A et al. Hidden or unnoticed? Multiple lines of evidence support the recognition of a new species of Pseudocorynopoma (Characidae: Corynopomini). Journal of Fish Biology 2021;98:219–36. https://doi.org/10.1111/jfb.14572
- Mariguela TC, Benine RC, Abe KT et al. Molecular phylogeny of Moenkhausia (Characidae) inferred from mitochondrial and nuclear DNA evidence. Journal of Zoological Systematics and Evolutionary Research 2013;51:327–32. https://doi.org/10.1111/jzs.12025
- Marinho MMF, Ohara WM, Dagosta FCP. A new species of *Moenkhausia* (Characiformes: Characidae) from the rio Madeira basin, Brazil, with

comments on the evolution and development of the trunk lateral line system in characids. *Neotropical Ichthyology* 2021;**19**:1–20.

- Mateussi NT, Melo BF, Ota RP et al. Phylogenomics of the Neotropical fish family Serrasalmidae with a novel intrafamilial classification (Teleostei: Characiformes). *Molecular Phylogenetics and Evolution* 2020;**153**:106945. https://doi.org/10.1016/j.ympev.2020.106945
- Mathubara K, Toledo-Piza M. Taxonomic study of *Moenkhausia cotinho* Eigenmann, 1908 and *Hemigrammus newboldi* (Fernández-Yépez, 1949) with the description of two new species of *Moenkhausia* (Teleostei: Characiformes: Characidae). *Zootaxa* 2020;**4852**:1–40.
- Mattox GMT, Conway KW. Osteology of *Tucanoichthys tucano* Géry and Römer, an enigmatic miniature fish from the Amazon basin, Brazil (Teleostei: Characiformes: Characidae). *Vertebrate Zoology* 2021;71:645–67. https://doi.org/10.3897/vz.71.e71886
- Mattox GMT, Toledo-Piza M. Phylogenetic study of the Characinae (Teleostei: Characiformes; Characidae). Zoological Journal of the Linnean Society 2012;165:809–915. https://doi.org/10.1111/j.1096-3642.2012.00830.x
- Mattox GMT, Britz R, Toledo-Piza M *et al. Cyanogaster noctivaga*, a remarkable new genus and species of miniature fish from the Rio Negro, Amazon basin (Ostariophysi: Characidae). *Ichthyological Exploration of Freshwaters* 2013;**23**:297–318.
- Mattox GMT, Britz R, Toledo-Piza M. Skeletal development and ossification sequence of the characiform Salminus brasiliensis (Teleostei: Ostariophysi: Characidae). Ichthyological Exploration of Freshwaters 2014;25:103–58.
- Mattox GMT, Britz R, Toledo-Piza M. Osteology of *Priocharax* and remarkable developmental truncation in a miniature Amazonian fish (Teleostei: Characiformes: Characidae). *Journal of Morphology* 2016;277:65–85.
- Mattox GMT, Britz R, Souza CS *et al*. Two new species of miniature tetras of the fish genus *Priocharax* from the Rio Juruá drainage, Acre, Brazil (Teleostei: Characiformes: Characidae). *Canadian Journal of Zoology* 2023a;**101**:248–66.
- Mattox GM, Cetra M, Souza CS *et al. Spintherobolus papilliferus* in the rio Ribeira de Iguape basin: implications for the biogeography and conservation of an endangered species (Ostariophysi: Characiformes). *Neotropical Ichthyology* 2023b;**21**:e230026.
- Melo BF, Benine RC, Mariguela TC *et al*. A new species of *Tetragonopterus* Cuvier, 1816 (Characiformes: Characidae: Tetragonopterinae) from the rio Jari, Amapá, northern Brazil. *Neotropical Ichthyology* 2011;**9**:49– 56. https://doi.org/10.1590/s1679-62252011000100002
- Melo BF, Benine RC, Silva GS et al. Molecular phylogeny of the Neotropical fish genus Tetragonopterus (Teleostei: Characiformes: Characidae). Molecular Phylogenetics and Evolution 2016;94:709–17. https://doi.org/10.1016/j.ympev.2015.10.022
- Melo BF, Sidlauskas BL, Near TJ *et al*. Accelerated diversification explains the exceptional species richness of tropical characoid fishes. *Systematic Biology* 2022a;**71**:78–92. https://doi.org/10.1093/sysbio/syab040
- Melo BF, de Pinna MCC, Rapp Py-Daniel LH *et al.* Paleogene emergence and evolutionary history of the Amazonian fossorial fish genus *Tarumania* (Teleostei: Tarumaniidae). *Frontiers in Ecology and Evolution* 2022b;**10**:924860.
- Menezes NA, Weitzman SH. Two new species of *Mimagoniates* (Teleostei: Characidae: Glandulocaudinae), their phylogeny and biogeography and a key to the glandulocaudin fishes of Brazil and Paraguay. *Proceedings of the Biological Society of Washington* 1990;**103**:380–426.
- Menezes NA, Weitzman SH. Systematics of the Neotropical subfamily Glandulocaudinae (Teleostei: Characiformes: Characidae). *Neotropical Ichthyology* 2009;7:295–370. https://doi.org/10.1590/ s1679-62252009000300002
- Menezes NA, Ferreira KM, Netto-Ferreira AL. A new genus and species of inseminating characid fish from the rio Xingu basin (Characiformes: Characidae). Zootaxa 2009;2167:47–58.
- Mirande JM. Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). *Cladistics* 2009;**2009**:574–613.
- Mirande JM. Phylogeny of the family Characidae (Teleostei: Characiformes) from characters to taxonomy. *Neotropical*

Ichthyology 2010;8:385–568. https://doi.org/10.1590/ s1679-62252010000300001

- Mirande JM. Morphology, molecules and the phylogeny of Characidae (Teleostei: Characiformes). *Cladistics* 2019;**35**:282–300. https://doi.org/10.1111/cla.12345
- Mirande JM, Aguilera G, Azpelicueta M. A threatened new species of *Oligosarcus* and its phylogenetic relationships, with comments of *Astyanacinus* (Teleostei: Characidae). *Zootaxa* 2011;**2994**:1–20.
- Mirande JM, Jerep FC, Vanegas-Ríos JA. Phylogenetic relationships of the enigmatic *Carlastyanax aurocaudatus* (Eigenmann) with remarks on the phylogeny of the Stevardiinae (Teleostei: Characidae). *Neotropical Ichthyology* 2013;**11**:747–66. https://doi.org/10.1590/ s1679-62252013000400003
- Moreira CR, Lima FCT. *Thayeria tapajonica* (Characiformes: Characidae), a new species from rio Tapajós basin, Brazil. *Zootaxa* 2017;**4344**:137–46. https://doi.org/10.11646/zootaxa.4344.1.5
- Müller J. Beobachtungen über die Schwimmblase der Fische, mit Bezug auf einige neue Fischgattungen. Archiv für Anatomie, Physiologie, und wissenschaftliche Medicin 1842;**9**:307–29.
- Myers GS. Descriptions of new South American fresh-water fishes collected by Dr. Carl Ternetz. Bulletin of the Museum of Comparative Zoology 1927;68:107–35.
- Myers GS. Suppression of some preoccupied generic names of fishes (*Kessleria, Entomolepis, Pterodiscus* and *Nesiotes*), with a note on *Pterophyllum. Stanford Ichthyological Bulletin* 1940;**2**:35–6.
- Myers GS, Böhlke JE. The Xenurobryconini, a group of minute South American characid fishes with teeth outside the mouth. *Stanford Ichthyological Bulletin* 1956;7:6–12.
- Nakatani M, Miya M, Mabuchi K et al. Evolutionary history of Otophysi (Teleostei), a major clade of the modern freshwater fishes: Pangaean origin and Mesozoic radiation. BMC Evolutionary Biology 2011;11:177–177. https://doi.org/10.1186/1471-2148-11-177
- Near TJ, Thacker CE. Phylogenetic classification of living and fossil ray-finned fishes (Actinopterygii). Bulletin of the Peabody Museum of Natural History 2024;65:3–302.
- Nelson JS, Grande TC, Wilson MVH. Fishes of the World, 5th edn. New York: John Wiley and Sons, 2016.
- Netto-Ferreira AL, Birindelli JLO, Sousa LM *et al.* A new miniature characid (Ostariophysi: Characiformes: Characidae), with phylogenetic position inferred from morphological and molecular data. *PLoS One* 2013;8:e52098.
- Ohara WM, Lima FCT. *Moenkhausia uirapuru*, a new species from the upper rio Guaporé, Chapada dos Parecis, Mato Grosso, Brazil (Teleostei: Characidae). *Ichthyological Exploration of Freshwaters* 2015;**26**:159–70.
- Ohara WM, Mirande JM, Lima FCT. *Phycocharax rasbora*, a new genus and species of Brazilian tetra (Characiformes: Characidae) from Serra do Cachimbo, rio Tapajós basin. *PLoS One* 2017;**12**:e0170648.
- Oliveira C, Avelino GS, Abe KT *et al.* Phylogenetic relationships within the speciose family Characidae (Teleostei: Ostariophysi: Characiformes) based on multilocus analysis and extensive ingroup sampling. *BMC Evolutionary Biology* 2011;**11**:1–25.
- Ortí G, Meyer A. Molecular evolution of ependymin and the phylogenetic resolution of early divergences among euteleost fishes. *Molecular Biology and Evolution* 1996;13:556–73. https://doi.org/10.1093/ oxfordjournals.molbev.a025616
- Ortí G, Meyer A. The radiation of characiform fishes limits of resolution of mitochondrial ribosomal DNA sequences. *Systematic Biology* 1997;46:75–100. https://doi.org/10.1093/sysbio/46.1.75
- Ota RP, Lima FCT, Pavanelli CS. A new species of *Hemigrammus* Gill, 1858 (Characiformes: Characidae) from the rio Madeira and rio Paraguai basins, with a redescription of *H. lunatus. Neotropical Ichthyology* 2014;**12**:265–79. https://doi.org/10.1590/1982-0224-20130176
- Ota RP, Lima FCT, Hidalgo MH. Description of a new *Hemigrammus* Gill (Characiformes: Characidae) from the río Madeira basin in Peru and Bolivia. *Zootaxa* 2019;**4577**:335–47.
- Ota RR, Carvalho FR, Pavanelli CS. Taxonomic review of the Hyphessobrycon panamensis species-group (Characiformes: Characidae). Zootaxa 2020;4751:401–36.

- Pattengale ND, Alipour M, Bininda-Emonds ORP *et al.* How many bootstrap replicates are necessary? *Lecture Notes in Computer Science* 2009;**5541**:184–200.
- Quagio-Grassioto I, Malabarba LR, Azevedo MA *et al.* Unique derived features in spermiogenesis and sperm morphology supporting a close relationship between the species of *Hollandichthys* and *Rachoviscus* (Characiformes: Characidae). *Copeia* 2012;**2012**:609–25.
- de Queiroz K, Gauthier J. Phylogeny as a central principle in taxonomy: phylogenetic definition of taxon names. Systematic Zoology 1990;39:307–22. https://doi.org/10.2307/2992353
- de Queiroz K, Gauthier J. Toward a phylogenetic system of biological nomenclature. Trends in Ecology and Evolution 1994;9:27–31. https:// doi.org/10.1016/0169-5347(94)90231-3
- Rambaut A, Drummond AJ, Xie D et al. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 2018;67:901-4. https://doi.org/10.1093/sysbio/syy032
- Regan CT. The classification of the teleostean fishes of the order Ostariophysi.—I. Cyprinoidea. *The Annals and Magazine of Natural History (Zoology)* 1911;8:13–32.
- Reia L, Vicensotto AMPF, Oliveira C et al. Taxonomy of Moenkhausia australis Eigenmann, 1908 (Characiformes, Characidae) with a discussion on its phylogenetic relationships. Zootaxa 2019;4688:213–31.
- Reinhardt JT. Om trende, formeentligt ubeskrevne fisk af characinernes eller Karpelaxenes familie. Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger og dets Medlemmers Arbeider 1867;1866:49-68.
- Reis RE. Systematic revision of the Neotropical characid subfamily Stethaprioninae (Pisces, Characiformes). *Comunicações do Museu de Ciências PUCRS, Serie Zoologia* 1989;**2**:3–86.
- Reis RE. Subfamily Tetragonopterinae. In: Reis RE, Kullander SO, Ferraris CJ Jr (eds), Check List of the Freshwater Fishes of South and Central America. Porto Alegre: Edipucrs, 2003, 212.
- Reis RE, Kullander SO, Ferraris CJ (eds). Checklist of the Freshwater Fishes of South and Central America. Porto Alegre: Edipucrs, 2003.
- Reis RE, Albert JS, Di Dario F *et al.* Fish biodiversity and conservation in South America. *Journal of Fish Biology* 2016;**89**:12–47. https://doi.org/10.1111/jfb.13016
- Ribeiro AC, Menezes NA. Phylogenetic relationships of the species and biogeography of the characid genus *Oligosarcus* Günther, 1864 (Ostariophysi, Characiformes, Characidae). *Zootaxa* 2015;**3949**:41– 81. https://doi.org/10.11646/zootaxa.3949.1.2
- Roberts TR. The glandulocaudine characid fishes of the Guayas Basin in western Ecuador. *Bulletin of the Museum of Comparative Zoology* 1973;**144**:489–514.
- Román-Valencia C, Ruiz-C RI, Barriga R. Una nueva especie ecuatoriana del género de peces andinos *Grundulus* (Characiformes: Characidae). *Revista de Biología Tropical* 2005;**53**:537–44.
- Román-Valencia C, Vanegas-Ríos JA, Ruiz-C RI. Phylogenetic and biogeographic study of the Andean genus *Grundulus* (Teleostei: Characiformes: Characidae). *Vertebrate Zoology* 2010;60:107–22.
- Rossini BC, Oliveira CAM, Melo FAG *et al.* Highlighting *Astyanax* species diversity through DNA Barcoding. *PLoS One* 2016;11:e0167203. https://doi.org/10.1371/journal.pone.0167203
- Roxo FF, Ochoa LE, Sabaj MH et al. Phylogenomic reappraisal of the Neotropical catfish family Loricariidae (Teleostei: Siluriformes) using ultraconserved elements. *Molecular Phylogenetics and Evolution* 2019;135:148–65. https://doi.org/10.1016/j.ympev.2019.02.017
- Ruiz-C RI, Román-Valencia C, Taphorn DC et al. Revision of the Astyanax orthodus species-group (Teleostei: Characidae) with descriptions of three new species. European Journal of Taxonomy 2018;402:1–45.
- Sabaj MH. Codes for Natural History Collections in ichthyology and herpetology. *Copeia* 2020;**108**:593–669.
- Sabaj MH. Codes for Natural History Collections in Ichthyology and Herpetology (online supplement), v.9.0. Washington, DC: American Society of Ichthyologists and Herpetologists, 2022. https://asih.org
- Sánchez-Romero O, Abad CQ, Cordero PQ *et al.* First description of the karyotype and localization of major and minor ribosomal genes in *Rhoadsia altipinna* Fowler, 1911 (Characiformes, Characidae)

from Ecuador. Comparative Cytogenetics 2015;9:271-80. https://doi.org/10.3897/CompCytogen.v9i2.4504

- Schultz LP. The fishes of the family Characinidae from Venezuela, with descriptions of seventeen new forms. *Proceedings of the United States National Museum* 1944;**95**:235–367, 27 figs. https://doi. org/10.5479/si.00963801.95-3181.235
- Scopoli JA. Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae. Prague: Wolfgang Gerle, 1777.
- Shibatta OA. Family Pseudopimelodidae. In: Reis RE, Kullander SO, Ferraris CJ Jr (eds), Checklist of the Freshwater Fishes of South America. Porto Alegre: Edipucrs, 2003, 401–5.
- Shibatta OA, Vari RP. A new genus of Neotropical rheophilic catfishes, with four new species (Teleostei: Siluriformes: Pseudopimelodidae). *Neotropical Ichthyology* 2017;15:1–30.
- Silva GSC, Melo BF, Oliveira C *et al*. Morphological and molecular evidence for two new species of *Tetragonopterus* (Characiformes: Characidae) from central Brazil. *Journal of Fish Biology* 2013;**82**:1613– 31. https://doi.org/10.1111/jfb.12094
- Silva GSC, Melo BF, Oliveira C et al. Revision of the South American genus *Tetragonopterus* Cuvier, 1816 (Teleostei: Characidae) with description of four new species. *Zootaxa* 2016;**4200**:1–46.
- Silva GSC, Melo BF, Roxo FF *et al.* Phylogenomics of the bumblebee catfishes (Siluriformes: Pseudopimelodidae) using ultraconserved elements. *Journal of Zoological Systematics and Evolutionary Research* 2021a;**59**:1662–72.
- Silva GSC, Roxo FF, Melo BF *et al.* Evolutionary history of Heptapteridae catfishes using ultraconserved elements (Teleostei, Siluriformes). *Zoologica Scripta* 2021b;**50**:543–54.
- Simion P, Delsuc F, Philippe H. To what extent current limits of phylogenomics can be overcome? In: Scornavacca C, Delsuc F, Galtier N (eds), *Phylogenetics in the Genomic Era*. Authors open access book, 2020, 2.1.1:1–34.
- Slobodian V, Akama A, Dutra GM. A new species of *Pimelodella* (Siluriformes: Heptapteridae) from the Guiana Shield, Brazil. Zootaxa 2017;4338:85–100. https://doi.org/10.11646/zootaxa.4338.1.4
- Slobodian V, Abreu-Santos B, Pastana MNL. The rediscovery of Pimelodella longipinnis (Borodin, 1927), an enigmatic Atlantic rainforest catfish species from southeastern Brazil (Siluriformes: Heptapteridae). Papéis Avulsos de Zoologia, Museu de Zoologia da Universidade de São Paulo 2021;61:1–13.
- Soares IM, Bührnheim CM. A new species of *Moenkhausia* Eigenmann, 1903 (Characiformes: Characidae) from Amazon basin, Brazil. *Zootaxa* 2016;**4208**:392–400.
- Soares IM, Ota RP, Lima FCT et al. Redescription of Moenkhausia melogramma (Characiformes: Characidae), a poorly known tetra from the western Amazon basin. Neotropical Ichthyology 2020;18:e200025.
- Souza CS, Melo BF, Mattox GMT et al. Phylogenomic analysis of the Neotropical fish subfamily Characinae using ultraconserved elements (Teleostei: Characidae). Molecular Phylogenetics and Evolution 2022;171:107462. https://doi.org/10.1016/j.ympev.2022.107462
- Stamatakis A. RAxML v.8: a tool for phylogenetic analysis and postanalysis of large phylogenies. *Bioinformatics* 2014;**30**:1312–3. https://doi.org/10.1093/bioinformatics/btu033
- Steindachner F. Beiträge zur Kenntniss der Characinen des Amazonenstromes. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche 1876;72:6–24.
- Steindachner F. Über einige neue und seltene Fische von dem canarischen Archipel, aus den Flüssen Südamerika's und von Madagascar unter dem Titel: 'Ichthyologische Beiträge' (XV). Anzeiger der Kaiserlichen Akademie der Wissenschaften, Wien, Mathematisch-Naturwissenschaftliche Classe 1891;28:171–4.
- Tagliacollo VA, Lanfear R. Estimating improved partitioning schemes for ultraconserved elements. *Molecular Biology and Evolution* 2018;35:1798–811. https://doi.org/10.1093/molbev/msy069
- Tagliacollo VA, Souza-Lima R, Benine RC et al. Molecular phylogeny of Aphyocharacinae (Characiformes, Characidae) with

morphological diagnoses for the subfamily and recognized genera. *Molecular Phylogenetics and Evolution* 2012;**64**:297–307. https://doi.org/10.1016/j.ympev.2012.04.007

- Tan M, Armbruster JW. Phylogenetic classification of extant genera of fishes of the order Cypriniformes (Teleostei: Ostariophysi). Zootaxa. 2018;4476:6–39. https://doi.org/10.11646/zootaxa.4476.1.4
- Taphorn DC. The Characiform Fishes of the Apure River drainage, Venezuela. BioLlania Edición Especial—No. 4. Venezuela: Monografias Cientificas del Museo de Ciencias Naturales, UNELLEZ—Guanara, estado Portuguesa, 1992.
- Terán GE, Benitez MF, Mirande M. Opening the Trojan horse: phylogeny of Astyanax, two new genera and resurrection of Psalidodon (Teleostei: Characidae). Zoological Journal of the Linnean Society 2020;190:1217–34.
- Thomaz AT, Arcila D, Ortí G et al. Molecular phylogeny of the subfamily Stevardiinae Gill, 1858 (Characiformes: Characidae): classification and the evolution of reproductive traits. BMC Evolutionary Biology 2015;15:1–25.
- Thompson DW. A Glossary of Greek Fishes. London: Oxford University Press, 1947.
- Toledo-Piza M, Mattox GMT, Britz R. *Priocharax nanus*, a new miniature characid from the rio Negro, Amazon basin (Ostariophysi: Characiformes), with an updated list of miniature neotropical freshwater fishes. *Neotropical Ichthyology* 2014;**12**:229–46. https://doi. org/10.1590/1982-0224-20130171
- Toledo-Piza M, Baena EG, Dagosta FCP *et al.* Checklist of the species of the Order Characiformes (Teleostei: Ostariophysi). *Neotropical Ichthyology* 2024;**22**:1–548.
- Urbanski BQ, Melo BF, Silva GSC et al. A new species of Tetragonopterus (Characiformes: Characidae) from Central Amazon lowlands, Brazil. Neotropical Ichthyology 2018;16:e170158.
- Van der Laan R, Eschmeyer WN, Fricke R. Family-group names of recent fishes. Zootaxa 2014;3882:1–230. https://doi.org/10.11646/ zootaxa.3882.1.1
- Vanegas-Ríos JA. Phylogeny of the Neotropical genus Gephyrocharax (Characiformes: Characidae: Stevardiinae), with remarks on the tribe Stevardiini. Zoological Journal of the Linnean Society 2018;182:808– 29. https://doi.org/10.1093/zoolinnean/zlx045
- Vanegas-Ríos JA, Faustino-Fuster DR, Meza-Vargas V et al. Phylogenetic relationships of a new genus and species of stevardiine fish (Characiformes: Characidae: Stevardiinae) from the Río Amazonas basin, Peru. Journal of Zoological Systematics and Evolutionary Research 2020;58:387–407.
- Varella HR, Kullander SO, Menezes NA et al. Revision of the generic classification of pike cichlids using an integrative phylogenetic approach (Cichlidae: tribe Geophagini: subtribe Crenicichlina). Zoological Journal of the Linnean Society 2023;198:982–1034. https://doi. org/10.1093/zoolinnean/zlad021
- Vari RP. Anatomy, relationships and classification of the families Citharinidae and Distichodontidae (Pisces, Characoidea). Bulletin of the British Museum (Natural History - Zoological Series) 1979;36:261–344.
- Vari RP. Systematics of the Neotropical Characiform genus Cyphocharax Fowler (Pisces, Ostariophysi). Smithsonian Contributions to Zoology 1992;529:1–137.
- Vari RP. Higher level phylogenetic concepts within Characiformes (Ostariophysi), a historical review. In: Malabarba LR, Reis RE, Vari RV, Lucena ZMS, Lucena CA (eds), *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre: EDIPUCRS, 1998, 111–22.
- Vari RP, Harold AS. Neotropical fishes of the genus Creagrutus (Teleostei: Ostariophysi: Characiformes): a phylogenetic study and a revision of the species east of the Andes. *Smithsonian Contributions to Zoology* 2001;612: 1–239.
- Vari RP, Melo BF, Oliveira C. Protocheirodon, a new genus of Characidae (Teleostei: Characiformes) with the redescription of the poorly known Protocheirodon pi. Neotropical Ichthyology 2016;14:315–22.
- Weitzman SH. A new species of characoid fish, *Hyphessobrycon diancistrus*, from the Rio Vichada, Orinoco River drainage, Colombia,

South America (Teleostei: Characidae). Proceedings of the Biological Society of Washington 1977;**90**:348–57.

- Weitzman SH, Fink WL. Relationships of the neon tetras, a group of South American freshwater fishes (Teleostei: Characidae), with comments on the phylogeny of new world characiforms. Bulletin of the Museum of Comparative Zoology 1983;150:339–95.
- Weitzman SH, Fink SV. Xenurobryconin phylogeny and putative pheromone pumps in Glandulocaudine fishes (Teleostei: Characidae). *Smithsonian Contributions to Zoology* 1985;421:1–121. https://doi. org/10.5479/si.00810282.421
- Weitzman SH, Malabarba LR. Systematics of spintherobolus (Teleostei: Characidae: Cheirodontinae) from Eastern Brazil. Ichthyological Exploration of Freshwaters 1998;10:1-44.
- Weitzman SH, Menezes NA. Relationships of the tribes and genera of the Glandulocaudinae (Ostariophysi: Characiformes: Characidae) with a description of a new genus, *Chrysobrycon*. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CA (eds), *Phylogeny and Classification of Neotropical Fishes*. Porto Alegre: Edipucrs, 1998, 171–92.
- Weitzman SH, Palmer L. A new species of *Hyphessobrycon* (Teleostei: Characidae) from the Neblina region of Venezuela and Brazil, with comments on the putative 'rosy tetra clade'. *Ichthyological Exploration* of Freshwaters 1997;7:209–42.
- Weitzman SH, Vari RP. Miniaturization in South American freshwater fishes; an overview and discussion. Proceedings of the Biological Society of Washington 1988;101:444–65.
- Weitzman SH, Menezes NA, Britski HA. Nematocharax venustus, a new genus and species from the Rio Jequitinhonha, Minas Gerais, Brazil (Teleostei: Characidae). Proceedings of the Biological Society of Washington 1986;99:335–46.
- Weitzman SH, Menezes NA, Weitzman MJ. Phylogenetic biogeography of the Glandulocaudini (Teleostei: Characiformes: Characidae) with comments on the distribution of other freshwater fishes in eastern and southeastern Brazil. In: Vanzolini PE, Heyer WR (eds), Proceedings

of a Workshop on Neotropical Distribution Patterns. Rio de Janeiro: Academia Brasileira de Ciências, 1988, 379–427.

- Weitzman SH, Menezes NA, Evers H-G *et al.* Putative relationships among inseminating and externally fertilizing characids, with a description of a new genus and species of Brazilian inseminating fish bearing an anal-fin gland in males (Characiformes: Characidae). *Neotropical Ichthyology* 2005;**3**:329–60.
- Youngh D, Gillung JP. Phylogenomics—principles, opportunities and pitfalls of big-data phylogenetics. *Systematic Entomology* 2020;45:225–47.
- Zanata AM. *Jupiaba*, um novo gênero de Tetragonopterinae com osso pélvico em forma de espinho (Characidae, Characiformes). *Iheringia, Série Zoologia* 1997;**83**:99–136.
- Zanata AM, Akama A. *Myxiops aphos*, new characid genus and species (Characiformes: Characidae) from the rio Lençóis, Bahia, Brazil. *Neotropical Ichthyology* 2004;2:45–54. https://doi.org/10.1590/ s1679-62252004000200001
- Zanata AM, Camelier P. A new species of Characidium (Characiformes: Crenuchidae) from small coastal drainages in northeastern Brazil, with remarks on the pseudotympanum of some species of the genus. *Neotropical Ichthyology* 2014;**12**:333–42. https://doi. org/10.1590/1982-0224-20130168
- Zanata AM, Camelier P. Two new species of *Characidium* Reinhardt (Characiformes: Crenuchidae) from northeastern Brazilian coastal drainages. *Neotropical Ichthyology* 2015;**13**:487–98. https://doi. org/10.1590/1982-0224-20140106
- Zanata AM, Lima FCT. New species of *Jupiaba* (Characiformes: Characidae) from Rio Tiquié, Upper Rio Negro Basin, Brazil. *Copeia* 2005;**2005**:272–8. https://doi.org/10.1643/ci-04-155r1
- Zarske A. Der Kolibrisalmer- *Trochilocharax ornatus* gen. et spec. nov.—ein neuer Salmler aus Peru (Teleostei: Characiformes: Characidae). *Vertebrate Zoology* 2010;**60**:75–98. https://doi.org/10.3897/vz.60.e30995
- Zerbino DR, Birney EV. algorithms for de novo short read assembly using de Bruijn graphs. *Genome Research* 2008;**18**:821–9.