Neotropical Ichthyology

Original article

https://doi.org/10.1590/1982-0224-2024-0108

urn:lsid:zoobank.org:pub:77F9CE7F-F821-4D64-9DDB-A9CB358F0119

New tribe-level classification of Hypostominae (Loricariidae) based on optimization of morphological states on DNA-based relationships, with descriptions of three new tribes and two new genera

Correspondence:
Jonathan W. Armbruster
armbrjw@auburn.edu

Jonathan W. Armbruster[1] and Nathan K. Lujan[2]

Hypostominae tribe-level taxonomy is revised with new recognition and cladistic diagnoses of previously proposed family-level names for the *Acanthicus* (Acanthicini), *Chaetostoma* (Chaetostomatini), and *Hemiancistrus* (Spectracanthicini) clades. Three new tribes are described for the *Peckoltia*, *Pseudancistrus*, and '*Pseudancistrus*' clades, with a new tribe erected for two new monotypic genera containing the sister species '*Pseudancistrus*' *sidereus* and '*P.*' *pectegenitor*. This third new tribe is known only from the upper Orinoco and Negro Rivers and is identifiable by having an accentuated keel on the caudal peduncle formed by dorsal laminae of the ventral plate series being strongly concave. The new genera are distinguishable by '*P.*' *pectegenitor* having extremely long cheek odontodes reaching to the third plate of midventral plate series (*vs.* anterior to opercular opening in '*P.*' *sidereus*) and 10 (*vs.* 7) branched dorsal-fin rays. We re-optimized morphological character-state change by mapping states previously used to infer evolutionary history onto a composite phylogenetic tree inferred from DNA-sequence data. This revealed the strong influence on morphology-based phylogenies of a correlated suite of opercular character states related to the mechanism for cheek odontode eversion. These states appear to be plesiomorphic within Hypostominae and to have been independently lost or reduced multiple times.

Keywords: Character analysis, Morphology, Phylogeny, *Pseudancistrus*, Venezuela.

Submitted July 11, 2024
Accepted October 31, 2024
by George Mattox
Epub January 10, 2025

Online version ISSN 1982-0224
Print version ISSN 1679-6225

Neotrop. Ichthyol.
vol. 22, no. 4, Maringá 2024

1 Auburn University Museum of Natural History, 101 Life Sciences Building, 120 W. Samford Avenue, Auburn University, AL, 36849, USA. armbrjw@auburn.edu (corresponding author).

2 Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, M5S 2C6, Canada, and Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario, M5S 3B2, Canada. nlujan@rom.on.ca.

A taxonomia no nível da tribo Hypostominae é revisada, com novo reconhecimento e diagnoses cladísticas de nomes previamente propostos em nível de família para os clados de *Acanthicus* (Acanthicini), *Chaetostoma* (Chaetostomatini) e *Hemiancistus* (Spectracanthicini). Três novas tribos são descritas para os clados de *Peckoltia*, *Pseudancistrus* e '*Pseudancistrus*', com uma nova tribo erigida para dois novos gêneros monotípicos contendo as espécies irmãs '*Pseudancistrus*' *sidereus* e '*P.*' *pectegenitor*. Essa terceira nova tribo é conhecida somente das partes superiores dos rios Negro e Orinoco e pode ser identificada pela presença de uma quilha acentuada no pedúnculo caudal, formada por uma lâmina dorsal das placas da série ventral, que são fortemente côncavas. Os novos gêneros se distinguem por '*P*'. *pectegenitor* possuir odontódeos extremamente longos na região opercular, alcançando até a terceira placa da série médio-ventral (*vs*. anterior à abertura opercular em '*P*'. *sidereus*) e 10 (*vs*. 7) raios ramificados na nadadeira dorsal. Nós otimizamos novamente as mudanças de estado dos caracteres morfológicos colocando os estados previamente utilizados para inferir histórias evolutivas em uma árvore filogenética composta, inferida a partir de sequências de DNA. Isso revelou que um conjunto correlacionado de estados de caracteres operculares envolvidos com o mecanismo de eversão dos odontódeos da região opercular tem influência historicamente forte nas filogenias baseadas em morfologia. Esses estados parecem ser plesiomórficos dentro de Hypostominae, sendo perdidos, ou reduzidos, de maneira independente múltiplas vezes.

Palavras-chave: Análise de caracteres, Filogenia, Morfologia, *Pseudancistrus*, Venezuela.

INTRODUCTION

The suckermouth armored catfish family Loricariidae is the fifth-richest family of vertebrates and richest family of catfishes with over 1,060 species described (Fricke *et al*., 2024). Within Loricariidae, nearly half of all species (508; 48%) are assigned to the subfamily Hypostominae, with most remaining species being distributed across subfamilies Loricariinae (276; 26%), Hypoptopomatinae (263; 25%), Delturinae (7), Rhinelepinae (6), and Lithogeninae (3; Fricke *et al*., 2024).

Systematic study of Hypostominae was dominated by phenetic approaches (Regan, 1904; Isbrücker *et al*., 2001) until the first morphology-based cladistic analyses of Howes (1983) and Schaefer (1986), which marked the beginning of a gradual shift toward exclusively cladistic methodologies. Cladistic studies progressively encompassed more taxa and characters until the essentially comprehensive morphology-based analyses by Armbruster (2004a, 2008) and Armbruster, Taphorn (2011). DNA-based studies of Hypostominae began with a study of two mitochondrial rRNA gene regions (12S, 16S) and eight genera (Montoya-Burgos *et al*., 1997) and progressively included more loci and taxa, resulting most recently in the Lujan *et al*. (2015a) study of 49 genera using two mitochondrial and three nuclear markers and the Roxo *et al*. (2019) study of 30 genera using genome-wide ultraconserved elements. Regardless of taxonomic breadth and

data magnitude, the revised systematic understanding of Hypostominae provided by DNA-based analyses has been largely consistent across studies, and consistently highly divergent from previous morphology-based inferences.

Comparisons of Hypostominae intergeneric relationships based on DNA versus morphology highlight two major types of discrepancy: morphological support for assigning species to genera that DNA-based studies later find to be paraphyletic, and morphological support for various distinct genera that later DNA-based studies find to be nested within an existing genus. Armbruster's (2004a,b) lumping of many species into *Pseudancistrus* Bleeker, 1862 is an example of the former, with later DNA-based studies (Covain, Fisch-Muller, 2012; Lujan *et al*., 2015a) finding this broader *Pseudancistrus* to be polyphyletic. Examples of the latter include Lujan, Ambruster's (2011) morphology-based description of *Micracanthicus vandragti* Lujan & Armbruster, 2011 and *Soromonichthys stearleyi* Lujan & Armbruster, 2011 as new genera, with Lujan *et al*. (2015a) finding the former to be nested within *Hypancistrus* Isbrücker & Nijssen, 1991 and the latter within *Pseudolithoxus* Isbrücker & Werner, 2001 (in Isbrücker *et al*., 2001). Deeper in the phylogeny, molecular analyses also support clades that would probably never have been considered based on morphology alone, such as the close relationship of *Corymbophanes* Eigenmann, 1909 with *Hopliancistrus* Isbrücker & Nijssen, 1989 (Lujan *et al*., 2015a). *Corymbophanes* lacks evertible cheek odontodes (Armbruster, Provenzano, 2000; Lujan *et al*., 2019) while *Hopliancistrus* has the most extreme cheek odontode eversion capability known (Oliveira *et al*., 2021).

Numerous such examples of molecular-morphological discrepancies just within Hypostominae illustrate the complexity of loricariid morphological evolution, with homoplastic characters appearing to have heavily influenced the classification schemes still in use today. These numerous and pervasive discrepancies illustrate the growing need for a thoroughly updated tribe and genus-level classification of Hypostominae based on an integration of results from both data sources. We begin that process by mapping character states described by Armbruster (2004a) onto the phylogeny of Lujan *et al*. (2015a), with additional species added per Lujan *et al*. (2015b, 2017, 2018, 2019). Results of this analysis provide a cladistic foundation for not only a revised classification, but also our description of three new tribes and two new genera. The resulting understanding of character state change across Hypostominae further demonstrates that several major loricariid clades currently lack morphological synapomorphies.

Two of the more enigmatic and recently described members of the now polyphyletic genus *Pseudancistrus* are *Pseudancistrus sidereus* Armbruster, 2004b and *P. pectegenitor* Lujan, Armbruster & Sabaj, 2007, both of which were described from the upper Orinoco and Negro River basins in southern Venezuela. *Pseudancistrus pectegenitor* is a wide-bodied, truncate species with a dark-brown base color, tiny light spots or vermiculations, a rounded dorsal fin with 10 or 11 branched dorsal-fin rays, and a caudal fin with a straight margin (Fig. 1A). Mature specimens have cheek odontodes that are among the longest seen in the Hypostominae (up to 60 mm) and a snout margined with enlarged odontodes up to 7 mm long. In contrast, *Pseudancistrus sidereus* is elongate for a hypostomine, has a dark gray base color with golden spots, a falcate dorsal fin with seven branched dorsal-fin rays, and a strongly asymmetrical caudal fin with the lower lobe much longer than the upper, and even mature males have very short cheek odontodes and no hypertrophied odontodes along the snout margin (Fig. 1B). Despite the dramatic

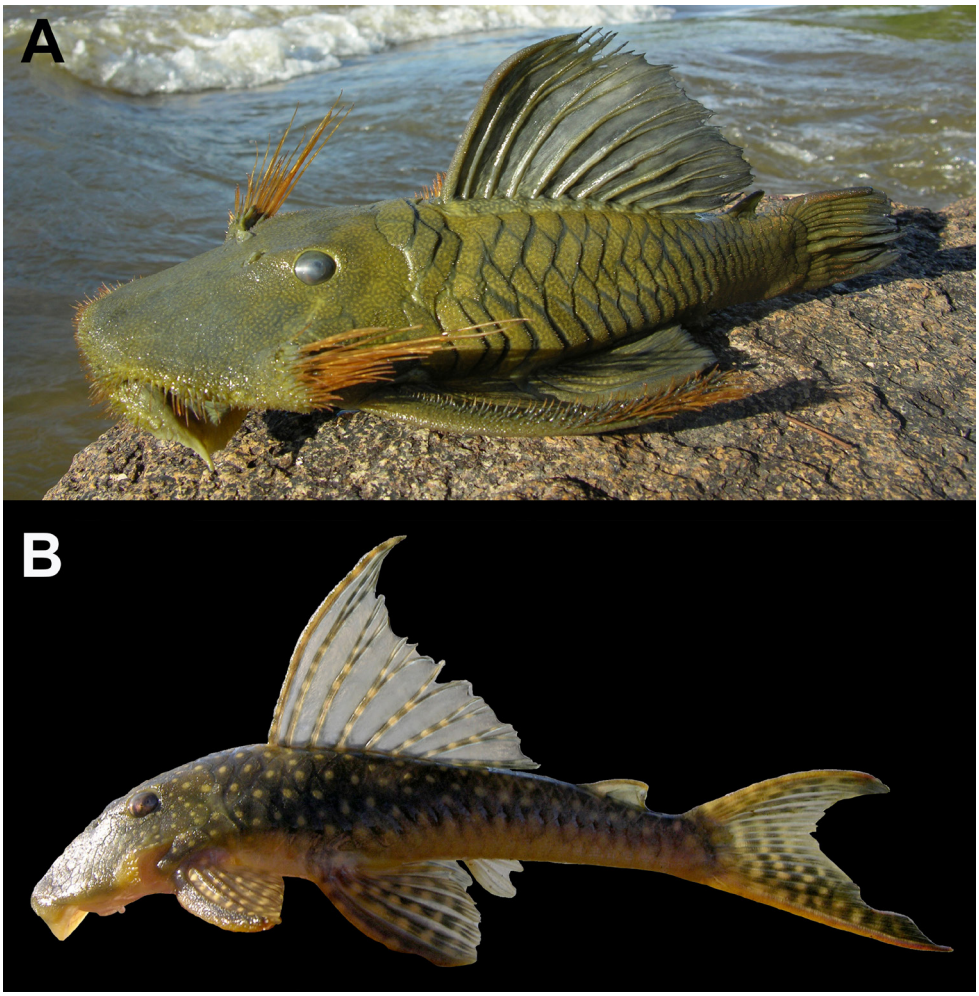

FIGURE 1 | **A.** *Colossimystax pectegenitor*, Holotype, MCNG 54797, 241.6 mm SL. Photo by NKL. **B.** *Stellantia siderea*, AUM 43443, 147.1 mm SL. The two genera are described below. Photo by M. H. Sabaj.

morphological contrast between these species, molecular analyses have consistently strongly supported them as each other's sister species, forming a clade that is distantly related to *Pseudancistrus sensu stricto* (*i.e.*, clade containing the type-species *Pseudancistrus barbatus* Valenciennes, 1840; Covain, Fisch-Muller, 2012; Lujan *et al.*, 2015a; Roxo *et al.*, 2019). To indicate this, Lujan *et al.* (2015a) referred to them as '*Pseudancistrus*' with single quotation marks. Despite their radically divergent appearance, they do share a unique characteristic. Armbruster (2004b) first noted that the caudal peduncle of '*P.*' *sidereus* has a strongly accentuated keel formed by the strongly concave dorsal laminae of the ventral series of plates (Fig. 2B). While a keel in this region of the caudal peduncle is not unusual in Hypostominae, due to the necessity that the ventral plates bend medially to follow the flattened ventral profile of the caudal peduncle, the degree of concavity and the accentuation of the curve was considered unique in '*P.*' *sidereus*. This keel is even more strongly formed in '*P.*' *pectegenitor* (Lujan *et al.*, 2007, Fig. 2C).

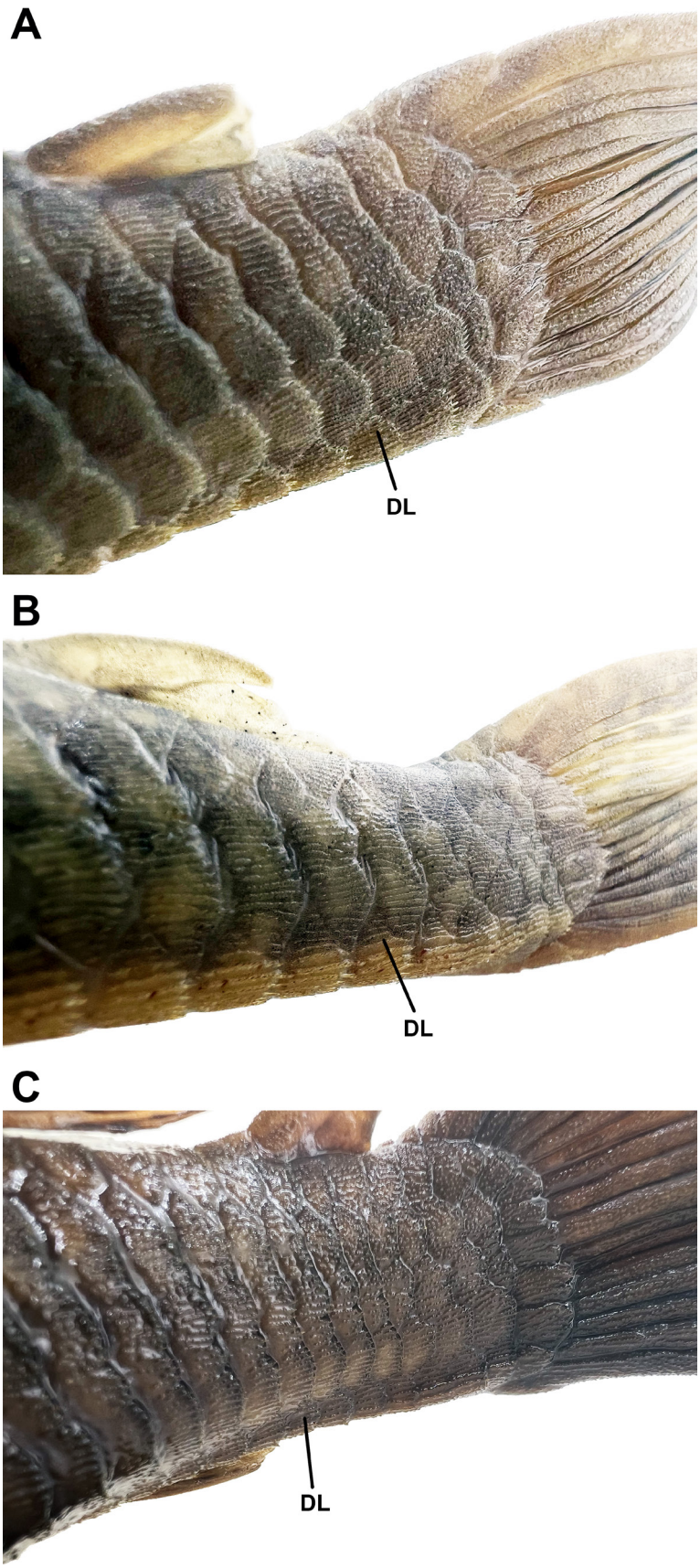

FIGURE 2 | Caudal peduncles of **A.** *Pseudancistrus nigrescens*, AUM 35742, 137.2 mm SL; **B.** *Stellantia siderea*, AUM 42185, 180.0 mm SL; and **C.** *Colossimystax pectegenitor*, paratype, AUM 42202, 227.0 mm SL. DL is the dorsal lamina of the indicated plate, and the keel lies just ventral. In **A**, there is only a slight keel (~3 plates) with the dorsal laminae straight to very slightly concave while the keel extends in front of the adipose fin in **B** and **C** and the dorsal laminae are concave.

While molecular phylogenies have revealed many new candidate genera in Hypostominae, these southern Venezuelan '*Pseudancistrus*' species are among the best studied, most morphologically distinct, and easiest to diagnose from other Hypostominae genera. The species are clearly very different from one another such that one would likely not posit them to be closely related at first glance; thus, we erect two monotypic genera for these species.

MATERIAL AND METHODS

Specimens for osteological examination were either cleared and double-stained following Taylor, Van Dyke (1985) or µCT-scanned at varying resolutions (1.4–14.0 µm) using either a GE vltomelx s240 dual tube 240/180 kV system (General Electric, Fairfield, CT, USA) or a Bruker Skyscan 1173 high-energy micro-CT (Bruker Inc, Billerica, MA, USA). CT data were edited, segmented, and colorized using VGStudio Max (v. 3.3–v2023.3; Volume Graphics, Heidelberg, Germany).

Counts and measurements follow Armbruster (2003). To determine character polarity a tree was constructed in Mesquite (Maddison, Maddison, 2023) based on Lujan *et al*. (2015a, 2015b, 2017, 2018, and 2019) with the characters of Armbruster (2004a, 2008) mapped to the phylogeny. *Araichthys* Zawadzki, Bifi & Mariotto, 2016 was added per the characters listed in Zawadzki *et al*. (2016), *Paulasquama* Armbruster & Taphorn, 2011 per Armbruster, Taphorn (2011), and *Hemiancistrus medians* (Kner, 1854) per Armbruster *et al*. (2015) (matrix and tree in Tab. **S1**). Taxa were entered and a tree created in Mesquite v. 3.8 (Maddison, Maddison, 2023). The tree was transferred into MacClade v. 4.05 (Maddison, Maddison, 2002) to produce a table of character state changes (Tab. **S2**). Characters are predominantly osteological and meristic and are presented as the number: state or state change (*i.e*., 11: 0>1 represents character 11 changing from 0 to 1 at the node) with character numbers from Armbruster (2004a). Phylogenetic diagnoses are given as summaries of the character state changes on the tree. An additional comparative diagnosis summarizes the most useful external characters for visually distinguishing each taxon from other members of the Hypostominae. Clades for which tribe-level names are available have those names assigned and new tribes are described for the *Peckoltia*, *Pseudancistrus*, and '*Pseudancistrus*' clades *sensu* Lujan *et al*. (2015a; relationships in fig. 3).

Geographic distributions were mapped in QGIS, v. 3.30.0 (QGIS Development Team, 2023). Rivers are from the HydroRIVERS v. 1.0 (Lehner, Grill, 2013), and river widths are represented as interpolated lines based on average discharge (DIS_AV_CMS) with only streams of six cubic meters per second or greater shown. Lakes are from the HydroLAKES v. 1 (Messager *et al*., 2016). Digital Elevation Model and Hillshade from Mapzen (https://www.mapzen.com). Country borders are from NaturalEarth (1:10m, file ne_10m_admin_countires, v. 5.1.1, naturalearthdata.com). Localities are from Armbruster (2004b), Lujan *et al*. (2007), and additional records added into the AUM database since publication. Museum acronyms are per Sabaj (2020).

RESULTS

Tribes. Four previously recognized family-level names are recognized for the following clades as named in Lujan *et al*. (2015a): Acanthicini Bleeker, 1862 for the *Acanthicus* Clade, Chaetostomatini Fowler, 1958 for the *Chaetostoma* clade, Lithoxini Isbrücker, 1980 for the *Lithoxus* clade (also recognized in Lujan *et al*., 2018), and Spectracanthicini Isbrücker & Nijssen, 1989 for the *Hemiancistrus* clade. We additionally describe three new tribes (Peckoltini, Pseudancistrini, and Stellantini) for the *Peckoltia*, *Pseudancistrus*, and '*Pseudancistrus*' clades *sensu* Lujan *et al*. (2015a) as well as two new genera for Stellantini, new tribe.

Phylogeny. Tribe-level nodes for Acanthicini (8 characters), Lithoxini (31 characters), and Chaetostomatini (18 characters) were well supported following our placement of the morphological characters of Armbruster (2004a, 2008) on the composite molecular phylogeny. Many other nodes were supported by few or no character states (Fig. 3). For example, Peckoltini and its relationship with Hypostomini is not supported by any characters and Hypostomini is supported by only one. Within Ancistrini, no characters support the clade of *Corymbophanes*, *Yaluwak*, *Araichthys*, *Cryptancistrus*, *Hopliancistrus*, and *Guyanancistrus* nor that clade plus *Dekeyseria*. Also in Ancistrini, no characters support the clade of *Neblinichthys* plus *Paulasquama* nor that clade plus *Lithoxancistrus*. The clade of *Neblinichthys*, *Paulasquama*, and *Lithoxancistrus* is supported as sister to the remaining Ancistrini by three characters; however, in other analyses we have run, this clade is not part of the Ancistrini and will need further exploration. Taxa that were not supported within their current clades in the morphological analyses often have very strong support because what had been synapomorphies for larger clades are now autapomorphies for the individual elements. Examples include *Guyanancistrus* (18 characters), *Corymbophanes* (28), *Paulasquama* (17), *Neblinichthys* (11), *Stellantia*, new genus (9), *Colossimystax*, new genus (14), *Panaque* (19), *Spectracanthicus* (11), *Parancistrus* (15), and *Scobinancistrus* (9). The large numbers of characters along these branches suggests that morphological change in loricariids can be quite rapid.

Subfamily Hypostominae

Included tribes (with unrecognized tribes and subtribes listed as synonyms).

Acanthicini Bleeker, 1862–63:2. Synonym: Pseudacanthicini Isbrücker, 1980.

Ancistrini Kner, 1854:256. Synonyms: Corymbophanini Armbruster, 2004a, Hopliancistrini Isbrücker & Nijssen, 1989.

Chaetostomatini Fowler, 1958:14

Hypostomini Kner, 1853a:279. Synonyms: Plecostiformes Bleeker, 1862, Pterygoplichthyini Armbruster, 2004a

Lithoxini Isbrücker, 1980:77

Peckoltini, new tribe

Pseudancistrini, new tribe

Spectracanthicini Isbrücker & Nijssen, 1989

Stellantini, new tribe

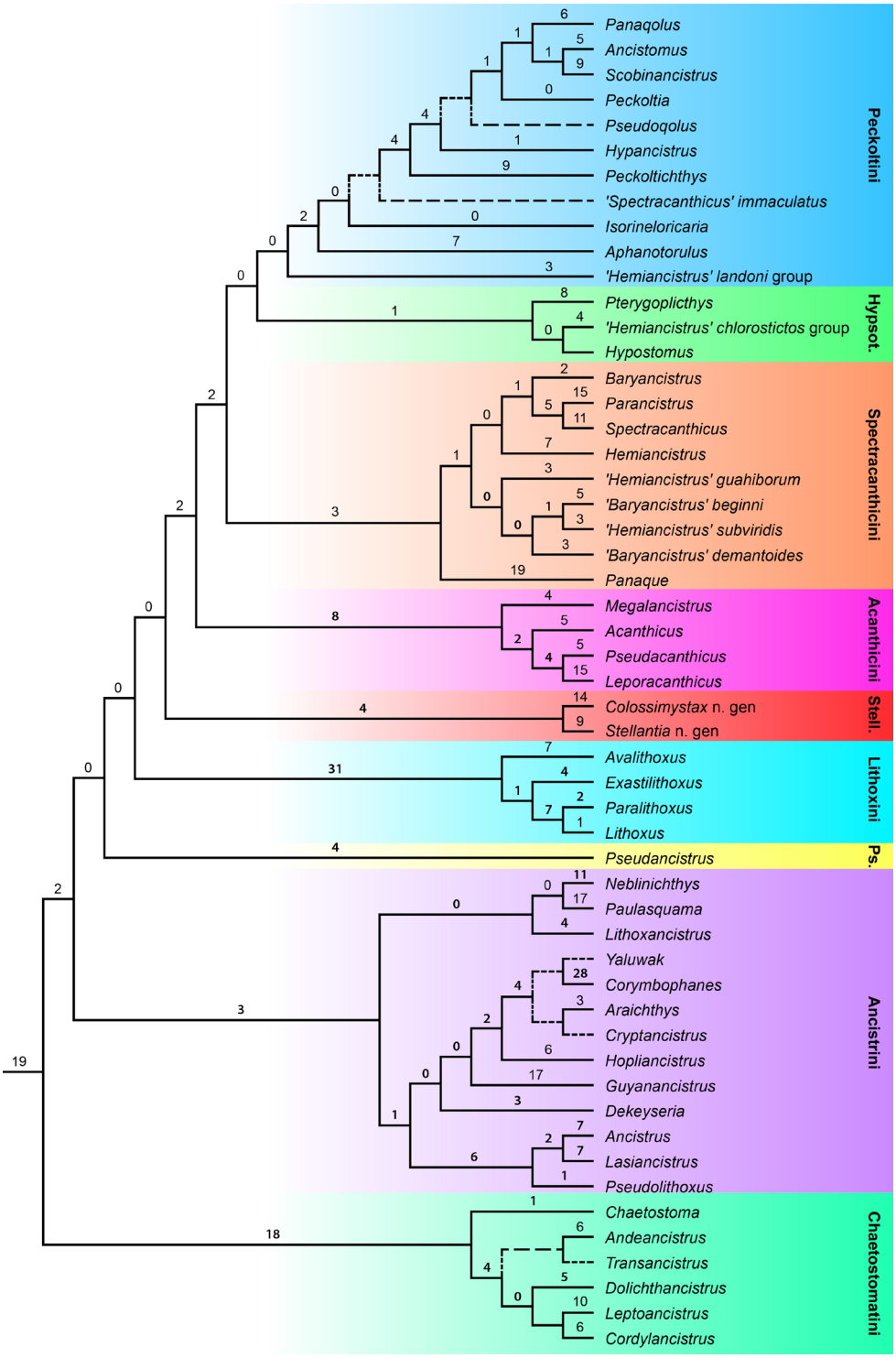

FIGURE 3 | Relationships of the clades of the genera of Hypostominae based on Lujan *et al.* (2015a,b, 2017, 2018, 2019). Stellantini, new tribe (abbreviated as Stell.), Peckoltini, new tribe, and Pseudancistrini, new tribe (abbreviated as Ps.) are described herein. Dashed lines represent species that were not available for morphological analysis. Numbers above branches represent the number of character state changes from Tab. **S2**.

Phylogenetic diagnosis. Accessory process of first ceratobranchial same length as main body and wide (7:2, 8:2), interhyal contacting bony portion of quadrate (26:2), either hyomandibula, quadrate or both with projections towards one another or sutured (33:1), preopercle with short posterior section appearing to be oriented almost vertically (61:1), quadrate with posteroventral projection that extends below symplectic foramen (66:1), a sickle-shaped opercle (75:1; note that opercle shape is especially variable within Hypostominae), one or more plates between suprapreopercle and opercle (81:1), one small canal plate (83:1), canal plate contacting the suspensorium (85:1), two or more plates between canal plate and opercle (88:2), 8–11 vertebrae from first normal neural spine behind dorsal fin up to, but not including, the hypural plate (121:2), ventral half of hypural plate longer than dorsal (123:1), reversal to a V-shaped spinelet (148:0), anterolateral process of basipterygium wide through entire length (169:1), posterovenral ridge of basipterygium present (173:1), hypertrophied cheek odontodes present regardless of season or sex (183:2), fully or slightly evertible cheek plates (184:1–2; ability to at least partially evert cheek plates is unique to Hypostominae with the possible exception of '*Pseudancistrus*' *genisetiger*), pectoral fin inserted ventrally such that it is aligned with and reaches or overlaps the pelvic fin (190:1; only seen in *Pogonopoma* outside of Hypostominae and reversed in *Corymbophanes*).

Comparative diagnosis. There are no universal character states that diagnose all Hypostominae from all other Loricariidae. The most widely diagnostic character states are cheek plates that evert forming a 30° to just greater than 90° from side of head (*vs*. not evertible; angle depends on species) and pectoral fin inserted ventrally such that it is aligned with and reaches or overlaps the pelvic fin (*vs*. pectoral fins distinctly dorsal to pelvic fins in all loricariids except *Pogonopoma*; *Corymbophanes* of the Hypostominae has the pectoral fins just slightly dorsal to the pelvics). Hypostominae can be separated from Lithogeninae by having the body fully plated (*vs*. anterior plates missing or non-overlapping); from Delturinae by having an adipose-fin spine followed by a membrane or a postdorsal ridge made of azygous plates with maximally a very small membrane (*vs*. postdorsal ridge made of azygous plates followed by an adipose-fin spine and membrane); from Rhinelepinae and Loricariinae by generally having an adipose fin or postdorsal ridge of azygous plates (*vs*. adipose fin and postdorsal ridge absent), from Rhinelepinae by generally having an iris operculum (*vs*. absent, some hypostomines lack an iris operculum, but they all have adipose fins or postdorsal ridges); from Loricariinae by generally not being extremely dorsoventrally flattened and elongated (only exceptions may be members of Lithoxini, which have evertible cheek plates present *vs.* absent and an adipose fin, and *Isorineloricaria* which has an adipose fin and five rows of plates on the caudal peduncle *vs.* three); from Hypoptopomatinae (except Neoplecostomini) by having maximally the lateral portion of the pectoral girdle exposed and supporting odontodes (*vs*. most or all of pectoral girdle exposed and supporting odontodes); from Hypoptopomatinae: Neoplecostomini by having hypertrophied odontodes generally absent along the snout of nuptial males or, when hypertrophied odontodes are present, they are not in thick integument (*vs.* generally having males with hypertrophied snout odontodes that are embedded in integument skin); and from '*Pseudancistrus*' *genesetiger* and '*P.*' *papariae* by having three or five rows of plates on the caudal peduncle (*vs.* four), and by either not having hypertrophied odontodes along the snout or on the cheek or

having them clearly separated by plates contiguous with remaining plates of the snout and head (*vs.* hypertrophied snout and cheek odontodes supported by deeply embedded, flesh-covered, hidden plates that are sunken medially such that other snout plates and the opercle form a shelf dorsal and lateral to the bases of the odontodes).

Geographical distribution. Hypostominae is broadly distributed throughout cis-Andean South America from the Parana basin northward, and throughout trans-Andean drainages from the Tumbes basin in northern Peru to the Terraba River in eastern Costa Rica.

Tribe Acanthicini Bleeker, 1862–1863

Included genera.

Acanthicus Agassiz, 1829:2 (in Spix, Agassiz, 1829). Type-species: *Acanthicus hystrix* Spix & Agassiz, 1829.

Leporacanthicus Isbrücker, Nijssen, 1989:544. Type-species: *Leporacanthicus galaxias* Isbrücker & Nijssen, 1989.

Megalancistrus Isbrücker, 1980:52. Type-species: *Chaetostoma gigas* Boulenger, 1895.

Pseudacanthicus Bleeker, 1862:2. Type-species: *Chaetostomus serratus* Valenciennes, 1840 (in Cuvier, Valenciennes, 1840). Synonym: *Stoniella* Fowler, 1914.

Phylogenetic diagnosis. Anterohyal greatest width greater than half its length (1:1), loss of flap on quadrate extending below symplectic foramen (66:0), mesethmoid disk extending anterior to main body of mesethmoid (101:1), large fenestrae in compound pterotic (109:1, reversed in *Leporacanthicus*), tip of transverse process of Weberian complex centrum not contacting compound pterotic (135:1, reversed in *Leporacanthicus*), eight or more dorsal-fin rays (142:1), hypertrophied odontodes along snout margin (188>1), and keels of lateral plates well developed (198:1).

Comparative diagnosis. Acanthicini can be separated from all other Hypostominae except some *Pterygoplichthys* Gill, 1858 (particularly *P. weberi*) by having lateral-plate keels made of long, stout odontodes, from all other Hypostominae except *Colossimystax* and *Pterygoplichthys* by having more than seven dorsal-fin rays, and from *Pterygoplichthys* with keels by having strongly evertible cheek odontodes (*vs.* weakly evertible), by having fewer odontodes dorsal and ventral to keel rows (*vs.* odontodes normally distributed). In addition, *Acanthicus* can be separated from *Pterygoplichthys* by lacking an adipose fin (*vs.* adipose fin present), *Acanthicus* and *Megalancistrus* can be separated from *Pterygoplichthys* by having compound pterotic extending beyond posteriormost insertion of pectoral fin (*vs.* maximally through ~3/4 of pectoral-fin base); and *Leporacanthicus* and *Pseudacanthicus* can be separated from *Pterygoplichthys* by having 10 or fewer teeth per jaw ramus (*vs.* more than 20).

Geographical distribution. Restricted to larger, main river channel habitats in cis-Andean drainages from the Paraná and São Francisco basins northward, including the Amazon and Orinoco basins and north-flowing Guiana Shield basins.

Tribe Ancistrini Kner, 1854

Included genera.

Ancistrus Kner, 1854:272. Type-species: *Hypostomus cirrhosus* Valenciennes, 1836 (in Valenciennes, 1834–39). Synonyms: *Pristiancistrus* Fowler, 1945, *Thysanocara* Regan, 1906, and *Xenocara* Regan, 1904.

Araichthys Zawadzki *et al*., 2016:362. Type-species: *A. loro* Zawadzki, Bifi & Mariotto, 2016.

Corymbophanes Eigenmann, 1909:5. Type-species: *Corymbophanes andersoni* Eigenmann, 1909.

Cryptancistrus Fisch-Muller *et al*., 2018:50. Type-species: *C. similis* Fisch-Muller, Mol & Covain, 2018.

Dekeyseria Rapp Py-Daniel, 1985:178. Type-species: *D. amazonica* Rapp Py-Daniel, 1985. Synonym: *Zonancistrus* Isbrücker, 2001 (in Isbrücker *et al*., 2001).

Guyanancistrus Isbrücker, 2001:19 (in Isbrücker *et al*., 2001). Type-species: *Lasiancistrus brevispinis* Heitmans, Nijssen & Isbrücker, 1983.

Hopliancistrus Isbrücker, Nijssen, 1989:543. Type-species: *H. tricornis* Isbrücker & Nijssen, 1989.

Lasiancistrus Regan, 1904:224. Type-species: *Chaetostomus heteracanthus* Günther, 1869. See Armbruster, 2005.

Neblinichthys Ferraris *et al*., 1986:70. Type-species: *N. pilosus* Ferraris, Isbrücker & Nijssen, 1986.

Lithoxancistrus Isbrücker *et al*., 1988:14. Type-species: *L. orinoco* Isbrücker, Nijssen & Cala, 1988.

Paulasquama Armbruster, Taphorn, 2011:46. Type-species: *P. callis* Armbruster & Taphorn, 2011.

Pseudolithoxus Isbrücker, Werner, 2001:21 (in Isbrücker *et al*., 2001). Type-species: *Lasiancistrus tigris* Armbruster & Provenzano, 2000. Synonym: *Soromonichthys* Lujan & Armbruster, 2011.

Yaluwak Lujan, Armbruster, 2019 (in Lujan *et al*., 2019). Type-species: *Yaluwak primus* Lujan, Armbruster & Werneke (in Lujan *et al*., 2019).

Phylogenetic diagnosis. No characters unite tribe Ancistrini as all character state changes at the node are reversed in a majority of taxa. Character state changes found at the node are hypertrophied odontodes along snout margin (188:1), snout and pectoral-fin odontode sheaths separated from odontode forming short tentacules (208:1, 209:1).

Comparative diagnosis. The diversity of forms within Ancistrini results in no characteristics that can readily separate it from all other tribes. *Ancistrus*, *Araichthys*, *Corymbophanes*, *Dekeyseria*, *Lasiancistrus*, *Neblinichthys*, and *Pseudolithoxus* can be separated from all Hypostomini by having three rows of plates on the caudal peduncle (*vs.* five, rarely four). *Araichthys*, *Corymbophanes*, some *Neblinichthys*, and *Yaluwak* can be separated from most other Hypostominae by lacking an iris operculum (the dorsal flap that bifurcates the dorsal part of the eye in most loricariids). *Hopliancistrus* can be separated from all other Hypostominae by generally having three large, stout, continuously curved evertible cheek odontodes (*vs.* no hypertrophied cheek odontodes or more or less than three with odontodes generally slender and hooked only distally, not curved throughout). *Cryptancistrus*, *Hopliancistrus*, and *Lasiancistrus* can be separated from all other Hypostominae by having hypertrophied odontodes at anterior corner of snout (see Armbruster, 2005). *Guyanancistrus* is not readily diagnosable from other Hypostominae, see Fisch-Muller *et al*. (2018) for review.

Geographical distribution. Found in all cis-Andean drainages from the La Plata River basin northward (including Trinidad) and trans-Andean basins from southern Ecuador to just east of the Herrera Peninsula, Panamá.

Tribe Chaetostomatini Fowler, 1958

Included genera.

Andeancistrus Lujan *et al*., 2015b:652. Type-species: *Chaetostomus platycephalus* Boulenger, 1898.

Chaetostoma Tschudi, 1846:25. Type-species: *Chaetostomus loborhynchos* Tschudi, 1846. Synonyms: *Hypocolpterus* Fowler, 1943, *Lipopterichthys* Norman, 1935, and *Loraxichthys* Salcedo, 2013.

Cordylancistrus Isbrücker, 1980:48. Type-species: *Pseudancistrus torbesensis* Schultz, 1944.

Dolichancistrus Isbrücker, 1980:47. Type-species: *Pseudancistrus pediculatus* Eigenmann, 1918 [a junior synonym of *Dolichancistrus fuesslii* (Steindachner, 1911].

Leptoancistrus Meek, Hildebrand, 1916:254. Type-species: *Acanthicus canensis* Meek & Hildebrand, 1913.

Transancistrus Lujan *et al*., 2015b:657. Type-species: *Cordylancistrus santarosensis* Tan & Armbruster, 2012.

Phylogenetic diagnosis. Anterior edge of the anterohyal sinusoidal (2:1, reversed in *Cordylancistrus torbesensis* and *Dolichancistrus cobrensis*), mesial facing process on branchiostegal 3 (6:1, unique), reversal to a large interhyal (27:0), long opercular condyle of the hyomandibula (38:1), tall levator arcus palatini crest (44:2), mesial wall of metapterygoid channel much taller than lateral wall (55:1, reversed in *Cordylancistrus torbesensis*), ventral process on quadrate for articulation with canal plate (65:1), wide, blunt articular condyle of quadrate (67:1), bar-shaped opercle (75:2), maximum forward position of opercle to posterolateral corner of the quadrate (77:1, reversed in *Andeancistrus* and some *Chaetostoma*), canal plate covered in skin or plates and not directly supporting odontodes (84:1, unique), tall ridge on lateral ethmoid for contact with metapterygoid (97:2), mesethmoid flares anteriorly (102:1), eight or more dorsal-fin rays (142:1), nuchal plate covered by skin or plates (147:1, nuchal plate may be exposed and supporting odontodes in nuptial male *Dolichancistrus*), reversal to a large space between posterior process of coracoid strut and posterior process of coracoid (164:0), reversal to tall ventral ridge of pelvic basipterygium (172:0), and widened first (unbranched) ray of pelvic fin (177:1, reversed in *Dolichancistrus*).

Comparative diagnosis. Chaetostomatini can be separated from all other Hypostominae except Acanthicini, *Collosimystax* new genus, and *Pterygoplichthys* by having eight or more branched dorsal-fin rays (*vs.* seven); from Acanthicini and *Pterygoplichthys* by lacking elongate patches of sharp odontodes on lateral plate keels (most species lack lateral plate keels entirely, *Andeancistrus platycephalus* and *Chaetostoma spondylus* have round patches of elevated, keel-like odontodes on lateral plates); from *Collosimystax* new genus by mature males having usually zero and maximally two cheek odontodes extending past the head (*vs.* >40), and by having plates in ventral series posterior to anal fin broadly convex (*vs.* dorsal halves of plates concave, forming a strong keel); and from *Pterygoplichthys* by lacking plates on abdomen (*vs.* abdominal plates present), and by having caudal fin truncate or maximally emarginate (*vs.* forked).

Geographical distribution. Most species with exclusively Andean distribution, including cis-Andean streams from southern Peru to the Caribbean Andes west of Caracas (including the Caribbean slope) and trans-Andean basins from the Tumbes River

in Northern Peru to the Chagres River of Panamá. Three species of *Chaetostoma* occur in scattered drainages east of the Andes, such as the Caroni, Caura, and Branco rivers draining the Guiana Shield north in Venezuela and south in Brazil, and a few northern and southern tributaries of the lower Amazon in Brazil (Meza-Vargas *et al*., 2022).

Tribe Hypostomini Kner, 1853

Included genera.

'*Hemiancistrus*' *chlorostictus* group (Armbruster *et al*., 2015).

Hypostomus Lacépède, 1803:144. Type-species: *Hypostomus guacari* Lacépède, 1803. Synonyms: *Cheiridodus* Eigenmann, 1922, *Cochliodon* Heckel, 1854 (in Kner, 1854), *Plecostomus* Gronow 1763, and *Watawata* Isbrücker & Michels, 2001 (in Isbrücker *et al*., 2001).

Pterygoplichthys Gill, 1858:408. Type-species: *Hypostomus duodecimalis* Valenciennes, 1840 (in Cuvier, Valenciennes, 1840). Synonyms: *Glyptoperichthys* Weber, 1991 and *Liposarcus* Günther, 1864.

Phylogenetic diagnosis. No unambiguous character states were found to support Hypostomini.

Comparative diagnosis. Hypostomini contains most of the large, stout-bodied loricariids, but these can be difficult to distinguish from other Hypostominae except by genus or species group. *Hypostomus* (with the exception of *H. cerrado*) differs from all other Hypostomini as well as all other tribes (except *Corymbophanes* of the Ancistrini, *Aphanotorulus*, *Isorineloricaria*, and *Peckoltia relictum* of the Peckoltini, and *Spectracanthicus murinus* of the Spectracanthicini) by having the cheek plates evertible to only about 30° from the head and lacking hypertrophied odontodes (*vs.* 75°+ from the head and having hypertrophied odontodes; *Pseudancistrus* have hypertrophied cheek odontodes, but cannot evert their cheek odontodes beyond 30°); from *Corymbophanes* by having either an adipose fin or fin completely missing without replacement by azygous plates (*vs.* adipose fin replaced by postdorsal ridge of raised azygous plates) and by having an iris operculum (*vs.* iris operculum absent); from *Aphanotorulus* and *Isorineloricaria* by lacking hypertrophied odontodes on the lateral trunk plates of nuptial males (*vs.* lateral plates and/or caudal-fin spines covered in large odontodes in nuptial males), by generally being brown with black spots or saddles or dark gray with light spots (*Hypostomus yaku* is uniformly brown, Martins *et al*., 2014) (*vs.* almost white to light tan with black spots); and by having a small buccal papilla (*vs.* single large or many small buccal papillae); from *Peckoltia relictum* by completely lacking hypertrophied cheek odontodes (*vs.* very small cheek odontodes); and from *S. murinus* by having dorsal fin free from adipose (*vs.* posterior membrane of dorsal fin expanded, entirely adnate to body reaching adipose-fin spine).

Pterygoplicthys can be separated from all other Hypostominae except Acanthicini, Chaetostomatini, and *Colossimystax* by having nine to 14 dorsal-fin rays (*vs.* seven); from Acanthicini by having relatively weak lateral plate keels and associated odontodes (*vs.* strong/sharp), by having odontodes evenly distributed across lateral plates (*vs.* odontodes reduced above and below keel rows), and by having a weaker ability to evert cheek-odontodes; and from Chaetostomatini and *Colossimystax* by having elongate

lateral plate keels (*vs.* keels absent or with rounded clusters of odontodes in *Andeancistrus platycephalus* and *Chaetostoma spondylus* Salcedo & Ortega, 2015) and by having plates on the abdomen (*vs.* plates absent). *Hypostomus cerrado* and the '*Hemiancistrus*' *chlorostictos* group have evertible cheek plates with hypertrophied odontodes.

Hypostomus cerrado can be separated from most other Hypostominae tribes by having weak lateral plate keels and a distally expanded pectoral-fin spine forming a club-like structure in adults (*vs.* no lateral plate keels in most other tribes or very strong keels and associated odontodes in Acanthicini and no expansion of the pectoral-fin spine). The '*Hemiancistrus*' *chlorostictos* group can be separated from *Ancistrus*, *Araichthys*, *Corymbophanes*, *Dekeyseria*, *Lasiancistrus*, *Neblinichthys*, and *Pseudolithoxus* by having five rows of plates on the caudal peduncle (*vs.* three); from *Ancistomus* by either being almost black with white spots or tan with black spots (*vs.* gray with black spots); from *Aphanotorulus* and *Isorineloricaria* by either being almost black with white spots or tan with medium black spots (*vs.* very light gray or tan with small black spots), by nuptial males lacking hypertrophied odontodes on lateral plates (*vs.* nuptial males with hypertrophied odontodes dense and widespread on lateral plates, especially caudally), from *Aphanotorulus* by having a small buccal papilla (*vs.* buccal papilla large or numerous and widespread); from *Baryancistrus*, '*Baryancistrus*', *Parancistrus*, and *Spectracanthicus*, by having a small posterior membrane of the dorsal fin (*vs.* posterior membrane of dorsal fin expanded, reaching the adipose-fin spine in all except *B. longipinnis*); from *Panafilus*, *Panaqolus*, *Panaque*, many *Peckoltia*, *Peckoltichthys*, *Pseudoqolus*, and *Scobinancistrus* by having dentaries long and forming an oblique angle with many small teeth (*vs.* dentaries short and forming an acute angle with fewer, larger teeth) and from remaining *Peckoltia* by being either almost black with white spots or tan with large black spots (*vs.* with dorsal saddles, with very large dark spots, being almost colorless, or having a golden tan background color with no spots); from '*B.*' *demantoides,* '*H.*' *guahiborum*, and '*H.*' *subviridis* by lacking a light edge to the dorsal and/or caudal fins (*vs.* yellow or orange bands along edges of dorsal and/or caudal fins).

Geographical distribution. Hypostomini is broadly distributed across cis-Andean South American drainages from the La Plata River northward (including Trinidad), and trans-Andean drainages from northern Ecuador to the Terraba River of Costa Rica (extending further into Central America than any other loricariid lineage). Introduced populations of mainly *Pterygoplichthys* but also *Hypostomus* are found in tropical and subtropical regions around the world.

Tribe Lithoxini Isbrücker, 1980

Included genera.

Avalithoxus Lujan *et al*., 2018:10. Type-species: *Lithoxus jantjae* Lujan, 2008

Lithoxus Eigenmann, 1910:405. Type-species: *Lithoxus lithoides* Eigenmann, 1912.

Exastilithoxus Isbrücker, Nijssen in Isbrücker, 1979:88. Type-species: *Pseudacanthicus* (*Lithoxus*) *fimbriatus* Steindachner, 1915.

Paralithoxus Boeseman, 1982:46. Type-species: *Ancistrus bovallii* Regan, 1906.

Phylogenetic diagnosis. Reversal to a short, narrow accessory process of the first ceratobranchial (7:1, 8:1), reversal to a narrow fifth ceratobranchial (10:0), loss of the accessory process on the first epibranchial (14:0), loss of the posterior shelf on the fourth epibranchial (17:0), reversal to a narrow hypohyal (20:0), an elongate first hypobranchial (23:1), reversal to the anterohyal being located on or behind the hyomandibula (26:0), reversal to a round upper pharyngeal jaw with evenly distributed teeth (30:0), lateral wall of posterohyal absent so that posterohyal forms a half cylinder (32:1), reversal to no mesial contact of hyomandibula and quadrate (33:0), posterior portion of hyomandibula forming a shelf dorsally such that suture to pterotic-supracleithrum is nearly perpendicular to preoperculo-hyomandibular ridge (40:1), posterior process of hyomandibula incorporated into main body of hyomandibula (41:1, unique), branched preoperculo-hyomandibular ridge (48:1), reversal to loss of metapterygoid channel and dorsal surface of the metapterygoid being only slightly split, forming a narrow channel (52:1, 53:0), dentary tooth rows forming acute angle (69:0), maxilla expanded ventrally (71:1), bar-shaped opercle (75:2), two to four plates between canal plate and opercle (88:2), reversal to small mesethmoid disk (100:1), wide ventral process of sphenotic (116:1), bifid hemal spines (122:1), first neural spine anterior to first dorsal-fin pterygiophore (125:1), tip of transverse process of Weberian complex centrum not contacting compound pterotic (135:1), reduction of exposed portion of cleithral process (157:1), reversal to large space between posterior process of coracoid strut and posterior process of cleithrum (164:0), curved anterolateral processes of basipterygium meeting or nearly meeting at midline (167:0), loss of posteroventral ridge of basipterygium (173:0), enlarged teeth (205:2).

Comparative diagnosis. The Lithoxini can be separated from all except *Leporacanthicus* by having a nearly round, flat oral disk with mandibular barbels located and directed anterolaterally (*vs*. lips oval and mandibular barbels located and directed posterolaterally) and from *Leporacanthicus* by having more than two premaxillary teeth and all teeth of similar length (*vs.* two teeth per premaxilla and premaxillary teeth much longer than dentary teeth; see Lujan *et al*., 2018, for more detail).

Geographical distribution. Lithoxini is distributed exclusively within the Guiana Shield, from right bank tributaries of the Orinoco River, to the upper Negro and Branco rivers, to north-flowing basins from the Essequibo eastward to the Oyapock, and drainages flowing south from the Guianas into the lower Amazon.

Tribe Peckoltini, new tribe

urn:lsid:zoobank.org:act:C1105224-245D-4807-A57A-C91C39D34EDC

Included genera.

Ancistomus Isbrücker, Seidel in Isbrücker *et al*., 2001:17. Type-species: *Ancistrus snethlageae* Steindachner, 1911.

Aphanotorulus Isbrücker, Nijssen, 1983:105. Type-species: *Aphanotorulus frankei* Isbrücker & Nijssen, 1983 (synonym of *A. unicolor* (Steindachner, 1908)). Synonym: *Squaliforma* Isbrücker & Michels, 2001 (in Isbrücker *et al*., 2001).

'Baryancistrus' beggini Lujan, Arce, Armbruster, 2009:51.

'Baryancistrus' demantoides Werneke, Sabaj Pérez, Lujan, Armbruster, 2005a:535.

'Hemiancistrus' guahiborum Werneke, Armbruster, Lujan, Taphorn, 2005b:544.

'*Hemiancistrus*' *landoni* group (includes '*H.*' *landoni* Eigenmann, 1916 (with '*H.*' *hammarlundi* Rendahl, 1937 as a synonym) and '*H.*' *furtivus* Provenzano & Barriga Salazar, 2017).

'Hemiancistrus' subviridis Werneke, Sabaj Pérez, Lujan, Armbruster, 2005a:538.

Hypancistrus Isbrücker, Nijssen, 1991:347. Type-species: *H. zebra* Isbrücker & Nijssen, 1991. Synonym: *Micracanthicus* Lujan & Armbruster, 2011.

Isorineloricaria Isbrücker, 1980:15. Type-species: *Plecostomus spinosissimus* Steindachner, 1880.

Panafilus Lujan *et al*., 2017:332. Type-species: *Panaque albomaculatus* Kanazawa, 1958.

Panaqolus Isbrücker, Schraml, in Isbrücker *et al*., 2001:20. Type-species: *Panaque gnomus* Schaefer & Stewart, 1993. With three subgenera (*Panafilus*, *Panaqolus* and *Panaqoco* per Lujan *et al*., 2017).

Peckoltia Miranda Ribeiro, 1912:1912. Type-species: *Chaetostomus vittatus* Steindachner, 1881. Synonym: *Etsaputu* Lujan, Armbruster & Rengifo, 2011.

Peckoltichthys Miranda Ribeiro, 1917:49. Type-species: *Peckoltichthys filicaudatus* Miranda Ribeiro, 1917 (synonym of *Chaetostomus bachi* Boulenger, 1898). Synonym: *Sophiancistrus* Isbrücker & Seidel, 2001 (in Isbrücker *et al*., 2001).

Pseudoqolus Lujan *et al*., 2017:333. Type-species: *Panaqolus koko* Fisch-Muller, Covain, 2012 (in Fisch-Muller, Montoya-Burgos, le Bail, Covain, 2012).

Scobinancistrus Isbrücker, Nijssen, 1989:542. Type-species: *Scobinancistrus pariolispos* Isbrücker & Nijssen, 1989.

'Spectracanthicus' immaculatus Chamon, Rapp Py-Daniel, 2014:12.

Phylogenetic diagnosis. No unambiguous character states were found to support Peckoltini.

Comparative diagnosis. Peckoltini is a diverse group of genera not easily separated as a group from other members of the Hypostominae. Peckoltini genera tend to have hypertrophied odontodes on lateral plates, especially along the caudal peduncle, while this character is not seen in other Hypostominae; however, these hypertrophied caudal trunk odontodes are also unknown or presumed absent in some species of Peckoltini. Of Peckoltini genera, only *Ancistomus* lacks a recent taxonomic review, and it is largely separated from all other Hypostominae by having a gray head and body base color with black spots (*vs.* base color, white, tan, brown, or black).

Geographical distribution. Peckoltini is widely distributed throughout the Amazon, Orinoco, Essequibo and other coastal basins of the Guianas as well as the trans-Andean Guayas and Esmeraldas drainages in Ecuador, the Magdalena River, and the Lake Maracaibo basin.

Tribe Pseudancistrini, new tribe

urn:lsid:zoobank.org:act:CE2CF701-3692-40FF-A9FE-D926399A8807

Included genera.

Pseudancistrus Bleeker, 1862:2. Type-species: *Hypostomus barbatus* Valenciennes, 1840 (in Cuvier, Valenciennes, 1840).

Phylogenetic diagnosis. With *Pseudancistrus megacephalus*, Pseudancistrini is diagnosed by hyomandibula contacting only the compound pterotic (no prootic contact; 35:0>1), walls of metapterygoid channel tall (56: 0>1), straight, spoon-shaped anterior process on metapterygoid (58: 0>1, shared with Stellantini), sphenotic lacking external contact with posteriormost infraorbital (117: 0>1).

All taxa except *P. megacephalus* are diagnosed by: anterohyal greatest width greater than half length (1: 0>1), hyomandubula deflected beyond posterior margin such that posterior margin is visible when mesial surface of hyomandibula is viewed (46: 0>1), almost vertically-oriented preopercle (61: 1>0), reduction in gap between anterior process of compound pterotic and main body (111: 2>1), forward extension of anterior process of compound pterotic halfway or greater through orbit (112: 0>1), distal margin of rib of sixth vertebral centrum flared distally such that tip is wider than shaft (128: 0>1), reversal to moderately evertible cheek plates (184: 2>1), hypertrophied odontodes along snout margin (188: 0>1), sheaths of snout odontodes long and well separated from odontode, forming tentacules (208: 0>1).

Comparative diagnosis. Pseudancistrini (except *P. megacephalus*) differs from most other Hypostominae except *Corymbophanes*, *Cryptancistrus* Fisch-Muller, Mol & Covain, 2018, some *Guyanancistrus* Isbrücker, 2001 (in Isbrücker *et al*., 2001), *Hopliancistrus*, *Lithoxancistrus* Isbrücker, Nijssen & Cala, 1988, *Neblinichthys* Ferraris, Isbrücker & Nijssen, 1986, and *Pseudolithoxus* by having hypertrophied odontodes along snout margin of nuptial males; from *Corymbophanes* by having hypertrophied, evertible cheek odontodes (*vs.* no evertible cheek odontodes); from *Cryptancistrus*, *Guyanancistrus*, and *Hopliancistrus* by having snout odontodes evenly arranged along entire snout margin and thin (*vs.* only at anterolateral corners and thick); from *Araichthys*, *Corymbophanes*, and *Neblinichthys* (and maybe *Paulasquama* and *Yaluwak* Lujan, Armbruster in Lujan *et al*., 2019) by lacking hypertrophied odontodes on top of snout; from *Lithoxancistrus* and *Colossimystax* by lacking enlarged papillae behind dentary teeth); and from Stellantini by having slight keel on midventral plate row on caudal peduncle, with dorsal laminae of plates largely flat (*vs.* plates strongly keeled with dorsal laminae strongly convex).

Geographical distribution. Found in north-flowing drainages of the eastern Guiana Shield from the Caroni and Essequibo basins east to the Oyapock, the south-flowing Branco, Negro, and Trombetas drainages, more eastward northern tributaries of the lower Amazon, and the Tapajós and Xingu rivers draining the northern Brazilian Shield.

Remarks. Placement of *P. megacephalus* in *Pseudancistrus* is uncertain, thus the phylogenetic diagnosis above is provided with and without *P. megacephalus*. *Pseudancistrus megacephalus* has a deeper body than congeners, lacks hypertrophied odontodes along the snout, and the skull (Fig. 4) contains significant differences. These include the posterior shelf of the pterotic being largely parallel with the main body of the hyomandibula in *P. megacephalus* (*vs.* bent medially), the anterior process of the pterotic being longer and more separated from the main body of the pterotic, and the lateral wall of the pterygoid channel being differently shaped. The orientation of the suspensorium (turquoise in Fig. 4, also indicated) forms almost a right angle at the posteroventral corner when viewed laterally (*vs.* forming almost a straight line), the preopercle lacks a process for articulation with the canal plate (*vs.* process present; the canal plate is the fulcrum for rotation of the evertible cheek odontodes), and the metapterygoid condyle to the suspensorium is tall (*vs.* short). *Pseudancistrus megacephalus* has not been collected within its range in Guyana and Suriname since 1909 despite several fairly intensive collecting efforts, suggesting it may be either regionally extirpated or extinct (Armbruster, 2023a). The MBUCV collection has five lots and 19 specimens identified as *Pseudancistrus megacephalus* from the Cuyuni River in Venezuela, all collected in 1987 and 1991. Thus the Cuyuni may remain a refuge, although it has suffered from even worse mining impacts than other parts of the species' range.

Tribe Spectracanthicini Isbrücker & Nijssen, 1989

Type-genus. *Sepctracanthicus* Nijssen & Isbrücker, 1987

Included genera.

Baryancistrus Rapp Py-Daniel, 1989:245. Type-species: *Hypostomus niveatus* Castelnau, 1855. See Rapp Py-Daniel *et al.* (2011).

Hemiancistrus Bleeker, 1862:2. Type-species: *Ancistrus medians* Kner, 1854. See Fisch-Muller *et al.* (2012) and Armbruster *et al.* (2015).

Parancistrus Bleeker, 1862:2. Type-species: *Hypostomus aurantiacus* Castelnau, 1855. See Rapp Py-Daniel (1989) and Rapp Py-Daniel, Zuanon (2005). Synonym: *Acanthodemus* Marschall, 1873.

Spectracanthicus Nijssen, Isbrücker, 1987:93. Type-species: *Spectracanthicus murinus* Nijssen & Isbrücker, 1987. See Rapp Py-Daniel (1989) and Chamon, Rapp Py-Daniel (2014).

Phylogenetic diagnosis. Posterior region of hyomandibula deflected mesially causing opercle to sit at almost right angle to main body axis (42:1), opercle not supporting odontodes (79:1), and curved anterolateral processes of basipterygium that meet or nearly meet at midline (167:0).

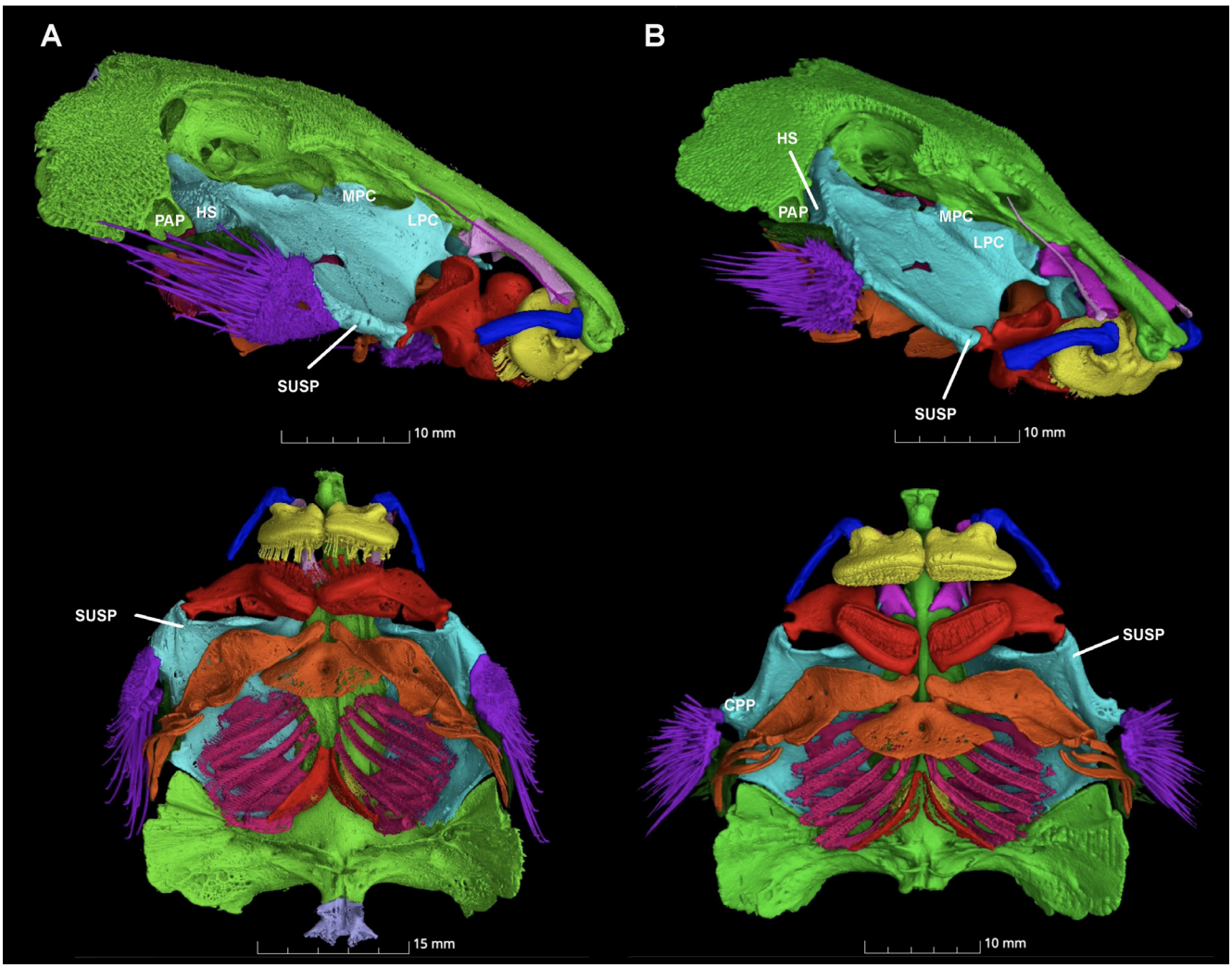

FIGURE 4 | µCT renderings of the crania of **A.** *Pseudancistrus megacephalus*, BMNH 1978.9.12.3, and **B.** *P. barbatus*, ROM 86176, in slightly anterolateral (top) and ventral views (bottom) emphasizing major differences between *P. megacephalus* and *Pseudancistrus sensu stricto*. CPP: canal plate process, HS: Hyomandibula posterior shelf, LPC: Lateral wall of the pterygoid channel, MPC: metapterygoid condyle, PAP: compound pterotic anterior process, SUSP: suspensorium.

Comparative diagnosis. Spectracanthicini cannot be separated from all other hypostomines as a group. *Baryancistrus,* '*B.*' *beggini*, '*B.*' *demantoides, Parancistrus*, and *Spectracanthicus* can be separated from all except '*Spectracanthicus*' *immaculatus* of the Peckoltini by having a fully adnate dorsal fin and a posterior extension of the dorsal-fin membrane that reaches either the adipose fin or at least two plates posterior to the insertion of the posteriormost dorsal-fin ray (*vs.* posterior dorsal-fin membrane maximally extending one plate from the insertion of the posteriormost dorsal-fin ray and never reaching adipose fin); all of these except '*B*'. *beggini* can be separated from '*S.*' *immaculatus* by having light spots (*vs.* solid gray or black). *Hemiancistrus medians* can be separated from all other hypostomines except the Acanthicini by having all odontodes on the head and lateral plates arranged in lines (*vs.* scattered) and from the Acanthicini by having many very small odontodes in lines (*vs.* very few, fairly large odontodes) and

by having seven dorsal-fin rays (*vs.* eight to 10). Some *Baryancistrus*, '*B.*' *demantoides*, '*H.*' *guahiborum*, and '*H.*' *subviridis* can be separated from most other Hypostominae by having a light-colored (white, yellow, or orange) margin to the dorsal fin.

Tribe ***Stellantini*** Armbruster & Lujan, new tribe

urn:lsid:zoobank.org:act:1D1E1710-3653-4CFA-A6BB-1975401D6ADF

(Fig. 1; Tabs. 1 and **S3**)

Type-genus. *Stellantia*, new genus

Included genera.
Colossimystax, new genus
Stellantia, new genus

Phylogenetic diagnosis. Hyomandibula contacting prootic (0>1), posteromedial invagination of ceratobranchial 5 (11: 0>1), straight, spoon-shaped anterior process on metapterygoid (58: 0>1, shared with Pseudancistrini), forward extent of anterior process of compound pterotic long, halfway through orbit or greater (112: 0>1), and straight anterolateral processes of pelvic basipterygium (167: 1>2). In addition, Stellantini uniquely possesses plates along ventral series on the caudal peduncle that are strongly bent to form a keel with the keel accentuated by having the dorsal lamina of the plates strongly concave.

Comparative diagnosis. Morphometric data reported in Tab. 1. The two species of Stellantini are dramatically different from one another, but the tribe can be identified from other Hypostominae by having a strong keel on the ventral plate series on the caudal peduncle made by the ventral lamina of each plate being strongly convex and the dorsal lamina of each plate being strongly concave (*vs.* maximally having a slight keel made predominantly of odontodes and the dorsal lamina of each ventral plate being flat to very slightly concave).

Geographical distribution. Both species of Stellantini are found in main channels of the upper Orinoco and Negro river basins, including the Casiquiare River, in Venezuela, Colombia, and possibly also northernmost Brazil, though no Brazilian specimens have been observed or reported (Fig. 5).

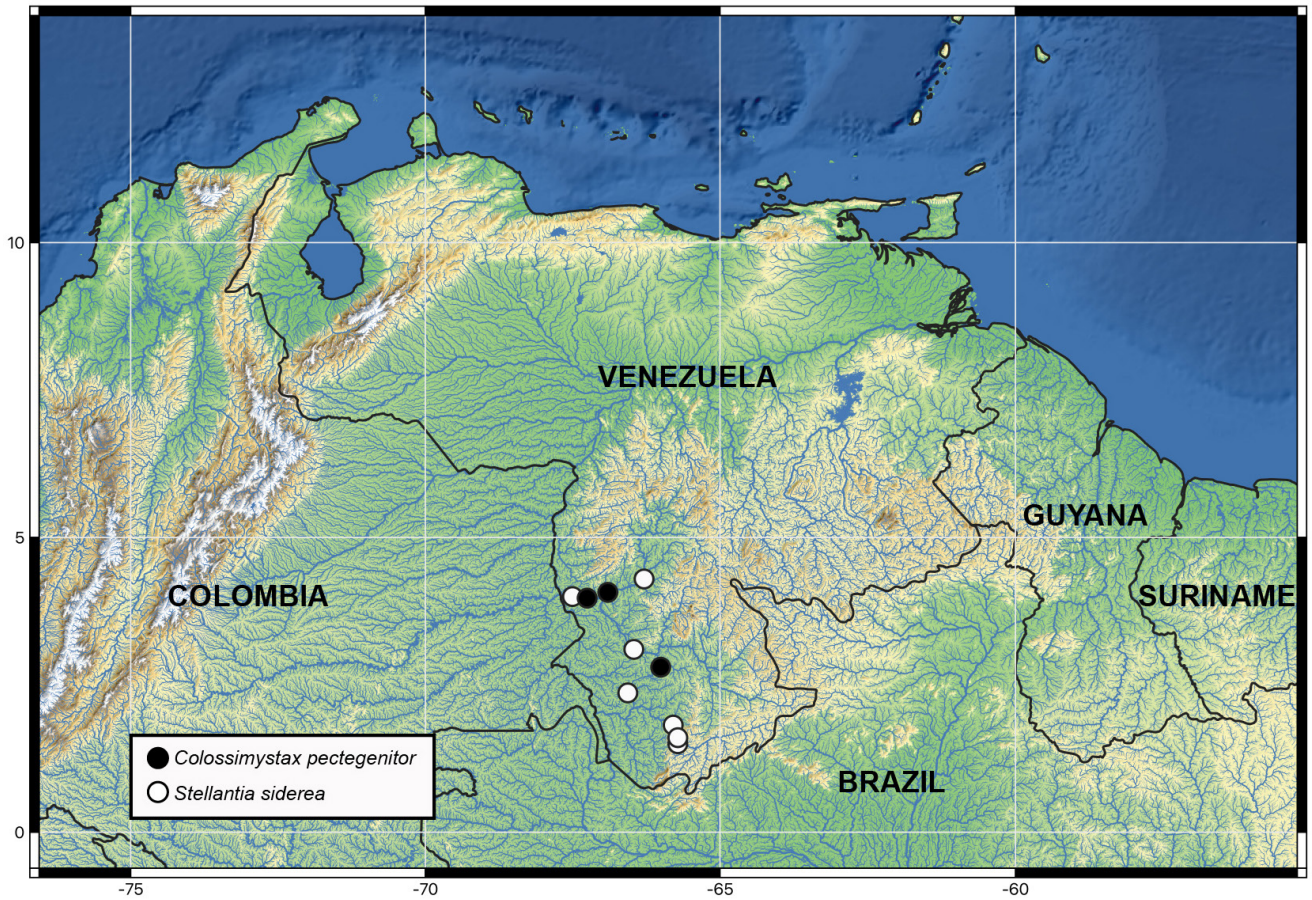

FIGURE 5 | Distribution of *Colossimystax pectegenitor* (black dots) and *Stellantia siderea* (white dots).

Colossimystax Armbruster & Lujan, new genus

urn:lsid:zoobank.org:act:3F6C7DC3-24AC-4BE2-8D7F-BE77FC4CAAD5

(Figs. 1A, 2C)

Type-species. *Pseudancistrus pectegenitor* Lujan, Armbruster & Sabaj Pérez, 2007

Included species.

Pseudancistrus pectegenitor Lujan, Armbruster, Sabaj Pérez, 2007:164, figs. 1b, 2–3. Río Casiquiare, 73 kilometers northeast of San Carlos de Río Negro, 02.3525°, -066.5753°, Amazonas, Venezuela.

Phylogenetic diagnosis. Spindle-shaped hypohyal (21: 0>1), upper pharyngeal jaw with invagination in shelf (29: 0>1), reversal to horizontally oriented preopercle (61: 1>0), wide, blunt articulating condyle of quadrate (67: 0>1), tall ridge on lateral ethmoid for contact with metapterygoid (97:2), reduction to three to eight vertebrae from first normal neural spine posterior to dorsal fin to spine under preadipose plate (120: 1>0; this is concomitant with a unique shortening of the body posterior to the dorsal fin), flared distal margin of rib of sixth vertebral centrum (128: 0>1), ten dorsal-fin rays

TABLE 1 | Morphometrics and counts for species of Stellantini.

	Colossimystax pectegenitor (N = 4)			*Stellantia siderea* (N = 17)		
Measurement	**Range**	**Mean**	**SD**	**Range**	**Mean**	**SD**
Standard length (mm)	173.6–241.6	216.8	–	110.7–183.0	155.4	–
Percentages of standard length						
Predorsal length	42.0–44.2	43.5	1.0	37.2–39.0	38.1	0.5
Head length	35.9–38.1	37.0	0.9	29.4–31.7	30.7	0.6
Head-dorsal length	5.6–6.8	6.2	0.6	6.9–8.3	7.7	0.4
Cleithral width	29.2–34.1	31.4	2.1	25.1–28.2	26.4	0.9
Head-pectoral length	30.6–32.9	31.9	1.2	24.2–26.8	25.7	0.8
Thorax length	22.9–25.1	24.0	1.0	20.3–25.0	22.8	1.1
Pectoral-spine length	38.3–42.2	40.1	1.9	25.5–32.1	27.9	1.4
Abdominal length	22.3–24.7	23.5	1.0	21.4–23.7	22.7	0.7
Pelvic-spine length	23.1–27.4	24.7	2.0	21.3–24.9	23.5	1.0
Postanal length	27.8–31.5	29.5	1.5	33.5–37.4	36.1	1.0
Anal-fin spine length	11.2–13.3	12.2	1.0	6.9–10.4	8.0	0.9
Dorsal-pectoral distance	24.6–26.4	25.7	0.8	22.7–24.2	23.6	0.5
Dorsal spine length	27.7–35.2	31.3	3.6	28.0–39.9	34.0	3.3
Dorsal-pelvic distance	22.6–25.5	23.9	1.5	17.1–21.9	20.5	1.1
Dorsal-fin base length	34.0–38.0	35.6	1.8	23.7–28.4	25.9	1.2
Dorsal-adipose distance	8.8–11.1	10.2	1.0	16.7–19.5	18.4	0.8
Adipose-spine length	5.6–7.8	6.6	1.1	6.3–9.6	8.5	0.8
Adipose-up. caudal distance	8.9–10.5	9.6	0.8	11.9–17.3	14.1	1.5
Caudal peduncle Dp.	12.1–13.6	12.7	0.7	7.5–9.2	8.4	0.4
Adipose-low. caudal distance	17.4–18.5	17.8	0.5	19.1–23.0	20.7	1.0
Adipose-anal distance	18.9–20.5	19.8	0.7	18.6–21.7	20.5	0.8
Dorsal-anal distance	14.4–16.4	15.5	0.9	11.7–13.8	13.0	0.5
Pelvic-dorsal distance	30.0–34.8	32.3	2.5	23.8–27.2	25.1	1.0
Percentages head length						
Head-eye length	25.3–29.9	27.5	1.9	27.5–36.2	30.5	2.7
Orbit diameter	14.6–16.0	15.0	0.6	15.0–18.1	16.5	0.9
Snout length	66.1–69.1	68.0	1.4	63.0–70.6	66.8	2.0
Internares width	11.0–12.2	11.4	0.5	9.6–12.9	10.9	1.0
Interorbital width	33.0–41.7	36.8	3.6	34.4–49.0	42.0	5.0
Head Dp.	62.8–64.4	63.4	0.7	61.4–68.2	63.8	1.7
Mouth length	49.4–58.4	52.3	4.1	48.4–58.5	52.8	2.6
Mouth width	62.3–75.9	70.3	6.2	59.9–72.7	65.5	2.8
Barbel length	9.3–10.9	10.1	0.8	3.2–8.2	6.2	1.4
Dentary tooth cup length	23.0–27.2	24.8	1.8	21.0–25.5	23.3	1.5
Premax. tooth cup length	21.5–26.5	24.5	2.2	20.4–25.5	23.3	1.6
Counts	**Range**	**Median**		**Range**	**Median**	
Plates in median row	24.0–24.0	24.0		25–25	25	
Plates in inframedian row	23.0–23.0	23.0		24–25	24	
Plates in supramedian row	24.0–25.0	24.0		25–26	25.0	
Dorsal-fin rays	I,10–I,11	I,10		I,7–I,7	I,7	
Pectoral-fin rays	I,6–I,6	I,6		I,6–I,6	I,6	
Pelvic-fin rays	i,5–i,5	I,5		i,5–i,5	i,5	
Anal-fin rays	i,5–i,5	I,5		i,4–i,4	i,4	
Caudal -fin rays	i,13,i–i,14,i	i,14,i		i,14,i–i,14,i	i,14,i	
Dentary teeth	126–134	128		63–102	81	
Premaxillary teeth	119–164	131		65–113	84	

(142: 0>1), reduction to five or six dorsal-fin radial elements with transverse processes (145: 1>0), reversal to wide posterior process of coracoid (158: 2>1), presence of dentary papillae (180: 0>1), presence of tentacules on hypertrophied snout and pectoral-fin spine odontodes, tentacules shorter than associated odontodes (208: 0>1, 209: 0>1). Further, *Colossimystax* has a larger supraoccipital crest than *Stellantia* or other species currently or formerly in *Pseudancistrus*, with crest most similar to *Hemiancistrus medians* but still taller and with a greater ventromedial lamina (Fig. 6).

Comparative diagnosis. *Colossimystax* is readily distinguished from all other Hypostominae except Acanthicini, Chaetostomatini, and *Pterygoplichthys* by having 10 dorsal-fin rays (*vs.* 7); from all other Hypostominae except *Stellantia* by having the dorsal lamina of each ventral plate of the caudal peduncle concave, accentuating the ventrolateral keel of the caudal peduncle (*vs.* ventral plates on caudal peduncle lacking strongly concave dorsal lamina or plates rounded and keel absent); from other species with more than seven dorsal-fin rays except *Dolichancistrus* by nuptial males having hypertrophied cheek odontodes reaching to at least the edge of the third plate of the midventral series (*vs.* maximally reaching the first plate); from *Dolichancistrus* by nuptial males having many hypertrophied cheek odontodes (*vs.* 1 or 2); from Hypostominae except *Chaetostoma* and *Lithoxancistrus* by having a single or small cluster of enlarged papillae located medially on dentaries interior to tooth rows (*vs.* all papillae small).

Description. See Tab. **S3** and Lujan *et al*. (2007).

Geographical distribution. Found in main channels and major tributaries of the Orinoco River upstream of San Fernando de Atabapo and in the Casiquiare River above its confluence with the Negro River, including the lower Ventuari River. Currently known exclusively from Venezuela but may also occur in neighboring basins of Colombia and Brazil (Fig. 5).

Etymology. *Colossimystax* is from the Latin *colossicon* for gigantic and *mystax* for moustache in reference to the very long cheek odontodes that look like a moustache, a masculine noun.

Conservation status. *Colossimystax pectegenitor* was evaluated as Least Concern (LC) by the IUCN (Echevarría, 2019). Only three disjunct localities are known, but all are main channel habitats, suggesting a likely contiguous distribution throughout a remote area of southern Venezuela in which the most threatening impact is gold mining.

Material examined. Amazonas, Venezuela. Holotype: MCNG 54797 [ex AUM 42130], 241.6 mm SL, Río Casiquiare. Paratypes: ANSP 182801 [ex AUM 42181], 1, 225.1 mm SL, Río Orinoco; AUM 42202, 1, 227.0 mm SL, Río Casiquiare; AUM 43192, 1 c&s, 173.6 mm SL, Río Orinoco.

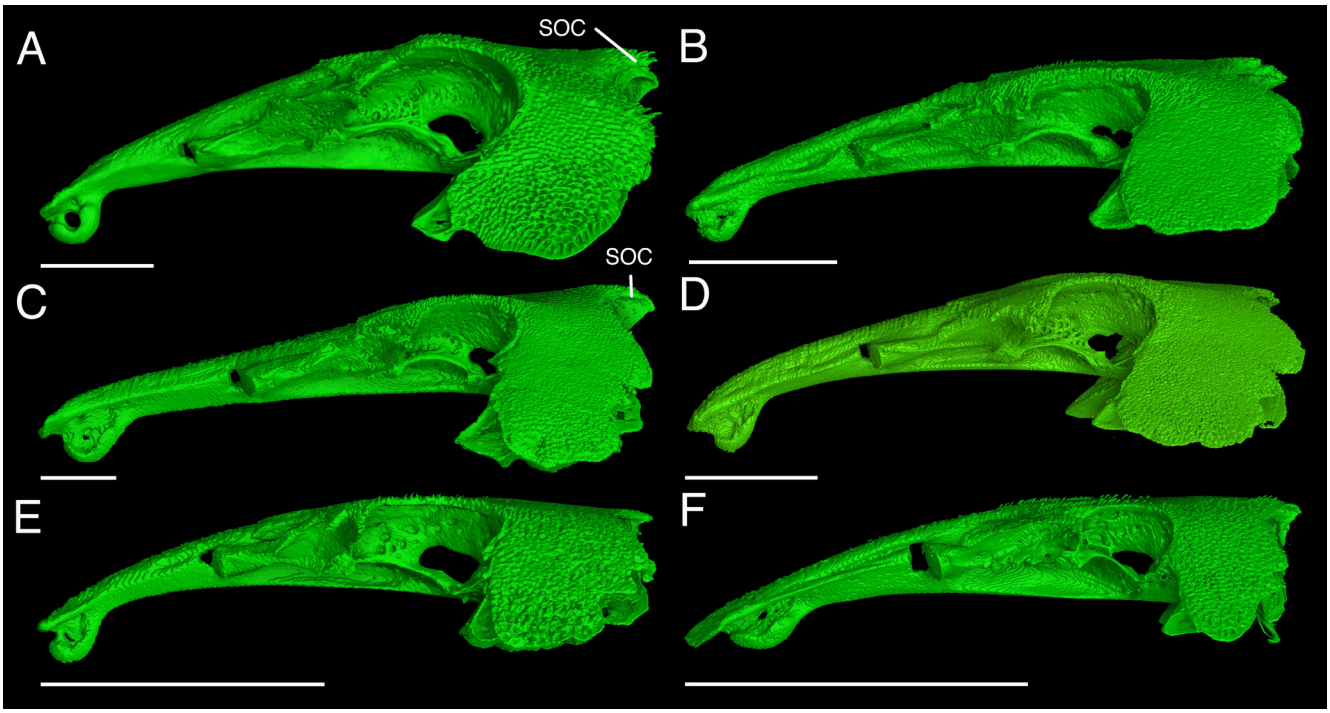

FIGURE 6 | µCT renderings of neurocrania (left, lateral view) of **A.** *Hemiancistrus medians*, ANSP 187122, **B.** *Pseudancistrus barbatus*, ROM 86176, **C.** *Colossimystax pectegenitor*, AUM 42130, **D.** *Stellantia siderea*, AUM 54310, **E.** *Lithoxancistrus coquenani*, AMNH 91025, **F.** *Lithoxancistrus yekuana*, AUM 39473. Scale bars = 1 cm.

Stellantia Armbruster & Lujan, new genus

urn:lsid:zoobank.org:act:894AA6EB-3851-4EA7-B4FB-24724F2A0491

(Figs. 1B, 2B)

Type-species. *Pseudancistrus sidereus* Armbruster, 2004b

Included species.

Pseudancistrus sidereus Armbruster, 2004b:8, fig. 3. Río Siapa from 10–15 kilometers downstream, Río Casiquiare - Río Negro drainage, 01.50000°, -065.71667°, Río Orinoco drainage, Amazonas, Venezuela.

Phylogenetic diagnosis. Reversal to large interhyal (27: 1>0), tall walls of metapterygoid channel (56: 0>1), reversal to narrow quadrate (64: 1>0), loss of flap of quadrate extending below symplectic foramen (66: 1>0), reversal to two to four cheek plates between canal plate and opercle (88: 3>2); no contact between infraorbital 4 and orbit (90: 1>2), anterior margin of mesethmoid flared (102: 0>1), loss of exterior contact between sphenotic and posteriormost infraorbital (117: 0>1), and increase in number of vertebrae to 12–15 from first normal neural spine posterior to dorsal fin up to and excluding the hypural (121:1).

Comparative diagnosis. *Stellantia* is readily identified from all other Hypostominae except *Colossimystax* by having the dorsal lamina of each ventral plate of the caudal

peduncle concave, accentuating the caudal peduncle keel (*vs.* caudal peduncle ventral plates rounded, lacking concave dorsal lamina, caudal peduncle keel weak or absent); and from *Colossimystax* by having seven branched dorsal-fin rays (*vs.* 10).

Geographical distribution. Known from main channels of the upper Orinoco River basin upstream of San Fernando de Atabapo, including the lower Ventuari River, and the Casiquiare River basin upstream of its confluence with the Negro River, including the lower Siapa River, exclusively in Amazonas, Venezuela.

Description. See Tab. **S3** and Armbruster (2004b).

Etymology. An abstract, feminine noun modified from the Latin adjective *stellans* for starry in reference to the dark body with white to yellow spots which appear like a field of stars, a feature that inspired the species epithet as well. *Stellantia* requires a change of ending for the single species in the genus: *Stellantia siderea*.

Conservation status. *Stellantia siderea* was evaluated as Least Concern (LC) by the IUCN (Armbruster, 2023b). The species is common throughout its range.

Material examined. Río Orinoco drainage, Amazonas, Venezuela. Holotype: MCNG 26125, 175.6 mm SL, Paratypes: AUM 37562, 1, 148.7 mm SL; FMNH 105294, 4, 149.5–176.7 mm SL; MCNG 48261, 1 c&s, 149.8 mm SL.

DISCUSSION

We present a new tribe-level taxonomy for the Hypostominae based on multiple genetic studies published over several decades. The first DNA-based hypotheses on Loricariidae interrelationships were those of Montoya Burgos *et al.* (1997, 1998), and the results of those studies have been largely confirmed in subsequent molecular analyses including more markers and taxa (Lujan, 2015a; Roxo *et al*., 2019). These results suggest that previous morphology-based phylogenetic studies (Schaefer, 1986; Armbruster, 2004a, 2008) are significantly biased by morphological homoplasy and, as the present study shows, rapid character evolution. The homoplastic presence and degree of development of a cheek odontode eversion mechanism driven by an anteroventral, lever-like process of the opercle has been a large source of this bias. This mechanism is unique to the Hypostominae, and it is easy to imagine how earlier research might have been biased by the assumption that such a complex structure is a derived state that is rarely lost.

Armbruster (2004a) described a transitional series in the complexity or degree of the cheek odontode eversion mechanism across Loricariidae, from no eversion (184:0; all but Hypostominae), to slight eversion (184:1; *Hypostomus*, *Pterygoplichthys*), to strong eversion (184:2). The opercle, which is the central bone of this mechanism, varies from a primitive triangular shape (75:0), to sickle-shaped (75:1), to bar-shaped (75:2) with the sickle shape considered intermediate. When applied at the scale of a clade as diverse as Loricariidae, morphology-based phylogenetics requires diverse and continuously variable morphologies to be binned into an arbitrarily small number of character states.

The opercles representing *Hemiancistrus* and species now or formerly in *Pseudancistrus* (all sickle-shaped) illustrate the complexity of form that must be collapsed into a single state (Fig. 7). Some species with highly evertible cheek plates have correlated modifications of the hyomandibula (37:1, 39:1, 40:1, 41:1, 42:1, 76:1), the quadrate articulating with the canal plate or other parts of the suspensorium (65:1, 85:1), increased fragmentation of the cheek plates (88:3) as well as other characters that influence or are influenced by cheek odontode evertibility. Such a functionally interrelated complex of characters easily overwhelms the phylogenetic signal from other characters, which are conversely too few and poorly correlated to correct the consequent bias.

DNA-based phylogenies show that many of the derived characters related to cheek odontode eversion occurred early in Hypostominae evolution and were lost or regained multiple times throughout the evolutionary history of the subfamily. Given the dominance of these characteristics, many clades lack morphological synapomorphies when the characters of Armbruster (2004a) are mapped onto the compound molecular phylogeny. While the molecular phylogeny could provide a fruitful foundation for the discovery of new characters to support such clades, it would be difficult to amass the specimens needed and it is beyond the scope of this study. The use of computed tomography to generate and archive three-dimensional digital libraries of skeletal morphology is accelerating our ability to compare individual bones in multiple standardized perspectives (Fig. 7). The near instant accessibility to such imagery allows for easier and more thorough assessments of character states than was ever historically possible using cleared and stained or dry skeletal material. Although molecular phylogenies are more likely to give results closer to the true tree than morphological phylogenies, future systematists will need to examine morphology in much greater detail, benefitting from new technologies, to truly understand character evolution in the Loricariidae.

Here we describe the new tribe Pseudancistrini for species once ascribed to *Pseudancistrus* sensu stricto. Armbruster (2004b) had recognized a broader *Pseudancistrus*; however, genetic evidence shows that this was in error, with several taxa once part of *Pseudancistrus*, such as *Collosimystax*, *Lithoxancistrus*, *Guyanancistrus*, and *Stellantia*, being removed from *Pseudancistrus* in recent studies. Most of the taxa removed from *Pseudancistrus* share with *Pseudancistrus* the presence of hypertrophied odontodes along the side of the head; however, this is a common trait across Loricariidae. Of the species now recognized in Pseudancistrini, *Pseudancistrus megacephalus* is the most curious, morphologically distinct, and ambiguous in its relationship to other species. This species has not been collected in its historical range in Guyana and Suriname in over 100 years and no genetic samples are currently available, thus we cannot test our taxonomic hypothesis with genetic data. We therefore define Pseudancistrini using distinct sets of character states that would be relevant whether *P. megacephalus* is included in Pseudanctrini or excluded.

We conclude this tribe-level reclassification of subfamily Hypostominae by erecting the new tribe Stellantini for two species from the upper Orinoco and Negro River drainages that are strongly supported as a clade in Lujan *et al*. (2015a). The phylogenetic position of Stellantini in Lujan *et al*. (2015a) is similar to that in the genomic analysis of Roxo *et al*. (2019), being one of four lineages (Ancistrini, Lithoxini, Pseudancistrini, Stellantini) that branch off after Chaetostomini but before the consistently supported crown-clade of Acanthicini + (Spectracanthicini + (Hypostomini + Peckoltini)), and

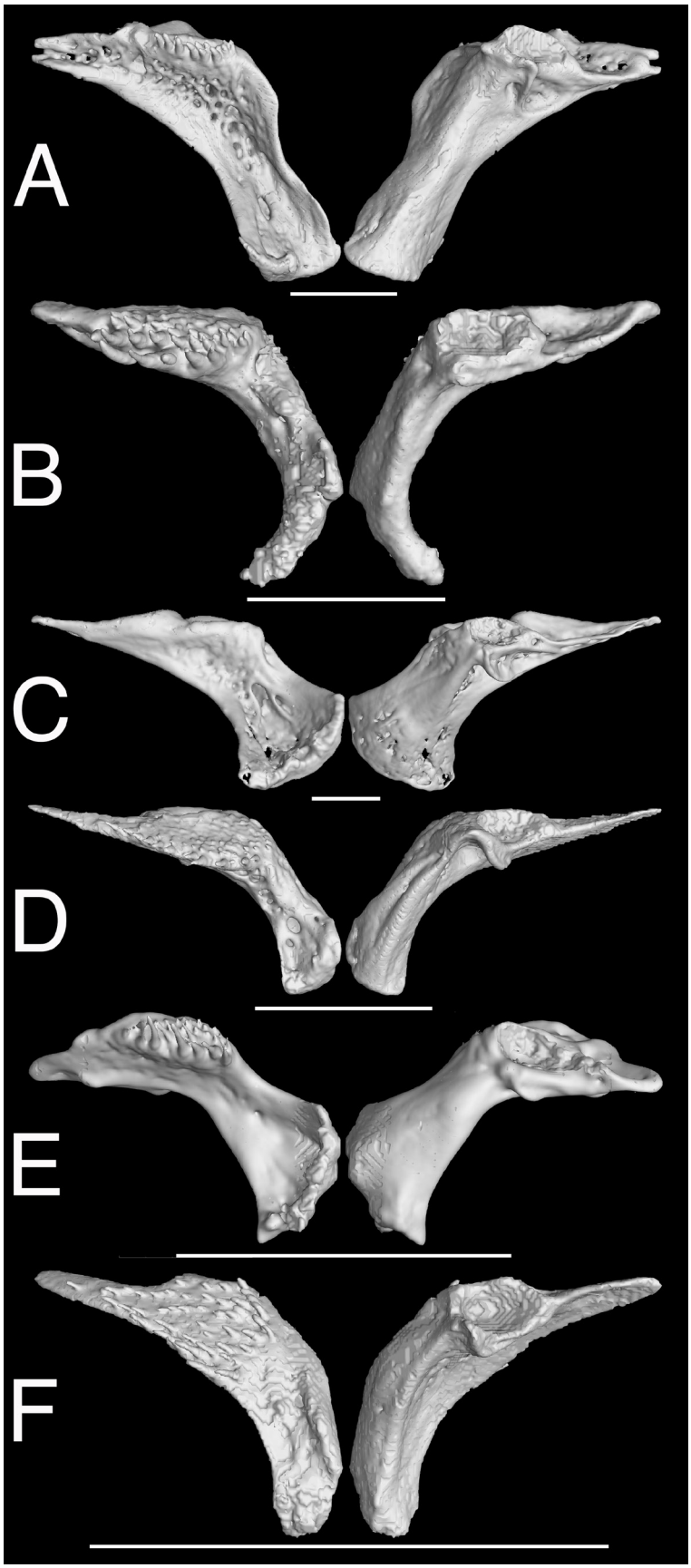

FIGURE 7 | µCT renderings of sickle-shaped opercles, right side in lateral (left) and medial (right) views of **A.** *Hemiancistrus medians*, ANSP 187122, **B.** *Pseudancistrus barbatus*, ROM 86176, **C.** *Colossimystax pectegenitor*, AUM 42130, **D.** *Stellantia siderea*, AUM 54310, **E.** *Lithoxancistrus coquenani*, AMNH 91025, **F.** *Lithoxancistrus yekuana*, AUM 39473. Scale bars = 1 cm.

whose interrelationships are weakly resolved in both studies. Nonetheless, both these studies and Covain, Fisch-Muller's (2012) phylogenetic analysis of *Pseudancstrius* sensu lato, found Stellantini to be more closely related to tribes other than Pseudancistrini, supporting our recognition of this clade as new. With the two Stellantini species so vastly different from one another, splitting them into two monotypic genera seems to be the best solution as there is very little to outwardly suggest that they are closely related except for the modified caudal peduncle keel.

Comparative material examined. *Hemiancistrus medians*, ANSP 187122, 155.1 mm SL, Lawa River, Marowijne drainage, Suriname. *Lithoxancistrus coquenani*, AMNH 91025, size not recorded, Orinoco drainage, Venezuela. *Lithoxancistrus yekuana*, AUM 39473, 42.7 mm SL, Orinoco drainage, Venezuela. *Pseudancistrus barbatus*, ROM 86176, 121.7 mm SL, Essequibo drainage, Guyana. *Pseudancistrus megacephalus*, BMNH 1978.9.12.3, holotype, size not recorded. *Pseudancistrus nigrescens*, AUM 35742, 137.2 mm SL, Essequibo drainage, Guyana.

ACKNOWLEDGMENTS

This project was partially funded by Planetary Biodiversity Inventory: All Catfish Species (Siluriformes), United States National Science Foundation Grant DEB–0315963 and NSF DEB–0707751 to JWA, NSF OISE–1064578 (International Research Fellowship), an NSERC Discovery Grant, and a National Geographic Committee for Research and Exploration grant #8721–09 to NKL, and various fieldwork grants from the Coypu Foundation to JWA and NKL. We thank Donald Taphorn and Oscar León (*in memoriam*) at the Museo de Ciencias Naturales in Guanare (MCNG) for aid in arranging field work in Venezuela and all those that helped in collecting specimens, particularly Mark Sabaj (ANSP) and David Werneke (AUM). We would like to thank them as well as Scott Schaefer, Tom Vigliotta, and Rad Arrindell (AMNH), James Maclaine, Oliver Crimmen, and Rupert Collins (BMNH), Mary Ann Rodgers and Kevin Swagel (FMNH), Raphael Covain and Sonia Fisch-Muller (MHNG), Richard Vari (*in memoriam*), Dianne Pitassy, and Sandra Raredon (NMNH), Erling Holm, Mary Burridge, and Don Stacey (ROM) for loan of materials and access to collections. We thank Hernán Lopéz-Fernandéz (ROM, UMMZ) and Nathan Lovejoy (University of Toronto Scarborough) for aid in developing the molecular phylogeny referred to in this paper, Emmanuel Neuhaus for translating the abstract to Portuguese, Morgan Chase (AMNH) and Alexander Tinius (University of Toronto) for assisting with CT-scanning, and University of Toronto student researchers Eunice Huang, Alice Lo, Jolie Nguyen, Amina Sharif, Christine Tang, Chunnan Yue for assistance with segmenting CT-data.

REFERENCES

- **Armbruster JW.** *Peckoltia sabaji*, a new species from the Guyana Shield (Siluriformes: Loricariidae). Zootaxa. 2003; 344(1):1–12. https://doi.org/10.11646/zootaxa.344.1.1
- **Armbruster JW.** Phylogenetic relationships of the suckermouth armored catfishes (Loricariidae) with emphasis on the Hypostominae and the Ancistrinae. Zool J Linn Soc. 2004a; 141(1):1–80. https://doi.org/10.1111/j.1096-3642.2004.00109.x
- **Armbruster JW.** *Pseudancistrus sidereus*, a new species from southern Venezuela (Siluriformes: Loricariidae) with a redescription of *Pseudancistrus*. Zootaxa. 2004b; 628(1):1–15. https://doi.org/10.11646/ZOOTAXA.628.1.1
- **Armbruster JW.** The loricariid catfish genus *Lasiancistrus* (Siluriformes) with descriptions of two new species. Neotrop Ichthyol. 2005; 3(4):549–69. https://doi.org/10.1590/S1679-62252005000400013
- **Armbruster JW.** The genus *Peckoltia* with the description of two new species and a reanalysis of the phylogeny of the genera of the Hypostominae (Siluriformes: Loricariidae). Zootaxa. 2008; 1822(1):1–76. https://doi.org/10.11646/ZOOTAXA.1822.1.1
- **Armbruster JW**. *Pseudancistrus megacephalus*. The IUCN Red List of Threatened Species. 2023a; e.T176016770A176016793. https://dx.doi.org/10.2305/IUCN.UK.2023-1.RLTS.T176016770A176016793.en. Accessed on 18 June 2024.
- **Armbruster JW.** *Pseudancistrus sidereus*. The IUCN Red List of Threatened Species 2023b:e.T176024212A176024225. https://dx.doi.org/10.2305/IUCN.UK.2023-1.RLTS.T176024212A176024225.en.
- **Armbruster JW, Provenzano F.** Four new species of the suckermouth armored catfish genus *Lasiancistrus* (Loricariidae: Ancistrinae). Ichthyol Explor Fres. 2000; 1:241–54.
- **Armbruster JW, Taphorn DC.** A new species of *Pseudancistrus* from the Río Caroni, Venezuela (Siluriformes: Loricariidae). Zootaxa. 2011; 1731(1):33–41. https://doi.org/10.11646/ZOOTAXA.1731.1.3
- **Armbruster JW, Werneke DC, Tan M.** Three new species of saddled loricariid catfishes and a review of *Hemiancistrus*, *Peckoltia* and allied genera (Siluriformes). ZooKeys. 2015; 480:97–123. https://doi.org/10.3897/zookeys.480.6540
- **Bleeker P.** Atlas ichthyologique des Indes Orientales Néêrlandaises, publié sous les auspices du gouvernement colonial néêrlandais. Tome II. Siluroïdes, Chacoïdes et Hétérobranchoïdes. Amsterdam : Frédéric Muller, 1862.
- **Boeseman M.** The South American mailed catfish genus *Lithoxus* Eigenmann, 1910, with the description of three new species from Surinam and French Guyana and records of related species (Siluriformes, Loricariidae). Proc Kon Ned Akad Wetensch C Biol Med Sci. 1982; 85(1):41–58.
- **Chamon CC, Rapp Py-Daniel LH.** Taxonomic revision of *Spectracanthicus* Nijssen & Isbrücker (Loricariidae: Hypostominae: Ancistrini), with description of three new species. Neotrop Ichthyol. 2014; 12(1):1-25. https://doi.org/10.1590/S1679-62252014000100001
- **Covain R, Fisch-Muller S.** Molecular evidence for the paraphyly of *Pseudancistrus* sensu lato (Siluriformes, Loricariidae), with revalidation of several genera. Cybium. 2012; 36(1):229–46. https://doi.org/10.26028/cybium/2012-361-013
- **Cuvier G, Valenciennes A.** Histoire naturelle des poissons. Tome quatorzième. Suite du livre seizième. Labroïdes. Livre dix-septième. Des Malacoptérygiens. Stasbourg, Ch. Pitois & Ve Levrault; 1840.
- **Echevarría G.** *Pseudancistrus pectegenitor*. The IUCN Red List of Threatened Species 2019:e.T118044065A118044070. http://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T118044065A118044070.en.
- **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. Ann Carnegie Mus. 1909; 6:4–54.
- **Eigenmann CH.** Catalogue of the fresh-water fishes of tropical and south temperate America. In: Scott WB, editor. Reports of the Princeton University expeditions to Patagonia 1896-1899. Princeton University & Stuttgart; 1910. p.375–511.

- **Ferraris Jr. CJ, Isbrücker IJH, Nijssen H.** *Neblinichthys pilosus*, a new genus and species of mailed catfish from the Rio Baria system, southern Venezuela (Pisces, Siluriformes, Loricariidae). Rev Fr Aquariol Herpétol. 1986; 13:69–72.
- **Fisch-Muller S, Mol JHA, Covain R.** An integrative framework to reevaluate the Neotropical catfish genus *Guyanancistrus* (Siluriformes: Loricariidae) with particular emphasis on the *Guyanancistrus brevispinis* complex. PLoS ONE. 2018; 13(1):e0189789. https://doi.org/10.1371/journal.pone.0189789
- **Fisch-Muller A, Montoya-Burgos JI, Le Bail P-Y, Covain R.** Diversity of the Ancistrini (Siluriformes: Loricariidae) from the Guianas: the *Panaque* group, a molecular appraisal with descriptions of new species. Cybium. 2012; 36:163–93.
- **Fricke R, Eschmeyer WN, Van der Laan R.** Eschmeyer's catalog of fishes: genera, species, references [Internet]. San Francisco: California Academy of Science; 2024. Available from: http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp
- **Gill TN.** Synopsis of the fresh water fishes of the western portion of the island of Trinidad, W. I. Ann Lyceum Nat Hist NY. 1858; 6:363–430.
- **Howes GJ.** Problems in catfish anatomy and phylogeny exemplified by the Neotropical Hypophthalmidae (Teleostei: Siloroidei). Bull Br Mus Nat Hist Zool. 1983; 45(1):1–39.
- **Isbrücker IJH, Nijssen H.** *Aphanotorulus frankei*, une espèce et un genre nouveaux de poissons-chats cuirassés du Bassin du Rio Ucayali au Pérou (Pisces, Siluriformes, Loricariidae). Rev Fr Aquariol Herpétol. 1983; 9:105–10.
- **Isbrücker IJH, Seidel I, Michels JP, Schraml E, Werner A.** Diagnose vierzehn neuer Gattungen der Familie Loricariidae Rafinesque, 1815 (Teleostei, Ostariophysi). DATZ-Sonderheft Harnischwelse. 2001; 2:17–24.
- **Kner R.** Über die Hypostomiden, oder die zweite Hauptgruppe der Panzerfische. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe. 1853; 10(3): 278–82.
- **Kner R.** Die Hypostomiden. Zweite Hauptgruppe der Familie der Panzerfische. (Loricata vel Goniodontes). Denk Kaiserl Akad Wiss [Wien] Math-Naturwiss Cl. 1854; 7:251–86.
- **Lacépède BGE.** Histoire naturelle des poissons. Paris, Plassan. 1803; 5:1–803.
- **Lehner B, Grill G.** Global river hydrography and network routing: baseline data and new approaches to study the world's large river systems. Hydrol Process. 2013; 27(15):2171–86. https://doi.org/10.1002/hyp.9740
- **Lujan NK, Armbruster JW.** Two new genera and species of Ancistrini (Siluriformes: Loricariidae) from the western Guiana Shield. Copeia. 2011; 2011(2):216–25. https://doi.org/10.1643/CI-10-008
- **Lujan NK, Armbruster JW, Lovejoy NR.** Multilocus phylogeny, diagnosis and generic revision of the Guiana Shield endemic suckermouth armoured catfish tribe Lithoxini (Loricariidae: Hypostominae). Zool J Linn Soc. 2018; 184(4):1169–86. https://doi.org/10.1093/zoolinnean/zly025
- **Lujan NK, Armbruster JW, Lovejoy NR, López-Fernández H.** Multilocus molecular phylogeny of the suckermouth armored catfishes (Siluriformes: Loricariidae) with a focus on subfamily Hypostominae. Mol Phylogenet Evol. 2015a; 82:269–88. https://doi.org/10.1016/j.ympev.2014.08.020
- **Lujan NK, Armbruster JW, Rengifo B.** A new basal Ancistrini genus and species from the Andes of northern Peru (Siluriformes: Loricariidae). Copeia. 2011; 2011(4):497–502. https://www.jstor.org/stable/41416568
- **Lujan NK, Meza-Vargas V, Astudillo-Clavijo V, Barriga-Salazar R, López-Fernández H.** A multilocus molecular phylogeny for *Chaetostoma* clade genera and species with a review of *Chaetostoma* (Siluriformes: Loricariidae) from the Central Andes. Copeia. 2015b; 103(3):664–701. https://doi.org/10.1643/CI-14-194
- **Lujan NK, Armbruster JW, Sabaj MH.** Two new species of *Pseudancistrus* (Siluriformes: Loricariidae) from southern Venezuela. Ichthyol Explor Freshw. 2007; 18:163–74.
- **Lujan NK, Armbruster JW, Werneke DC, Teixeira TF, Lovejoy NR.** Phylogeny and biogeography of the Brazilian–Guiana Shield endemic *Corymbophanes* clade of armoured catfishes (Loricariidae). Zool J Linn Soc. 2019; 188:1213–35. https://doi.org/10.1093/zoolinnean/zlz090

- **Lujan NK, Cramer CA, Covain R, Fisch-Muller S, López-Fernández H.** Multilocus molecular phylogeny of the ornamental wood-eating catfishes (Siluriformes, Loricariidae, *Panaqolus* and *Panaque*) reveals undescribed diversity and parapatric clades. Mol Phylogenet Evol. 2017; 109:321–36. https://doi.org/10.1016/j.ympev.2016.12.040
- **Maddison WP, Maddison DR.** MacClade, Version 4.05. Sinauer Associates, Sunderland; 2002.
- **Maddison WP, Maddison DR.** Mesquite: a modular system for evolutionary analysis. Version 3.81; 2023. Available from: http://www.mesquiteproject.org.
- **Meek SE, Hildebrand SF.** The fishes of the fresh waters of Panama. Publ Field Mus Nat Hist, Zool ser. 1916; 10:217–374.
- **Messager ML, Lehner B, Grill G, Nedeva I, Schmitt O.** Estimating the volume and age of water stored in global lakes using a geo-statistical approach. Nat Commun. 2016; 7:13603. https://doi.org/10.1038/ncomms13603
- **Meza-Vargas V, Calegari BB, Lujan NK, Ballen GA, Oyakawa O, Sousa LM, Rapp-Py Daniel L, Reis RE.** A new *Chaetostoma* species (Siluriformes: Loricariidae) expands the distribution of rubbernose plecos eastward into the lower Amazon basin of Brazil. Ichthyol Herpetol. 2022; 110(2):364–77. https://doi.org/10.1643/i2021068
- **Miranda Ribeiro A.** Loricariidae, Callichthyidae, Doradidae e Trichomycteridae. Commissão de Linhas Telegraphicas Estrategicas de Matto-Grosso ao Amazonas. 1912; 5:1–31.
- **Miranda Ribeiro A.** De scleracanthis. Fluvio "Solimões" anno MCMVIII a cl. F. Machado da Silva duce brasiliense inventis et in Museu Urbis "Rio de Janeiro" servatis. Rev Soc Bras Sci (Rio de Janeiro). 1917; 1:49–52.
- **Oliveira RR, Zuanon J, Py-Daniel LHR, Birindelli JLO, Sousa LM.** Taxonomic revision of *Hopliancistrus* Isbrücker & Nijssen, 1989 (Siluriformes, Loricariidae) with redescription of *Hopliancistrus tricornis* and description of four new species. PLoS ONE. 2021; 16:e0244894. https://doi.org/10.1371/journal.pone.0244894
- **Martins FO, Langeani F, Zawadzki CH.** A new spiny species of *Hypostomus* Lacépède (Loricariidae: Hypostominae) from thermal waters, upper rio Paraná basin, central Brazil. Neotrop Ichthyol. 2014; 12(4):729–36. https://doi.org/10.1590/1982-0224-20140035
- **Montoya-Burgos JI, Muller S, Weber C, Pawlowski J.** Phylogenetic relationships between Hypostominae and Ancistrinae (Siluroidei: Loricariidae): first results from mitochondrial 12S and 16S rRNA gene sequences. Rev suisse Zool. 1997; 104:185–98.
- **Montoya-Burgos JI, Muller S, Weber C, Pawlowski J.** Phylogenetic relationships of the Loricariidae (Siluriformes) based on mitochondrial rRNA gene sequences. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CAS, editors. Phylogeny and classification of Neotropical fishes. Porto Alegre: Edipucrs; 1998. p.363–74.
- **QGIS Development Team.** QGIS geographic information system. Chicago, IL: Open Source Geospatial Foundation Project; 2023. Available from: https://www.qgis.org
- **Rapp Py-Daniel LH.** *Dekeyseria amazonica*, novo gênero e nova espécie na região amzônica, Brasil, e *Dekeyseria scaphirhyncha* (Kner, 1854) nova combinação (Loricariidae: Siluriformes). Amazoniana. 1985; 9:177–91.
- **Rapp Py-Daniel LH.** Redescription of *Parancistrus aurantiacus* (Castelnau, 1855) and preliminary establishement of two new genera: *Baryancistrus* and *Oligancistrus* (Siluriformes, Loricariidae). Cybium. 1989; 13(3): 235–46. https://doi.org/10.26028/cybium/1989-133-004
- **Rapp Py-Daniel LH, Zuanon J, Oliveira RR.** Two new ornamental loricariid catfishes of *Baryancistrus* from rio Xingu drainage (Siluriformes: Hypostominae). Neotrop Ichthyol. 2011; 9(2):241–52. https://doi.org/10.1590/S1679-62252011000200001
- **Regan CT.** Notes on some loricariid fishes, with descriptions of two new species. Ann Mag Nat Hist Ser 7. 1906; 17:94–98.
- **Roxo FF, Ochoa LE, Sabaj MH, Lujan NK, Covain R, Silva GSC, Melo BF, Albert JS, Chang J, Foresti F, Alfaro ME, Oliveira C.** Phylogenomic reappraisal of the Neotropical catfish family Loricariidae (Teleostei: Siluriformes) using ultraconserved elements. Mol Phylogenet Evol. 2019; 135:148–65. https://doi.org/10.1016/j.ympev.2019.02.017

- **Sabaj MH.** Codes for natural history collections in ichthyology and herpetology. Copeia. 2020; 108(3):593–669. https://doi.org/10.1643/ASIHCODONS2020
- **Schaefer SA.** Historical biology of the loricariid catfishes: phylogenetics and functional morphology. [PhD Thesis]. Chicago: The University of Chicago; 1986.
- **von Spix JB, Agassiz L.** Selecta genera et species piscium quos in itinere per Brasiliam annis MDCCCXVII-MDCCCXX jussu et auspiciis Maximiliani Josephi Bavarie regis augustissmi peracto collegit et pingendos curavit Dr J. B. de Spix… J.B. Spix, L. Agassiz. Munich; C. Wolfe; 1829.
- **von Tschudi JJ.** Ichthyologie. In: Untersuchungen über die Fauna Peruana. St. Gallen: Scheitlin & Zollikofer; 1846.
- **Valenciennes A.** Poissons [plates]. In: A. d'Orbigny. Voyage dans l'Amérique méridionale. Paris: Pitois-Levrault; 1834–1839.
- **Werneke DC, Sabaj Pérez MH, Lujan NK, Armbruster JW.** *Baryancistrus demantoides* and *Hemiancistrus subviridis*, two new uniquely colored species of catfishes from Venezuela (Siluriformes: Loricariidae). Neotrop Ichthyol. 2005a; 3(4):533-42. https://doi.org/10.1590/S1679-62252005000400011
- **Werneke DC, Armbruster JW, Lujan NK, Taphorn DC.** *Hemiancistrus guahiborum*, a new suckermouth armored catfish from southern Venezuela (Siluriformes: Loricariidae). Neotrop Ichthyol. 2005b; 3(4):543-48. https://doi.org/10.1590/S1679-62252005000400012
- **Zawadzki CH, Bifi AG, Mariotto S.** *Araichthys loro*, a new genus and species of suckermouth armored catfish from the upper rio Tapajós basin, Brazil (Siluriformes: Loricariidae). Ichthyol Explor Freshw. 2016; 27:361–72.

AUTHORS' CONTRIBUTION

Jonathan W. Armbruster: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing-original draft, Writing-review and editing.

Nathan K. Lujan: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing-original draft, Writing-review and editing.

ETHICAL STATEMENT

Not applicable.

COMPETING INTERESTS

The authors declare no competing interests.

HOW TO CITE THIS ARTICLE

- **Armbruster JW, Lujan NK.** New tribe-level classification of Hypostominae (Loricariidae) based on optimization of morphological states on DNA-based relationships, with descriptions of three new tribes and two new genera. Neotrop Ichthyol. 2024; 22(4):e240108. https://doi.org/10.1590/1982-0224-2024-0108

Neotropical Ichthyology

OPEN ACCESS

SBI
Official Journal of the
Sociedade Brasileira de Ictiologia