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Phylogeny and biogeography of a new South American catfish genus (Siluriformes: Trichomycteridae) providing insights about role of Andean uplift in trichomycterine diversification

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ABSTRACT

Trichomycterine catfishes are widely distributed in the Neotropics, with a greater species concentration in the Andes and eastern South American mountain ranges. The focus of the present study is a trichomycterine clade endemic to a region of central Brazil under severe process of environmental degradation. It was provisionally placed in '*Trichomycterus*', but previous studies indicate that it is closely related to Andean genera. We performed a multigene phylogenetic analysis including representatives of all main trichomycterine lineages and a biogeographical analysis using ancestral area reconstruction in a time-calibrated phylogeny, aiming to test the positioning of that unnamed clade, here described as a new genus, and the role of Andean uplift in trichomycterine diversification. The analysis indicated an Andean origin for Trichomycterinae during the Eocene (about 50 million years ago, Ma) and occurrence of dispersal events from the Andes to other Neotropical areas and in the opposite direction, corroborating multiple biotic exchange as reported for other organisms. The divergence time between the new genus lineage and its sister group, a southern Andes clade, was estimated to have occurred in the Oligocene, about 30 Ma, thus synchronous with the uplift of the Central Andes and the formation of the Central Andean Orocline adjacent to Central Brazil.

Keywords: Ancestral area reconstruction; Mountain biodiversity; Biogeography; Multigene phylogeny; New genus

INTRODUCTION

Trichomycterinae is a diverse subfamily of trichomycterid catfishes exhibiting a wide distribution in the Neotropics, with greater concentration of species in South American mountains, mostly in the Andes and eastern mountain ranges (Costa et al., 2021a; Ochoa et al., 2020). Currently, the Trichomycterinae (hereafter trichomycterines) include over 325 species in nine genera (Fricke et al., 2025), but classification at the genus level has been the target of much criticism (*e.g.*, Costa & Bockmann, 1993; de Pinna, 1998; Fernandez et al., 2021). For many years, delimitation of the genera of Trichomycterinae was uniquely based on combinations of a few morphological characters (*e.g.*, Arratia, 1990a; Eigenmann, 1918), in which all genera, except *Trichomycterus* Valenciennes, 1832 were diagnosed by unique character states not found in other genera, whereas *Trichomycterus* was diagnosed by a combination of generalized character states (Costa, 2021; Datovo & Bockmann, 2010; de Pinna, 1998). *Trichomycterus* in this wide sense was considered a paraphyletic genus with a wide geographical distribution, containing the vast majority of the trichomycterine species (see Costa et al., 2021a for a historical overview of generic trichomycterine classification).

Both the wide geographical distribution of *Trichomycterus*, corresponding to the entire distribution of the Trichomycterinae, and the large number of species with uncertain phylogenetic position, many of them known only from brief original descriptions, have been a powerful obstacle to the recognition and description of new species. Molecular phylogenies have consistently corroborated the paraphyletic status of *Trichomycterus* and supported identification of monophyletic groups of species with well-defined phylogenetic positions (e.g., Fernandez et al., 2021; Katz et al., 2018; Ochoa et al., 2017, 2020), making possible major advances in the taxonomy of the Trichomycterinae. Greatest advances were mainly recorded in studies on taxa from southeastern and southern Brazil, a region that currently concentrates about half of all the species of this subfamily, including the type species of *Trichomycterus*, *Trichomycterus nigricans*

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Valenciennes, 1832 (Costa et al., 2019). *Trichomycterus* was then restricted to a monophyletic group of species endemic to southeastern and eastern Brazil, including *T. nigricans* (Costa, 2021; Katz *et al.*, 2018).

Trichomycterus in the sense of Katz et al. (2018) (i.e. *Trichomycterus s.s.*) is sister to a clade from eastern South America, containing *Scleronema* Eigenmann, 1918 and *Cambeva* Katz, Barbosa, Mattos & Costa, 2018 (Katz et al., 2018), with the three genera together comprising the CST-clade endemic to eastern South America. Today, *Cambeva*, *Scleronema* and *Trichomycterus* s.s. are stable genera, with well-corroborated phylogenies and a rapidly increasing number of species year after year. *Cambeva*, for example, was described in 2018 to include 24 species previously placed in *'Trichomycterus'* (Katz et al., 2018), but along the following six years 33 new species were described for this genus (Costa et al., 2023a, 2023b, 2024; Reis & de Pinna, 2023 and included references), indicating that formal delimitation of genera from a phylogenetic perspective facilitates studies and recognition of new species. However, many trichomycterine species still have an undetermined generic position (Fernandez et al., 2021; Ochoa et al., 2020), being so far allocated in the paraphyletic *'Trichomycterus'* (*e.g.*, Katz et al., 2018).

The majority of species of *'Trichomycterus'* are endemic to river basins draining the Andes and adjacent areas in southern Central America and northern South America, being necessary substantial collections from the several countries to revise and provide new generic status to them. An exception is a clade from central Brazil endemic to a region encompassing the mountain ranges that separate the Amazon and Paraguay river basins, presently comprising two nominal species recently described, *'Trichomycterus' chapadensis* Katz & Costa, 2021 and *'Trichomycterus' jatobensis* Costa, 2021 (Costa et al., 2021a). Our previous phylogenetic study indicated that this unnamed clade is more closely related to genera endemic to southern Andes (i.e. *Bullockia* Arratia, Chang, Menu-Marque & Rojas, 1978, *Hatcheria* Eigenmann, 1909, and *Silvinichthys* Arratia, 1998) than any other trichomycterine, including *Trichomycterus* (Costa et al., 2021a). Other phylogenetic studies and some collection records indicate that this unnamed clade contains some undescribed species from the Paraguay river basin (Ochoa et al., 2017, 2020), but the lack of clear generic placement inhibits descriptions.

The delay in formal descriptions is particularly problematic considering the accelerated state of intense environmental degradation observed in this region (see Conservation remarks below). Therefore, the recognition and formal description of endemic taxa is of utmost importance for the implementation of strategies aimed at the conservation of the remaining fragments of natural environments. Another fundamental aspect for justifying deeper studies on the unnamed clade from Central Brazil is their possible hypothesized relationships within a more inclusive clade, named as the HI-clade in Costa et al., 2021a). The HI-clade includes taxa from southern Andes, *Bullockia maldonadoi* Eigenmann, 1920, *Hatcheria macraei* Girard, 1855 and *Trichomycterus' areolatus* Valenciennes, 1846, and *Ituglanis* Costa & Bockmann, 1993, a geographically widespread genus in South American lowlands (Costa et al., 2021a). Thus deeper phylogenetic studies on the HI-clade may potentially opening new perspectives for our understanding of biogeographic relationships in South America and the possible role of the Andean uplift in the diversification of endemic groups. The first objective of this study is to perform a multigene phylogeny using four mitochondrial and two nuclear markers for representatives of all main trichomycterine lineages delimited in recent phylogenetic studies (*e.g.*, Katz et al., 2018; Ochoa et al., 2017, 2020), with emphasis in taxa of the HI-clade, with the aim of better positioning the central Brazilian clade, which is described here as a new genus. The second objective is to conduct a biogeographical analysis using ancestral area reconstruction methodology in a time-calibrated phylogeny to infer possible historical explanations for the present distribution of the main trichomycterine lineages.

MATERIALS AND METHODS

Terminal taxa

Terminal taxa used in the phylogenetic analysis included representatives of all major trichomycterine lineages delineated in previous studies (Costa et al., 2021a; Fernandez et al., 2021; Katz et al., 2018; Ochoa et al., 2017, 2020), with sequences available in GenBank. Special attention was given to include as many taxa as possible belonging to the HI-clade as outlined in Costa et al. (2021a), including taxa with at least two gene fragments compatible with our analysis, to effectively test the position of the central Brazilian clade within the HI-clade. In addition to '*T.*' *chapadensis* included in our previous analysis (Costa et al., 2021a), we now included another species from the Central Brazilian clade, Paraguay river basin, that is still undescribed and previously included in the analysis of Ochoa et al. (2017). The present analysis included a total of 49 terminal taxa, of which 20 are members of the HI-clade, 22 are trichomycterine species representing other lineages, and 7 are outgroups, including 2 other lineages of Trichomycteridae, 4 representing other lineages of Loricarioidei and one representing Diplomystidae, which together with Siluroidei form the sister group of Loricarioidei.

DNA extraction, amplification and sequencing

DNA extraction and amplification, sequencing reactions, thermal profiles, assessment of sequencing chromatograms and sequence annotation follow Costa et al. (2021a). The analyses included two additional sets of mitochondrially encoded genes synthetized with the following oligos: 16sar-L and 16sbr-H (Palumbi et al., 1991) for the mitochondrially encoded 16S rRNA (16S), and H3L11935 and H12857 (Palumbi et al., 1991) for the mitochondrially encoded NADH: ubiquinone oxidoreductase core subunit 4 (ND4).

Phylogenetic analysis

The concatenated molecular data matrix comprised 4 130 bp (16S 463 bp, CO1 522 bp, CYTB 1 088 bp, ND4 693 pb, MYH6 543 pb, RAG2 820 bp). GenBank accession numbers and the species list are provided in Table 1. Sequences were aligned in MEGA 11 (Tamura et al., 2021) using the ClustalW algorithm (Chenna et al., 2003) for each gene dataset. The best partition scheme and best-fit substitution models for the concatenated molecular data matrix, partitioned by gene and codon position, were calculated using PartitionFinder (Lanfear et al., 2017) implemented in IQTREE2 (Minh et al., 2020), allowing partition merging. The best score was assigned based on the Bayesian Information Criterion (BIC; Schwarz, 1978), as shown in Table 2. Two independent phylogenetic

Table 1 Terminal taxa and GenBank accessions numbers used in the molecular analysis

specie	16S	COX1	CYTB	ND4	MYH6	RAG2
Diplomystes nahuelbutaensis	NC_015823	NC_015823	MN640590	KJ174985	-	DQ492317
Nematogenys inermis	KY807229	KY857952	-	AY307250	JX190413	KY858182
Callichthys callichthys	KP959735	MZ051783	KP960058	HM114437	-	DQ492324
Trichogenes longipinnis	KY807238	MK123682	MK123704	MN389484	MF431104	MF431117
Microcambeva ribeirae	-	MN385807	OK334290	MN389502	MN385819	MN385832
Eremophilus mutisii	KY807207	PQ233849	-	MW415540	KY858086	KY858171
'Trichomycterus' striatus	KY807281	KY858003	KY858069	-	KY858154	KY858219
'Trichomycterus' guianensis	KY807251	MT017633	MT017625	FJ744657	KY858125	DQ492319
'Trichomycterus' sandovali	KY807261	KY857985	KY858052	-	KY858136	KY858205
'Trichomycterus' punctulatus	KY807259	KY857983	-	-	KY858134	KY858203
Trichomycterus giganteus	-	MK123693	MT470413	PP333226	MK123746	MT446426
Trichomycterus nigricans	MF434083	MN813005	MT470415	MN389488	MK123750	MK123765
Trichomycterus itatiayae	KY807254	MW671552	MT470425	OR948809	KY858128	KY858198
Trichomycterus albinotatus	-	MN813007	MT459172	OM324337	MK123743	MN812990
Trichomycterus brunoi	-	MW196751	MW196760	OM324345	MW196772	MW196785
Trichomycterus auroguttatus	-	MT435135	MT436452	OR356043	MT436450	OP699434
Cambeva barbosae	-	MK123689	MK123713	MN389487	MK123740	MN385820
Cambeva balios	-	OQ810040	MT002666	PP333230	-	OQ814193
Cambeva perkos	KY807257	MN995663	KY858050	-	KY858132	KY858202
Cambeva variegata	KY807269	KY857991	OQ110805	PP333239	-	PP333217
Cambeva iheringi	KY807286	KY858008	KY858074	-	KY858159	KY858223
Scleronema minutum	KY807234	KY857957	KY858031	MN389486	KY858109	KY858184
Scleronema macanuda	-	MK123686	MK123708	PP333229	MK123736	MK123760
Scleronema auromaculatum	-	OM037445	OM037134	-	OM037135	OM037136
Bullockia maldonadoi	KY807202	KY857926	FJ772237	MW415539	KY858081	KY858166
Hatcheria macraei	MW415491	-	FJ772225	MW415541	-	MW415456
'Trichomycterus' areolatus	KY807241	KY857964	FJ772214	AP012026	KY858115	KY858188
Oreiadoglanis chapadensis	PQ818298	MW196746	MW196756	PQ817546	MW196766	MW196778
Oreiadoglanis sp. 2	KY807283	KY858005	KY858071	-	KY858156	-
Silvinichthys mendozensis	MW415494	-	-	MW415544	-	MW415457
'Trichomycterus' barbouri	MW415496	-	-	MW415546	-	-
Ituglanis amphipotamus	-	MW250305	MW247140	-	MW247141	MW247142
Ituglanis boitata	KY807272	KY857994	MK123706	MN389485	MK123734	MN389485
Ituglanis amazonicus	MF434082	MZ051763	MK123705	MW415542	MF431105	KY858175
Ituglanis metae	MW415492	-	-	MW415543	-	-
Ituglanis eichorniarum	KY807215	KY857939	KY858021	-	KY858094	KY858176
Ituglanis paraguassuensis	-	MW196748	-	-	MW196768	MW196780
Ituglanis payaya	-	MW196747	MW196757	-	MW196768	MW196780
Ituglanis goya	KY807223	KY857945	-	-	KY858101	KY858180
Ituglanis parahybae	KY807219	-	KY858023	-	KY858098	-
Ituglanis herberti	KY807224	KY857947	KY858025	-	KY858103	-
'Trichomycterus' cachiraensis	KY807248	KY857971	-	-	KY858122	KY858195

reconstruction approaches, Bayesian Inference (BI) and Maximum Likelihood (ML) were used. BI was conducted using Beast v.1.10.4 (Suchard et al., 2018) with the Birth-Death Process model for tree reconstruction (Gernhard, 2008), and two independent Markov Chain Monte Carlo (MCMC) runs with 10^8 generations with a sampling frequency of 1000. Convergence and burn-in of the MCMC chains were determined by evaluating the achievement of the stationary phase and the effective sample size greater than 200 for all parameters using Tracer v.1.7.1 (Rambaut et al., 2018). Trees were combined in LogCombiner v.1.10.4 (Suchard et al., 2018) with 25% burn-in at the outset of each run. The consensus tree and posterior probabilities were calculated in TreeAnnotator v.1.10.4 (Drummond et al., 2012) to assess node support. ML was conducted using IQTREE v.2.2.2.6 (Minh et al., 2020), ultrafast bootstraps (Hoang et al., 2018) and the SH-like approximate likelihood ratio test (Guindon et al., 2010), both with 1000 replicates, was calculated to assess node support.

Divergence-time estimation and reconstruction of ancestral areas

The divergence time analysis was conducted in Beast v.1.10.4 along with the estimation of topology, using uncorrelated relaxed molecular clock model with lognormal distribution. The same dataset, partitions, evolutionary models, and parameters as described above were implemented. Calibration points were established as follows: the origin of the family Trichomycteridae with a normal prior distribution (mean=106 Ma, SD=7.0), following the estimative of Betancur-R et al.

Table 2 Best-fitting models, calculated by the BIC criterion, for the partition scheme and the number of base pairs for each partition used in the molecular analysis

Partition	Base pairs	Evolutive model
16S, CO1 1st, ND4 1st	869	GTR +I +G
CO1 2nd, CYTB 2nd, ND4 2nd	768	HKY +I +G
COI 3rd	174	TRN +G
CYTB 1st	363	K80 +I +G
CYTB 3rd, ND4 3rd	593	TRN +G
MYH6 1st, MYH6 2nd	362	JC +I +G
MYH6 3rd	181	K80 +G
RAG2 1st, RAG2 2nd	547	SYM +G
RAG2 3rd	273	K80 +G

(2015); and the origin of the corydoradine lineage (Callichthyidae) with a lognormal prior distribution (mean=55 Ma, SD=1), based on the dating of the oldest known callichthyid fossil species, *Hoplisoma revelatus* Cockerell, 1925 from the Late Paleocene of the Mais Gordo Formation in Salta, Argentina, about 58 Ma, following identification in Dias et al. (2025).

The best model to reconstruct the relationships among the ancestral areas was selected using BioGeoBEAR (Matzke, 2014), which was executed in RASP v.4.4 (Yu et al., 2020), then indicating the event-based analysis of Lagrange (Dispersal-Extinction-Cladogenesis model, referred here as DEC) (Ree & Smith, 2008). A total of seven areas of endemism were delimited. Delimitation of the three areas in the Andes were according to delimitation of major areas of endemism in the Andes in Schaefer (2011): (A) Northern Andes; (B) Central Andes; (C) and Southern Andes. Other four areas were coincident with the distribution of trichomycterine lineages as shown in previous studies: (D) Pakaraima Mountains; (E) Amazon lowlands; (F) Central Brazil; and (G) Eastern South America (Costa et al., 2021a; Katz et al., 2018; Ochoa et al., 2020; Vilardo et al., 2023).

Taxonomic accounts

Morphological examination and data were according to Costa et al. (2021a), with addition of 20 specimens of two undescribed species of the Central Brazilian clade, deposited in the fish collection of the Laboratory of Fish Biology, Universidade Estadual Paulista, Botucatu (LBP 5056, 3 ex.; LBP 5058, 7 ex.; LBP 5648, 10 ex. cleared and stained for osteological examination; LBP 30668, 3 ex.). Coordinates for specimens used in the phylogenetic analysis are provided in Costa et al. (2021a) and Ochoa et al. (2020). Terminology for osteological structures followed Costa (2021), with modifications described in Kubicek (2022). Nomenclature for pores of the cephalic latero-sensory system followed Arratia & Huaquin (1995), with modification proposed by Bockmann & Sazima (2004). '*Trichomycterus*' used in species names along the text refers to species still formally allocated in the genus *Trichomycterus*, but more closely related to other trichomycterine genera than to the clade containing the type species of the genus (i.e. *Trichomycterus* sensu strictum).

RESULTS

Phylogenetic analysis

The results corroborated Trichomycterinae as monophyletic, containing two more inclusive clades, all with high statistical support (Figure 1). The first clade comprises the CST-clade from eastern South America and a lineage with species with undetermined generic status from the central Andean region, corroborating previous studies (Fernandez et al., 2021; Ochoa et al., 2020). The second one comprises all other lineages of Trichomycterinae, including the HI-clade. The latter clade occurs in all the areas of the Neotropical Region and includes the genera *Bullockia*, *Eremophilus*, *Hatcheria*, *Ituglanis* and *Silvinichthys*, in addition to seven lineages with undefined generic status, including the Central Brazilian clade.

The Central Brazilian clade was supported as sister to a clade comprising two subclades from southern Andes: the *Hatcheria* clade, containing taxa from central Chile and adjacent areas in Argentina, and the *Silvinichthys* clade, from north-western Argentina (Figure 1). The *Hatcheria* clade includes *B. maldonadoi*, the only species of its genus according to Arratia et al. (1978), *H. macraei*, the only species of its genus according to Arratia & Menu-Marque (1981), and an unnamed clade comprising '*T.*' *areolatus* and '*Trichomycterus*' *chiltoni* Eigenmann, 1928. The *Silvinichthys* clade, includes *Silvinichthys mendozensis* Arratia et al., 1978, the type species of the genus, and an unnamed clade comprising '*Trichomycterus*' *alterus* Marini, Nichols & La Monte, 1933 and '*Trichomycterus*' *minus* Fernández & Vari, 2012.

Biogeography

Our analysis indicated an Andean origin, areas A and B (Figure 2), for the most recent common ancestor (MRCA) of Trichomycterinae, with age estimated in the Eocene. The analysis supported multiple dispersal and vicariance events throughout the Cenozoic generating the present geographical distribution; dispersal events occurred both from the Andes to other South American areas and in the opposite direction (see discussion below). Dispersal events between areas currently distant from each other, with no records of the clade in vast intermediate areas (*e.g.* from central Andes presently inhabited by the clade comprising '*Trichomycterus*' *rivulatus* Valenciennes, 1846 and '*Trichomycterus*' *quechuorum* Steindachner, 1900, to eastern South America presently inhabited by the CST-clade, Figure 2, with close relatives presently missing in central South America), suggest the existence of extinction processes or insufficient field studies in intermediate areas.

Taxonomic accounts

***Oreiadoglanis* Costa and Katz, gen. nov.**

Trichomycterus non *Trichomycterus* Valenciennes, 1832; Ochoa et al., 2017: 75.

Type species: *Trichomycterus chapadensis* Katz and Costa, 2021 in Costa et al. (2021a).

Diagnosis: *Oreiadoglanis* is distinguished from all other trichomycterine genera by a unique morphology of the

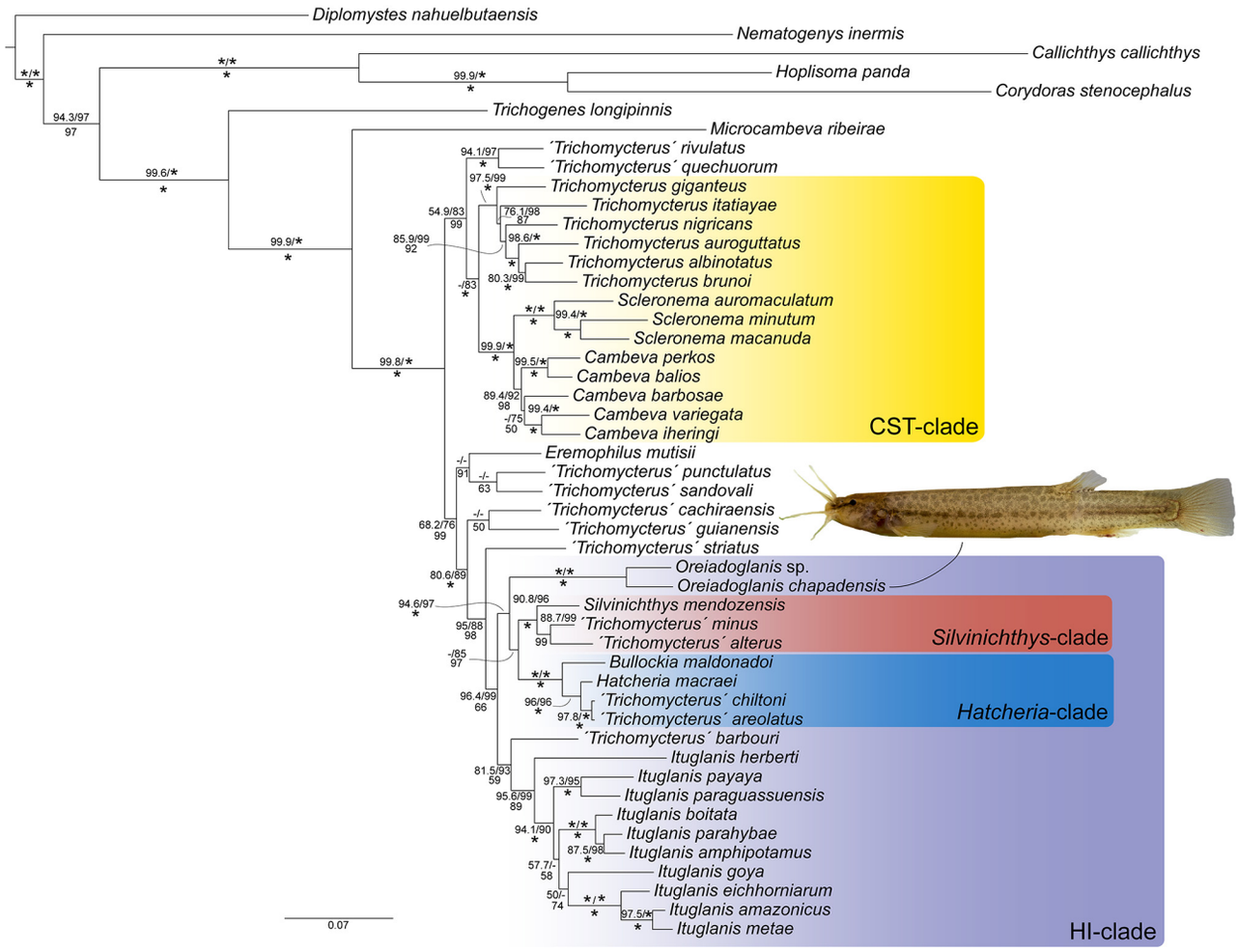

Figure 1 Bayesian inference tree estimated by BEAST 1.10.4 for 42 species of Trichomycterinae, two species from other trichomycterid subfamilies and five more distantly outgroup catfish species, using a multigene molecular dataset comprising 16S, CO1, CYTB, ND4, MYH6 and RAG2 (total of 4 130 bp)

Numbers above branches, separated by slashes (/), indicate ultrafast bootstrap (UFBoot) and Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT), respectively, and numbers below branches indicate Bayesian posterior probabilities. Asterisks (*) indicate maximum support values and dashes (-) indicate values below 50. CST refers to *Cambeva-Scleronema-Trichomycterus* clade, and HI to *Hatcheria-Ituglanis* clade. Fish in photo is a live paratype of *Oreiadoglanis chapadensis* (UFRJ 10 758, 58.0 mm SL), the type species of the genus.

quadrate, comprising an elongate postero-dorsal process, often terminating in sharp tip (Figure 3B; *vs.* quadrate never exhibiting this morphology, *e.g.* Arratia, 1990b) and by the poorly ossified hypobranchials 2 and 3, with ossification restricted to their anterior tip (Figure 3D; *vs.* hypobranchials 2 and 3 always more ossified, *e.g.* Costa et al., 2021a). *Oreiadoglanis* is also distinguished from *Bullockia* by having longer nasal and maxillary barbels, with the nasal barbel posteriorly reaching the opercular patch of odontodes or beyond it (*vs.* not reaching orbit) and maxillary barbel reaching the posterior margin of the interopercular patch of odontodes or beyond it (*vs.* reaching anterior margin of interopercular patch of odontodes), by the absence of the supraorbital s4 pore (*vs.* presence, Arratia & Huaquin, 1995), absence of infraorbital pores i6 and i9 (*vs.* presence, Arratia & Huaquin, 1995), and long anterior processes of the pelvic bone, longer than pelvic bone excluding anterior processes (*vs.* shorter, Arratia et al., 1978: Figure 5); from *Eremophilus* Humboldt, 1805 by the presence of well-developed pelvic fin and pelvic girdle (*vs.* absence), by having supraorbital canal with four pores, s1, s2, s3 and s6 (*vs.* two pores, s3 and s6, Arratia & Huaquin, 1995), and absence of a posteroventral process on the lateral ethmoid (*vs.* presence, Arratia, 1990a); from *Ituglanis* by the presence of 12 or 13 ribs (*vs.* 2 to 8) and a laterally directed sphenotic process (Figure 3C; *vs.* anteriorly directed, Costa et al., 2021a: Figure 2M); from *Rhizosomichthys* Miles, 1943 by the absence of a thick layer of adipose tissue between the skin and the body musculature (*vs.* presence, Schaefer & Fernández, 2009: Figure 1), the absence of two pillow-like masses of adipose tissue on nape, and the absence of a robust osseous ridge on the dorsolateral surface of the autopalatine (*vs.* presence, Schaefer & Fernández, 2009: Figure 10); from *Scleronema* by the absence of an skin crest similar to an adipose fin on the dorsal margin of the caudal peduncle (*vs.* presence, Ferrer & Malabarba, 2020: Figure 1), and the presence of the anterior portion of the supraorbital canal with pores s1 and s2 (*vs.* absence); from *Silvinichthys* by the absence of a conspicuously perforated skin body surface by pores of ampullary organs (*vs.* body skin surface highly perforated by pores of ampullary organs, Arratia, 1998), by having a long supraorbital canal, with four pores, S1, S2, S3 and S6 (*vs.* a short supraorbital canal, restricted to the snout region with two pores, S1 and S2, Arratia & Huaquin, 1995), one or two

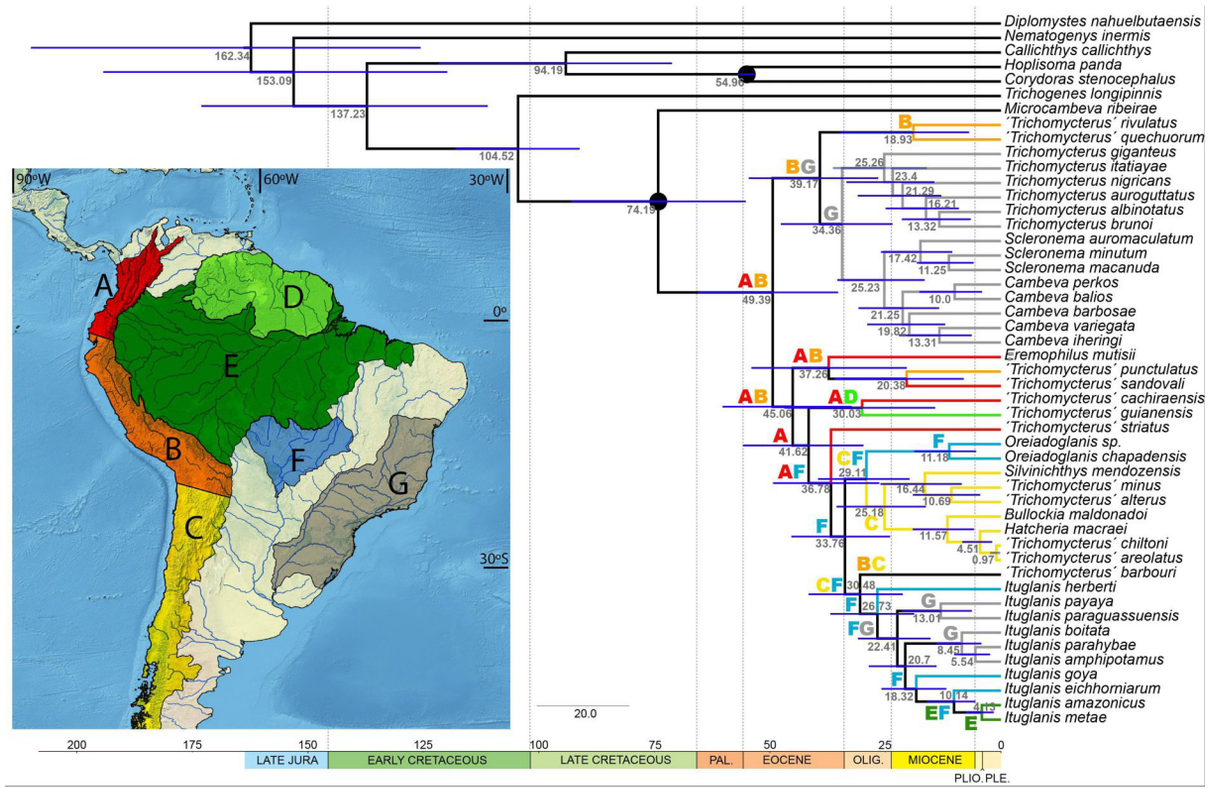

Figure 2 Time-calibrated phylogenetic tree and results of the reconstruction of ancestral areas analysis based on the analytical approach Lagrange-Dispersal-Extinction-Cladogenesis model (DEC)

Position of time calibrations are indicated by black circles, and the 95% highest posterior credibility intervals of divergence times are represented by blue bars. The map indicates areas of endemism used in the analysis: (A) Northern Andes; (B) Central Andes; (C) Southern Andes; (D) Pakaraima Mountains; (E) Amazon lowlands; (F) Central Brazil; and (G) Eastern South America.

segments of the infraorbital canal (*vs.* absence of any segment of the infraorbital canal, Arratia, 1998), anteromedial process of the pelvic bone anteromedially directed, making its anterior tip in contact or in close proximity to its symmetrical homologous process (Figure 3F; *vs.* anteriorly directed, its anterior tip distant from its symmetrical homologous process, Arratia, 1998: Figure 11B); from *Trichomycterus* by having the skin between the opercle and interopercle smooth, without striae (*vs.* with longitudinal striae); from *Bullockia*, *Cambeva*, *Eremophilus*, *Hatcheria*, *Ituglanis*, *Scleronema* and *Silvinichthys* by having a sharply pointed anterodorsal extremity of the metapterygoid (Figure 3B; *vs.* rounded to slightly pointed, e.g. Arratia, 1990b); from *Bullockia* and *Hatcheria* by having two pores in the lateral series of the trunk (*vs.* 3 to 6, Arratia & Huaquin, 1995), the dorsal process of the interopercle positioned near the anterior margin of the bone (Figure 3B; *vs.* more posteriorly placed, distant from the bone anterior margin, Arratia et al., 1978: Figure 3), and a dorsally pointed metapterygoid (Figure 3B; *vs.* rounded, Arratia & Menu-Marque, 1981: Figure 3A); from *Bullockia*, *Hatcheria*, *Rhizosomichthys*, and *Silvinichthys* by having a narrow and pointed lateral process on the sesamoid supraorbital (Figure 3A; *vs.* a broad lateral projection in *Silvinichthys*, Arratia, 1998: Figure 8A, and absence of lateral projections in *Bullockia*, *Rhizosomichthys*, and *Hatcheria*, Arratia et al., 1978); from *Bullockia*, *Hatcheria*, and *Silvinichthys* by having two dorsal hypural plates (Figure 3G; *vs.* single, Arratia et al., 1978: Figure 18); from *Bullockia* and *Scleronema* by having the maxilla shorter than the premaxilla (Figure 3A; *vs.* longer, Costa et al., 2022: Figure 2A, B); from *Cambeva*, *Eremophilus*, *Rhizosomichthys*, *Scleronema*, and *Silvinichthys* by having a pronounced concavity on the medial margin of the autopalatine (Figure 3A; *vs.* shallow concavity when concavity is present, *e.g.* Arratia, 1990b); from *Cambeva, Ituglanis*, *Scleronema* and *Trichomycterus s.s.* by the absence of the supralateral process of the coracoid (Figure 3E; *vs.* presence, Costa, 2021: Figure 5; Costa et al., 2021a: Figure 5O); from *Cambeva* and *Trichomycterus* by the rostral series of neuromasts being inconspicuous or absent (*vs.* conspicuous, with easily visible individual neuromasts); and from *Ituglanis* and *Silvinichthys* by having the anal-fin origin at a vertical approximately through the middle of the dorsal-fin base (*vs.* just posterior to the dorsal-fin base, Arratia et al., 1978).

Etymology: From the Greek *oreiades*, a nymph of the Greek mythology inhabiting and protecting the mountains, besides being the nymph name used by the Bavarian naturalist Karl Friedrich Philipp von Martius to naming the South American phytogeographical province of the savannah-like Cerrado; and *glanis*, a name of uncertain origin, used by Aristotle to name a catfish, also frequently used to compose generic names of trichomycterid catfishes. The name of this new genus refers to the occurrence of all included species in the Cerrado region of the high plateaus of central Brazil. Gender masculine.

Included species: *Oreiadoglanis* includes two nominal species, *Oreiadoglanis chapadensis* Katz & Costa, 2021 in Costa et al. (2021a) from the upper Rio Paraguai basin, Rio da Prata system, and *Oreiadoglanis jatobensis* (Costa, 2021) from the upper Rio Xingu drainage, Rio Amazonas basin. The latter species was described in the same paper as *O. chapadensis*, with both sharing all morphological derived features (Costa et al., 2021a), and therefore considered congeneric species, but material to extract DNA was not available. We here have

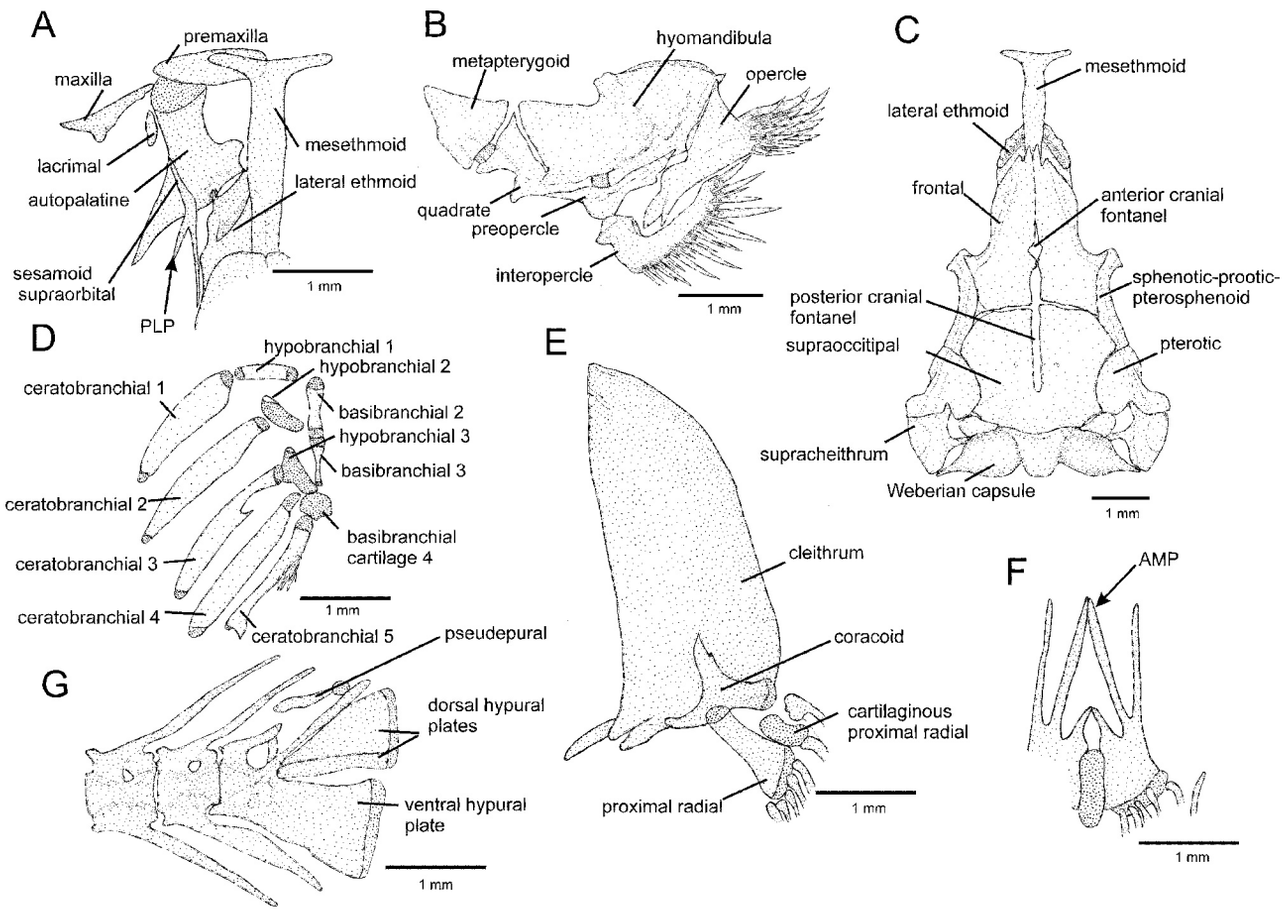

Figure 3 Osteological structures of *Oreiadoglanis chapadensis*

A: mesethmoidal region, median and left portion, dorsal view; B: left jaw suspensorium and opercular series, lateral view; C: neurocranium and adjacent structures, dorsal view; D: ventral branchial arches, left and median portions, dorsal view; E: shoulder girdle, ventral view; F: pelvic girdle, ventral view; G: caudal skeleton, left lateral view. AMP, anteromedian process; PLP, posterolateral process. Larger stippling represents cartilaginous areas.

examined two other species, still undescribed, from the upper Rio Paraguai basin and upper Rio Xingu drainage, respectively. All localities in Central Brazil.

Conservation remarks: The area of Central Brazil where *Oreiadoglanis* occurs remained well preserved until the mid-20th century, but environmental decline has been rapid and devastating in recent years. Records made by naturalists and government commissions between the end of the 18th century and the mid-20th century (Costa, 2017; Domingues, 2001; Lima & Sá, 2017; Sick, 1997) show that natural environments were little modified. However, we have recorded a marked process of deforestation and destruction of freshwater habitats throughout the region in our fieldworks between the 1990s and 2016. The native vegetation typical of the savannah-like Cerrado has been almost completely extirpated, giving way to immense fields of soybean plantations, while streams have often been channelled, dammed, or have disappeared completely after their waters were diverted for irrigation of plantations. Only small streams with thin marginal vegetation remain, often with high levels of pollution, or rare areas under protection, such as the Chapada dos Guimarães National Park and some tourist sites.

DISCUSSION

Relationships of *Oreiadoglanis*

Like in our previous study (Costa et al., 2021a), *Oreiadoglanis* is here supported as a member of the HI-clade as delineated in that study, but also containing four species that were not included in the previous analysis: '*Trichomycterus' barbouri* Eigenmann, 1911, a geographically widespread species in central and southern Andes, occurring in Argentina and Bolivia (Cardoso & Bogan, 2015; Fernández, 2000), which is supported as sister to *Ituglanis*, a genus occurring in the Amazon and other Cis-Andean lowlands (Costa et al., 2021b); '*T.*' *alterus* and '*T.*' *minus*, both from southern Andes in Argentina (Fernández & Vari, 2012), which together are supported as sister to *S. mendozensis* from the same area (Arratia, 1998); and, '*T.*' *chiltoni* from the southern Andes in Chile (Eigenmann, 1928), which together '*T.*' *areolatus* from the same area are supported as sister to *H. macraei*, also from southern Andes.

No morphological derived character state was found to be shared by species of the HI-clade in the present study. However, all species of *Oreiadoglanis* have a small ossification, sometimes represented by a cartilage or both a small cartilage and an elongate ossification in the caudal skeleton at the position of the epural bone (Figure 3G), here named as pseudepural, since a true epural in not present in trichomycterines. A similar ossification occurs in some specimens of the type species of *Bullockia*, *Hatcheria* and *Silvinichthys* (Arratia et al., 1978; Arratia & Menu-Marque, 1981; Arratia, 1990b), as well as in '*T.*' *barbouri* (Fernández, 2000) and eventually in other species from Argentinean Andes

(Arratia & Menu-Marque, 1984), but not in other trichomycterine taxa here examined, indicating a possible ancestral condition for the HI-clade with variable expression among extant species.

The present analysis supported monophyly of the clade comprising *Oreiadoglanis*, the type species of *Silvinichthys*, *Bullockia*, and *Hatcheria*, and '*T.*' *alterus*, '*T.*' *areolatus*, '*T.*' *minus* and '*T.*' *chiltoni* with high support values (Figure 1). As reported by Costa et al. (2021a), species of *Oreiadoglanis*, *Silvinichthys*, *Bullockia*, and *Hatcheria*, and '*T.*' *areolatus* share the absence of the supra-lateral process of the coracoid (Figure 3E; see also Arratia et al., 1978: Figure 4 and Arratia, 1990: Figure 11A), a condition not found in taxa out of this clade. Therefore, the absence of that process consists of a potential synapomorphy for this clade, although not being possible to confirm it in *'T.' alterus, 'T.' chiltoni*, and *'T.' minus*, for which data on informative osteological characters are not available. This process is present in other trichomycterines (*e.g.* Costa, 2021: Figure 5), although often being rudimentary in *Cambeva* and *Scleronema*. Species of *Oreiadoglanis*, *Bullockia* and *Hatcheria* also share an uncommon apomorphic morphology of the preopercle (Costa et al., 2021a), in which the middle portion is ventrally expanded (Figure 3B; see also Arratia, 1990b: Figure 7, Figure 10C), but this condition is not seen in the illustration of the opercular apparatus of *S. mendozensis* in Arratia (1998: Figure 9), therefore we assume that this condition is not present in every member of this clade and may not be informative to diagnose it.

The role of Andean uplift in diversification of Trichomycterinae catfishes

Recent studies have highlighted the relevance of the Andean uplift in diversification of South American biota (*e.g.* Antonelli et al., 2009; Boschman et al., 2023; Cassemiro et al., 2023; Chaves et al., 2011; Vieu et al., 2022) and a different situation would not be expected for Trichomycterinae, a group with most of its representatives typically living in mountain rivers and occurring in all Andean regions. The occurrence of members of all the major clades of Trichomycterinae in the Andes suggests that mountain building process in Andes also played a prominent role in the diversification of this fish group. Our biogeographical analysis (Figure 2) pointed to the origin of Trichomycterinae in the region comprising the northern and central portion of the Andes, with the beginning of diversification occurring during the early Eocene (about 50Ma), a time just after mountain building in northern Andes (Boschman, 2021). Diversification of the main Trichomycterinae clades occurred between the Eocene and the Oligocene, which is compatible with the beginning of diversification estimated for other Andean organisms (e.g. Boschman & Condamine, 2022; Ceccarelli et al., 2016). Considering that most Trichomycterinae live in mountain rivers with cold waters (*e.g.* Costa, 2021), the rapid diversification of species and geographical expansion at the end of the Eocene may be related to the global cooling recorded for the period (Mudelsee et al., 2014).

The Andean Cordillera may act both as a dispersal route for groups adapted to mountain life and as a barrier for typical lowland groups (Patterson et al., 2012). According to our analysis, at least two primary dispersal events of trichomycterines occurred from the Andes to other areas: dispersal of the lineage originating the CST-clade from central-northern Andes to eastern South America and dispersal of the lineage originating the HI-clade from northern Andes to Central Brazil, both during the Eocene (about 40Ma). More interestingly, our analysis indicated that the occupation of the southern Andes by trichomycterines occurred through two dispersal events from Central Brazil within the HI-clade, both during the late Eocene and early Oligocene (see below). These events corroborate the occurrence of multiple biotic exchange between Andes and other areas of South America, as reported for other Neotropical organisms (*e.g.*, Pérez-Escobar et al., 2022).

Oreiadoglanis from tropical central Brazil is supported as sister to a trichomycterine group endemic to subtropical southern Andes (Figure 2), with the time of divergence between these two lineages estimated as being occurred in the Oligocene (about 30 Ma), coincident with a first major shift in diversification rates of South American fish (Cassemiro et al., 2023). This estimated divergence timing is synchronous with the uplift of the Central Andes and the formation of the Central Andean Orocline (*e.g.*, Albert et al., 2021), that is adjacent to Central Brazil. At the same estimated time occurred the divergence of the '*T.*' barbouri lineage from central and southern Andes, and the MRCA of *Ituglanis* in Central Brazil, probably resulting from the same paleogeographic event. According to Boschman's (2021) paleoelevation reconstruction for Andean mountain building, the western Patagonian Andes had already reached its present elevation at about 55 Ma. However, episodes of deformation and uplift intensified during the early-mid Miocene, about 20 Ma, when occurred a broad marine transgression through the Austral basin, separating the southern Andean region from the central portion of South America, probably widening the geographical gap between the distribution of *Oreiadoglanis* in central Brazil and the distribution of its sister group in southern Andes.

Trichomycterine generic classification

Currently, Trichomycterinae includes about 325 nominal species, of which approximately half are currently placed in five stable monophyletic genera (*Cambeva*, *Ituglanis*, *Scleronema*, *Silvinichthys*, and *Trichomycterus s.s.*) and in four monotypic stable genera (*Bullockia*, *Eremophilus*, *Hatcheria*, and *Rhizosomichthys*). On the other hand, the other half of the species are taxa with undetermined generic position, still formally placed in the paraphyletic '*Trichomycterus*' (see Introduction above). To solve this taxonomical inconsistency, Fernandez et al. (2021) proposed to synonymize all trichomycterine genera with a single genus, *Trichomycterus*. If this proposal was feasible, this taxonomical act would have a great impact on the stability of the group classification, requiring at least 100 species being transferred from stable genera over time to *Trichomycterus*, in addition to dramatically impoverishing the phylogenetic information level of the classification. However, as discussed by Costa et al. (2021a), this proposal would not be feasible, since *Eremophilus* has chronological priority over *Trichomycterus* that was described by Valenciennes (1832) 27 years after the first genus, *Eremophilus*, described by von Humboldt (1805). In case of transferring all trichomycterines to *Eremophilus*, we would have about 325 generic transferences, causing a much deeper impact on the stability and phylogenetic content of the classification. Therefore, the best option seems to us to allocate those incertae sedis species in new monophyletic genera, as adopted here in describing *Oreiadoglanis*, and in

the past when describing *Cambeva* and *Ituglanis* (Costa & Bockmann, 1993; Katz et al., 2018; see discussion below).

Some resistance to accepting the description of new generic names for Trichomycterinae may arise from the difficulty of identifying new genera through external morphological characteristics, often having to use osteological preparations or DNA sequencing, impeding rapid identification in the field or in museum collections. We believe that ichthyological taxonomy should not be limited to common external morphological characteristics as effective tool for identification. It is common knowledge that many angiosperms can only have their genera morphologically identified through a few floral characteristics, often only accessible during very short flowering periods, as well as microorganisms are more easily and quickly identified through genetic approaches (e.g. Franco-Duarte et al., 2019). Furthermore, animal genera, such as certain groups of rodents (e.g. oryzomine rodents), can only be reliably identified by observing special characters of dentition and osteology (Weksler & Percequillo, 2011), which are not accessible during field studies and rapid examinations in collections by non-specialized biologists. Therefore, we believe that bringing special characters to the taxonomy of Trichomycterinae does not hinder but rather enriches and enables an informative and stable phylogenetic classification.

Good examples of the benefits of new genera descriptions to increase the flow of publications on species diversity are the genera *Cambeva* and *Ituglanis*. Both were originally described to include species previously allocated in '*Trichomycterus*' and are not objectively identifiable through characters of the external morphology. *Cambeva* had its number of species increased in 138% since its description in 2018 (see Introduction above) and the genus name has been explicitly used as valid in over 20 publications, including articles written by researchers belonging to different research groups (*e.g.* Donin et al., 2020; dos Reis et al., 2020; Ribeiro et al., 2021). The same increase in number of described species was obtained after the description of *Ituglanis* by Costa & Bockmann (1993), containing in 1993 a total of nine described species, but presently reaching 30 valid species, with over 30 articles conducted by different research groups adopting the name *Ituglanis* as valid (*e.g.* Bichuette & Trajano, 2008; Castro & Wosiacki, 2017; Datovo & Landim, 2005; de Pinna, 1998; Lima et al., 2013; Ochoa et al., 2017; Sarmento-Soares et al., 2006).

CONCLUSION

Tropical South America harbours some of the most rich and endangered biodiversity hotspots of the globe, including the savannah-like Cerrado (Myers et al., 2000), with many taxa still unknown for scientists. It is possible that some undescribed species of *Oreiadoglanis* may be on the verge of extinction or even extinct. Thus, we hope that the present formal description of *Oreiadoglanis* will be a starting point for better understanding the species diversity of the clade, which will be a fundamental step towards more comprehensive studies on both comparative biology and biodiversity conservation.

NOMENCLATURAL ACTS REGISTRATION

This study and the nomenclatural act it contains are registered with ZooBank, the official registry of the International Code of Zoological Nomenclature (ICZN). Publication ID: http:// zoobank.org/pub:78822B17-A5D6-4D10-8C5D-E4EBA0DFA9B9.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

Field studies have been made using with permits provided by ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade; permit numbers: 64415-5, 94649-1) and methods approved by the Ethics Committee for Animal Use of Federal University of Rio de Janeiro (permit numbers: 065/18, 084/23).

DATA AVAILABILITY

DNA sequences have been deposited in Genbank (Table 1).

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

W.J.E.M.C. conceived the research and wrote the manuscript; W.J.E.M.C. and A.M.K. collected specimens; W.J.E.M.C., J.L.O.M., P.F.A., and A.M.K. conducted lab work; W.J.E.M.C., J.L.O.M., P.F.A. analysed the data; J.L.O.M., P.F.A., and A.M.K. supplemented and revised the preliminary text. All authors read and approved the final version of the manuscript.

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