

REGULAR PAPER

Molecular delimitation and taxonomic revision of the wimple piranha *Catoprion* (Characiformes: Serrasalminidae) with the description of a new species

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Abstract

A taxonomic revision of wimple piranhas of the genus *Catoprion* is performed in combination with a molecular analysis using mtDNA. Molecular phylogenetic analyses of 49 specimens using genetic distances, conventional likelihood and four delimitation methods yielded two distinct lineages of *Catoprion*, with the morphological analyses of 198 specimens of *Catoprion* corroborating the molecular results. We provide a redescription of *Catoprion mento*, from the Paraguay, Orinoco, and tributaries of western Amazon basin, keeping *Mylesinus macropterus* as a junior synonym of *C. mento*, and the description of *Catoprion absconditus* n. sp., from the Amazon and Essequibo basins. *C. absconditus* n. sp. differs from *C. mento* by the presence of 86–94 perforated scales in the lateral line (vs. 65–86 scales) and the presence of 35–40 circumpeduncular scales (vs. 29–34 scales). The distribution of *C. mento* follows the Amazonas-Paraguay-Orinoco lowlands, whereas *C. absconditus* follows the eastern Amazon biogeographic pattern.

KEYWORDS

biodiversity, DNA barcoding, Neotropical region, systematics, Teleostei

1 | INTRODUCTION

Serrasalminidae is a Neotropical freshwater fish family comprising 100 species within 16 extant genera (Fricke *et al.*, 2020), morphologically identified by a combination of characters that includes a deep and laterally compressed body, a ventral keel composed of spines derived from modified abdominal scales and the presence of a predorsal spine in almost all genera, with the exception of *Colossoma* Eigenmann & Kennedy 1903, *Mylossoma* Eigenmann & Kennedy 1903 and *Piaractus* Eigenmann 1903 (Jégu, 2003). The dietary specializations for carnivory, frugivory, herbivory, and lepidophagy result in disparate morphological traits related to teeth shape and buccal apparatus (Goulding, 1980; Nico and Taphorn, 1988; Sazima, 1983; Sazima & Machado, 1990). The genus *Catoprion* Müller & Troschel, 1844 stands out for its singular lepidophagous habit (Roberts, 1970).

Catoprion was described to allocate *Serrasalmus mento* Cuvier, 1819 and has been considered monotypic, with a single

species *Catoprion mento*, since its description (*i.e.*, Müller & Troschel, 1844; Nico *et al.*, 2017). Although *Mylesinus macropterus* Ulrey, 1894 was included as a junior synonym of *C. mento* by Eigenmann (1912), the synonym was little discussed in the literature and never evaluated systematically. The genus *Catoprion* is easily distinguished from the other serrasalminid genera by presenting a lower jaw much more prominent and projecting past the upper jaw, and a distinctive arrangement of mamilliform teeth in both premaxilla and dentary (Géry, 1972), being considered an “aberrant condition” in the family (Gosline, 1951). Based on this condition, Géry (1972) proposed the subfamily Catoprioninae to include *Catoprion*, an arrangement followed by his subsequent studies (Géry, 1976, 1977). Nonetheless, the first cladistic study in Serrasalminidae, based on morphological characters, proposed *Catoprion* as a member of the clade, including the “piranhas” (*Pristobrycon* Eigenmann 1915, *Pygocentrus* Müller & Troschel, 1844, *Pygopristis* Müller & Troschel, 1844 and *Serrasalmus* Lacepède 1803) (Machado-Allison, 1982). This hypothesis was

corroborated by subsequent morphology- and molecular-based phylogenies with few variations in the exact position of the genus (Orti *et al.*, 1996, 2008; Jégu, 2004; Freeman *et al.*, 2007; Thompson *et al.*, 2014; Mateussi *et al.*, in review).

Although the phylogenetic position of the genus is well supported by several studies, an opportunity remains to explore the possibility of multiple or cryptic species within the genus throughout South America. Herein, the taxonomic revision of the genus was performed using morphological and molecular data, as well as the redescription of *C. mento* and the description of a new species from the Amazon basin.

2 | MATERIALS AND METHODS

2.1 | Ethical statement

Fishes were collected according to Brazilian environmental laws through SISBIO/MMA permit no. 3245, and procedures for collection, maintenance, and analyses of fishes followed the international guidelines for animal experiments through CEEAA IBB/UNESP protocol no. 1058.

2.2 | Molecular analysis

For the molecular approach, the authors analysed 49 specimens of *Catoprius* from all basins except the Essequibo river, plus one *Pygopristis denticulata* (Cuvier, 1819) as an outgroup. Samples were taken from fin or muscle tissues. Tissue samples were preserved and stored at 95% ethanol, whereas voucher specimens were first fixed in 10% formalin or 95% ethanol, and then stored at 70% ethanol. Specimens used in molecular analyses are listed in Table 1. Total DNA was isolated using the Qiagen "DNeasy Blood and Tissue kit" according to manufacturer's instructions. Then, the DNA barcode region of the *cytochrome c oxidase subunit I* (COI) was amplified by PCR using the primers Fish F1 (5'-TCAACCAACCACAAAGACATTGGCAC-3') and Fish R1 (5'-TAGACTTCTGGGTGGCCAAAGAATCA-3') described by Ward *et al.* (2005). The PCR was performed on a thermocycler with a final volume of 12 μ l containing 8.175 μ l distilled water, 0.5 μ l deoxynucleotide triphosphate (dNTP, 8 mM), 1.25 μ l 10 \times Taq buffer (500 mM KCl; 200 mM Tris-HCl), 0.375 μ l MgCl₂, 0.25 μ l each primer (10 μ M) and 0.2 μ l Taq PHT DNA polymerase. PCR conditions consisted of an initial denaturation at 94°C for 5 min, followed by 35 cycles including denaturation at 95°C for 60 s, annealing at 52°C for 60 s and extension at 68°C for 2 min, with a final extension at 68°C for 10 min. Amplified products were checked on 1% agarose gel.

The PCR products were purified with ExoSAP-IT (USB Corporation, Cleveland, OH, USA) following the manufacturer's protocol. The purified product was used as a template to sequence both DNA strands. The cycle sequencing reaction was carried out using a BigDye Terminator v3.1 Cycle Sequencing Ready Reaction kit (Applied Biosystems, Austin, TX, USA) in a final volume of 7 μ l containing 0.35 μ l primer (10 mM), 1.05 μ l buffer 5 \times , 0.7 μ l BigDye mix and 3.9 μ l

distilled water. The cycle sequencing conditions were initial denaturation at 96°C for 2 min followed by 30 cycles of denaturation at 96°C for 45 s, annealing at 50°C for 60 s and extension at 60°C for 4 min. The sequencing products were purified following the protocol suggested in the BigDye Terminator v3.1 Cycle Sequencing kit's manual (Applied Biosystems). All samples were sequenced on an ABI 3130 Genetic Analyser (Applied Biosystems) following the manufacturer's instructions.

Raw sequences were assembled in Geneious v4.8 (Kearse *et al.*, 2012) to obtain the consensus and check for deletions, insertions and stop codons. Then, all sequences were uploaded to GenBank (accession numbers MT519731–MT519762) and BoldSystems (IDs CATOP001-19–CATOP0032-19), and a Barcode Index Number (BIN) discordance analysis was performed (Ratnasingham & Hebert, 2013). Additional sequences were obtained from GenBank (accession numbers MG751919–MG751937; Table 1). Then, all sequences were aligned using Muscle algorithm (Edgar, 2004) implemented in Geneious under default parameters. Genetic distances were obtained using the Kimura-2-Parameter (K2P) model (Kimura, 1980), as estimated by BoldSystems (boldsystems.org). A neighbour-joining tree was generated using the K2P model with 1000 bootstrap replicates.

A maximum likelihood (ML) analysis was performed in RaxML v8.2 (Stamatakis, 2014) using the GTRGAMMA model. The best tree was accessed through five random searches, and a *posteriori* analysis of bootstrap replicates was conducted with the autoMRE function (Pattengale *et al.*, 2010). The resulting ML tree was used as an input tree for the Poisson Tree Process (PTP) analysis (Zhang *et al.*, 2013), which was performed on the PTP webserver (species.h-its.org/server) using 100,000 MCMC generations with 0.1 burn-in rate. In addition, the Automatic Barcode Gap Discovery (ABGD) analysis was performed (Puillandre *et al.*, 2012) on the ABGD webserver (bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) with Kimura (K2P; 2.0) distance model and other parameters at default (Pmin = 0.001; Pmax = 0.1).

A phylogenetic tree was estimated under Bayesian inference with a lognormal relaxed clock and a speciation birth-death model, on an arbitrary timescale, using BEAUTi and BEAST v.1.8.4 (Drummond *et al.*, 2012). The nucleotide evolutionary model used to estimate the ultrametric tree was the GTR + G model as estimated by PartitionFinder2 (Lanfear *et al.*, 2012). A random tree was used as a starting tree for the MCMC searches with two independent runs of 300 million generations each, and a tree sampled every 30,000 generations. Tracer v1.7.1 (Rambaut *et al.*, 2018) was used to examine the distribution of log-likelihood scores and determine the stationary phase for each search and to decide whether extra runs were required to achieve convergence. All sampled topologies beneath the asymptote were discarded as part of a burn-in procedure (10%), and the remaining trees were used to construct a 50% majority-rule consensus tree in TreeAnnotator v1.8.4. The resulting tree was checked in FigTree v1.4.3 and used as an input file for the General Mixed Yule Coalescent Model (GMYC; Pons *et al.*, 2006; Fujisawa & Barraclough, 2013) analysis performed at the GMYC webserver (species.h-its.org/gmyc/R) with a single threshold method.

TABLE 1 List of the specimens of *Catoptrion* and one related taxa (*Pygopristis*) used in the molecular analyses

Taxon	Voucher	Specimens	Locality, basin	Coordinates	Country	BOLD number	GenBank number	
<i>Catoptrion mento</i>	LBP 7556	35,625	Rio Cuiabá, Paraguay basin	16°11'39" S 55°48'25" W	Brazil	CATOP001-19	MT519732	
	LBP 7556	35,626	Rio Cuiabá, Paraguay basin	16°11'39" S 55°48'25" W	Brazil	CATOP002-19	MT519731	
	LBP 26133	93,487	Rio Paraguay, Paraguay basin	16°27'02" S 55°19'12" W	Brazil	CATOP003-19	MT519743	
	LBP 26133	93,488	Rio Paraguay, Paraguay basin	16°27'02" S 55°19'12" W	Brazil	CATOP004-19	MT519742	
	LBP 26133	93,489	Rio Paraguay, Paraguay basin	16°27'02" S 55°19'12" W	Brazil	CATOP005-19	MT519741	
	LBP 26133	93,490	Rio Paraguay, Paraguay basin	16°27'02" S 55°19'12" W	Brazil	CATOP006-19	MT519740	
	LBP 11127	50,884	Rio Purus, Amazon basin	07°29'34" S 63°35'03" W	Brazil	CATOP007-19	MT519739	
	LBP 11127	50,885	Rio Purus, Amazon basin	07°29'34" S 63°35'03" W	Brazil	CATOP008-19	MT519738	
	LBP 11127	50,886	Rio Purus, Amazon basin	07°29'34" S 63°35'03" W	Brazil	CATOP009-19	MT519737	
	LBP 11127	50,887	Rio Purus, Amazon basin	07°29'34" S 63°35'03" W	Brazil	CATOP010-19	MT519736	
	LBP 11127	50,888	Rio Purus, Amazon basin	07°29'34" S 63°35'03" W	Brazil	CATOP011-19	MT519735	
	UFRO 7501	5909	Rio Jaci-Paraná, Rio Madeira, Amazon basin	09°17'03" S 64°23'43" W	Brazil	CATOP012-19	MT519734	
	UFRO 7501	5912	Rio Jaci-Paraná, Rio Madeira, Amazon basin	09°17'03" S 64°23'43" W	Brazil	CATOP013-19	MT519733	
	<i>Catoptrion absconditus</i> sp. nov.	ANSP 198245	P 26431	Rio Xingu, Amazon basin	01°46'30" S 52°12'57" W	Brazil	CATOP028-19	MT519752
		INPA 37207	P 17948	Rio Jatapu, rio Uatumã, Amazon basin	02°10'31" S 58°10'26" W	Brazil	CATOP030-19	MT519750
		INPA 37246	P 19779	Rio Jatapu, rio Uatumã, Amazon basin	02°01'03" S 58°10'26" W	Brazil	CATOP029-19	MT519751
INPA 47302		P 26437	Rio Xingu, Amazon basin	01°46'30" S 52°12'57" W	Brazil	CATOP027-19	MT519753	
INPA 37862		P 27287	Rio Atuanã, rio Negro, Amazon basin	00°35'24" S 64°55'10" W	Brazil	CATOP031-19	MT519749	
LBP 4342		24,074	Rio Uraricoera, Rio Branco, Amazon basin	03°11'00" N 60°33'20" W	Brazil	CATOP014-19	MT519747	

(Continues)

TABLE 1 (Continued)

Taxon	Voucher	Specimens	Locality, basin	Coordinates	Country	BOLD number	GenBank number
	LBP 15148	62,389	Rio Branco, Amazon basin	03°08'16" N 60°16'33" W	Brazil	CATOP015-19	MT519746
	LBP 15148	62,391	Rio Branco, Amazon basin	03°08'16" N 60°16'33" W	Brazil	CATOP016-19	MT519748
	LBP 15148	62,392	Rio Branco, Amazon basin	03°08'16" N 60°16'33" W	Brazil	CATOP017-19	MT519744
	LBP 21615	63,663	Rio Cauamé, Rio Negro, Amazon basin	02°56'19" N 61°03'06" W	Brazil	CATOP018-19	MT519760
	LBP 21615	63,665	Rio Cauamé, Rio Negro, Amazon basin	02°56'19" N 61°03'06" W	Brazil	CATOP020-19	MT519759
	LBP 21615	63,666	Rio Cauamé, Rio Negro, Amazon basin	02°56'19" N 61°03'06" W	Brazil	CATOP021-19	MT519758
	LBP 15534	63,933	Rio Takutu, Rio Branco, Amazon basin	03°22'55" N 59°51'28" W	Brazil	CATOP022-19	MT519757
	LBP 15534	63,934	Rio Takutu, Rio Branco, Amazon basin	03°22'55" N 59°51'28" W	Brazil	CATOP023-19	MT519756
	LBP 15534	63,935	Rio Takutu, Rio Branco, Amazon basin	03°22'55" N 59°51'28" W	Brazil	CATOP024-19	MT519755
	MCP 51844	261	Rio Tapajós, Amazon basin	02°53'29" S 55°10'32" W	Brazil	CATOP032-19	MT519745
	INPA 23351		Rio Itá, rio Branco, Amazon basin		Brazil	PRNHA170-18	MG751919*
	INPA 46313		Rio Nhamundá, Amazon basin		Brazil	PRNHA486-18	MG751920*
	INPA 46314		Rio Nhamundá, Amazon basin		Brazil	PRNHA487-18	MG751921*
	INPA 46314		Rio Nhamundá, Amazon basin		Brazil	PRNHA488-18	MG751922*
	INPA 23423		Rio Capivara, rio Branco, Amazon basin		Brazil	PRNHA172-18	MG751923*
	UFAM 14604		Rio Capivara, rio Branco, Amazon basin		Brazil	PRNHA173-18	MG751924*
	UFAM 14605		Rio Capivara, rio Branco, Amazon basin		Brazil	PRNHA174-18	MG751925*
	INPA 23314		Rio Negro, Amazon basin		Brazil	PRNHA416-18	MG751926*
	INPA 23314		Rio Negro, Amazon basin		Brazil	PRNHA417-18	MG751927*
	UFAM 15086		Lago Aracu, Rio Aripuanã, Amazon basin		Brazil	PRNHA098-18	MG751928*
	INPA 37419		Rio Jatapu, Amazon basin		Brazil	PRNHA383-18	MG751929*
	INPA 37207		Rio Jatapu, Amazon basin		Brazil	PRNHA384-18	MG751930*
	INPA 37246		Rio Jatapu, Amazon basin		Brazil	PRNHA385-18	MG751931*
	INPA 37246		Rio Jatapu, Amazon basin		Brazil	PRNHA386-18	MG751932*
	INPA 46254		Rio Trombetas, Amazon basin		Brazil	PRNHA752-18	MG751933*
	INPA 46254		Rio Trombetas, Amazon basin		Brazil	PRNHA753-18	MG751934*

TABLE 1 (Continued)

Taxon	Voucher	Specimens	Locality, basin	Coordinates	Country	BOLD number	GenBank number
<i>Pygopristis denticulata</i>	INPA 46254	64,256	Rio Trombetas, Amazon basin	03°17'24" N 59°53'48" W	Brazil	PRNHA754-18	MG751935*
	INPA 46243		Rio Uatumã, Amazon basin		Brazil	PRNHA557-18	MG751936*
	UFAM Rneg16		Rio Negro, Amazon basin		Brazil	PRNHA419-18	MG751937*
	LBP 15609		Rio Takutu, Rio Branco, Amazon basin		Brazil	CATOP025-19	MT519762

Note: Sequences added from GenBank data set used in the molecular analysis are indicated by asterisk.

2.3 | Morphological analyses

For the taxonomic revision, 198 museum specimens from the Orinoco, Amazon, Essequibo, and Paraguay basins were analysed. Institutional abbreviations follow Sabaj (2019). Morphometric and meristic data were taken whenever possible on the left side of specimens using digital callipers (precision of 0.1 mm). Measurements and meristics followed Géry (1972), except the maxillary length and orbital diameter measurements, lateral line counts including the scales extending onto the caudal fin, and the addition of vertebrae and supraneural countings. All measurements are described in detail in Appendix S1. All measurements were presented as percentages of standard length (L_s), except for subunits of the head, which were presented as percentages of head length (L_H). Osteological data were obtained through specimens cleared and stained (cs) according to Taylor and VanDyke (1985) or radiographed (rd) with a Faxitron MX-60 digital X-ray system at LIRP-Ribeirão Preto, Brazil. Vertebrae incorporated into the Weberian apparatus were counted as four elements. Ventral-keel spines were divided into prepelvic spines (extending to the origin of pelvic fin and not including the spine lying over the pelvic-fin origin), post-pelvic spines (including the spine over the pelvic-fin origin, plus those from the pelvic-fin origin to the pair of spines) and anal spines (a pair of spines around anus). In the description, each count is followed by its frequency in parentheses. Counts of type specimens are marked with asterisks. In the list of examined specimens, the total number of specimens is first reported, followed by the number of examined specimens in parentheses (if different of the total number), and the number of cs or rd specimens. Given the large number of specimens of the new species, at least one lot from each basin and for each museum collection was chosen, and all remaining lots became non-type material. The map was prepared in the QGIS v2.18 software.

3 | RESULTS

3.1 | Species delimitation in *Catoprion*

Barcode sequences were obtained from 31 specimens and 19 additional sequences from GenBank, totalling 50 sequences in the final matrix (49 *Catoprion* and 1 *Pygopristis*). Stop codons, deletions or insertions were not observed in any of the sequences. After alignment and editing, the final matrix had 553 characters, with 469 conserved and 81 variable sites, with 23.2% adenine, 31.5% cytosine, 27.2% thymine and 18.1% guanine. The genetic distance analysis showed that the two species of *Catoprion* differ from each other by 0.069 ± 0.00 (Min Dist = 0.064 ± 0.00 ; Max Dist = 0.077 ± 0.00). Intraspecific genetic distances were 0.003 ± 0.00 for *Catoprion absconditus* sp. nov. (Min Dist = 0.000 ± 0.00 ; Max Dist = 0.008 ± 0.00) and 0.0009 ± 0.00 for *C. mento* (Min Dist = 0.000 ± 0.00 ; Max Dist = 0.005 ± 0.00).

The ML tree inferred through RAXML recovered the two groups consistent with the genetic distance analysis and the previous morphological identification of species and exhibited strong node support for each species, i.e., 94% for the *C. absconditus* sp. n. clade and 85% for *C. mento* clade (Figure 1). The species delimitation analyses BIN,

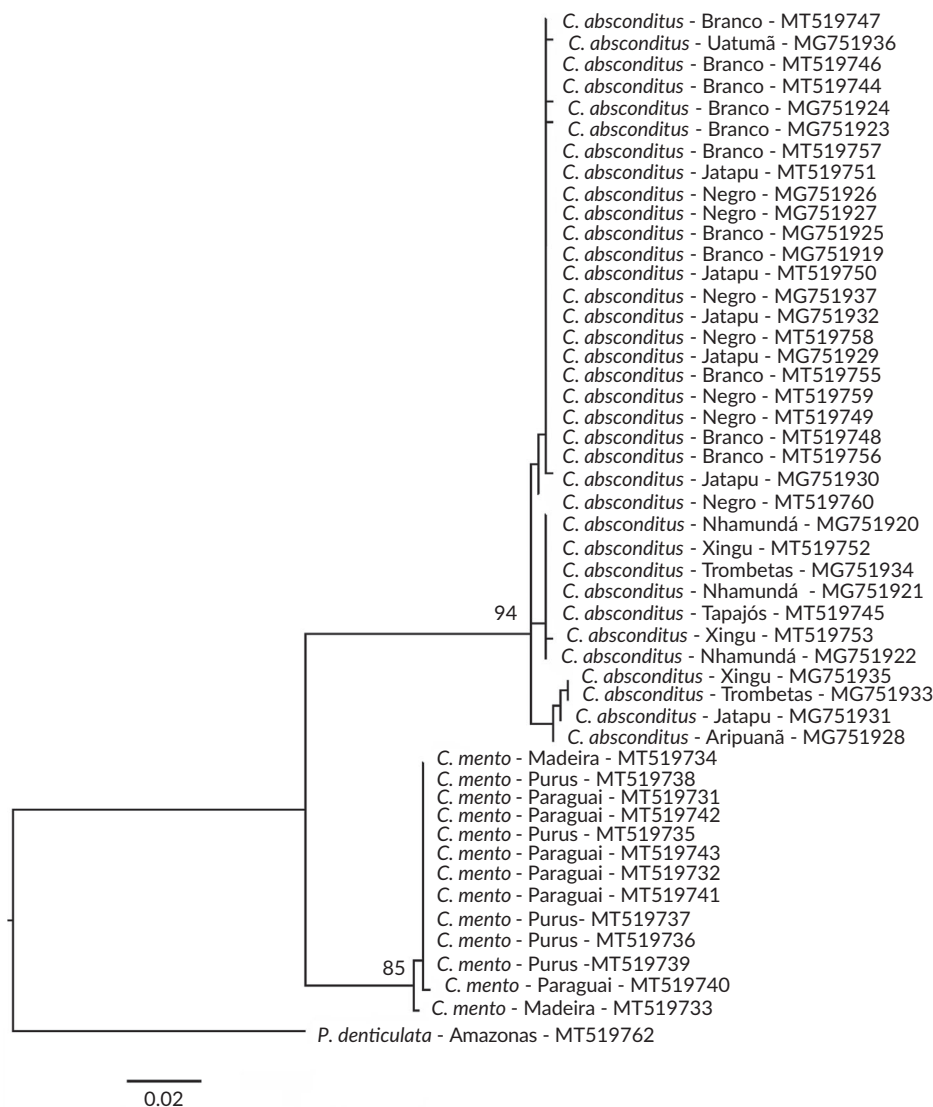


FIGURE 1 Maximum likelihood tree based on the cytochrome oxidase c subunit I gene evidencing the presence of two clades of *Catoprion*. Nodes labelled with number represent bootstrap support and those after tip names represent tissue numbers

PTP, ABGD and GMYC support the presence of two species of *Catoprion*, the first, *C. mento*, occurring in the Paraguay, Purus and Madeira Rivers (samples from Orinoco and upper Araguaia unavailable) and the second, *C. absconditus* sp. nov. described herein as a species occurring in the Branco, Japurá, Jatapu, Negro, Nhamundá, Tapajós, Trombetas, Uatumã and Xingu Rivers of the Amazon basin. The ABGD analysis resulted in nine partitions that ranged from 2 ($P = 0.059$) to 11 ($P = 0.001$) lineages, with five partitions ($P = 0.007$ – 0.059) suggesting two lineages of *Catoprion*.

3.2 | Taxonomic revision

3.2.1 | *Catoprion* Müller & Troschel, 1844

Catoprion Müller & Troschel, 1844: 96 (original description, type by monotypy: *S. mento* Cuvier, 1819. Gender: masculine). Müller & Troschel, 1845: 22 (description; dentition draw, plate II Figure 5). Eigenmann & Eigenmann, 1891: 61 (Serrasalmoninae).

Eigenmann, 1912: 386 (brief description; Mylinae). Gosline, 1951: 54 (brief description; Serrasalminae). Nelson, 1961: 610 (swim bladder morphology). Géry, 1972: 207 (Guyanas; Catoprioninae). Géry, 1976: 54 (checklist). Géry, 1977: 294 (Serrasalminae; Catoprioninae). Machado-Allison, 1982: 213 (phylogeny of Serrasalminae; autapomorphies). Taphorn, 1990: 252, 2003: 112 (Apure). Britski *et al.*, 1999: 58, Britski *et al.*, 2007: 78 (Pantanal). Jégu, 2003: 183 (checklist). Jégu & Ingenito, 2007: 40 (checklist). Nico *et al.*, 2017: 181 (Amazon, Orinoco and Guyanas).

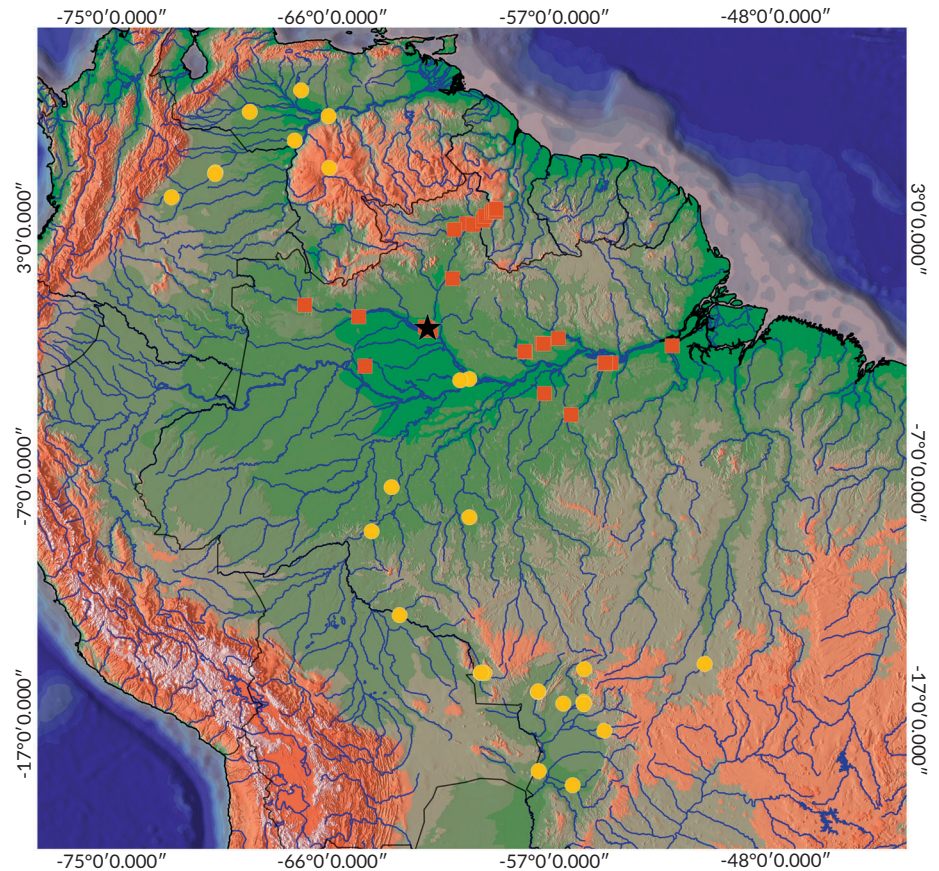
Amended diagnosis

Catoprion can be distinguished from the remaining Serrasalminae genera by presenting the upturned mouth with the lower jaw clearly longer than the upper jaw, with a strongly prognathic jaw, and the presence of mamilliform teeth in both premaxilla and dentary.

Distribution

Catoprion is widely distributed in lowlands of the Orinoco, Essequibo, Amazon, Tocantins-Araguaia and Paraguay river basins (Figure 2).

FIGURE 2 Map of central and northern South America showing the geographic distribution of the morphologically analysed specimens of *Catoprion absconditus* (red squares; black star = type locality) and *Catoprion mento* (yellow circles). One symbol may represent more than one locality



Etymology

Cato, from the ancient Greek *kata*, meaning down; *prion*, from the Greek *prion*, meaning saw; probably referring to the ventral keel with spines.

Remarks

In the original description, Müller and Troschel (1844) described two series of mamiliform teeth in the premaxilla in “Dentes ossis intermaxillaris biserialis,” later corroborated by Machado-Allison (1982) as an autapomorphy for *Catoprion*. Both papers described the outer premaxillary series as formed by two larger teeth and the inner series with three smaller teeth, whereas other authors consider them as a single irregular row, named a “zig-zag arrangement” (Cione *et al.*, 2009; Géry, 1972; Gosline, 1951; Jégu, 2004). Then, the morphology of *Catoprion*'s dentition would be an intermediate state between the condition “two rows of molariform/incisiform teeth” observed in *pacus* and the condition “single row of sharp multicuspid teeth” observed in all other piranhas and also shared with †*Megapiranha paranensis* (Cione *et al.*, 2009). Herein, in agreement with previous authors (Eigenmann, 1912; Machado-Allison, 1982; Müller & Troschel, 1844), the presence of two series of teeth in the premaxilla of *Catoprion* is stated; the outer premaxillary tooth row presents two larger teeth, whereas the inner row presents three small teeth (Figure 3).

In addition to the type and arrangement of the premaxillary and dentary teeth, a series of autapomorphies not analysed herein have

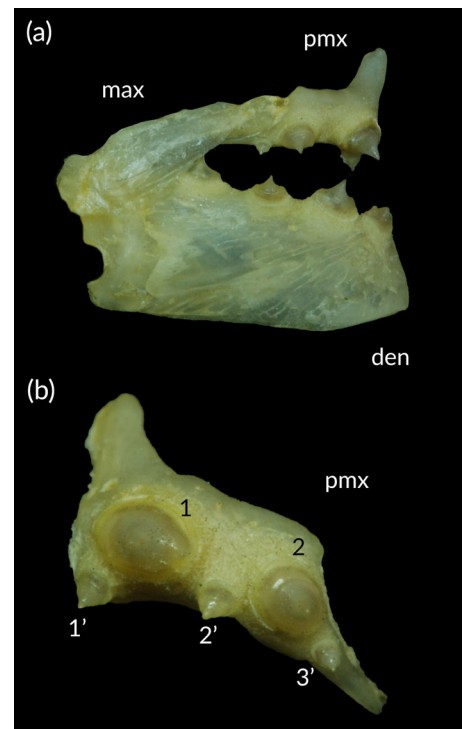


FIGURE 3 *Catoprion* dentition. (a) Lateral view of premaxilla (pmx), maxilla (max) and dentary (den); (b) superior view of the premaxilla; 1-2 outer row of premaxillary series, 1'-3' inner row of premaxillary teeth. INPA 37246, rio Jatapu, rio Uatumã basin. Photos by Victória Pereira

been identified in *Catoprion*. Machado-Allison (1982) reported a total of 14 autapomorphies, mostly related to lepidophagy, such as a reduction on the basal plate of gill rakers and reduction and/or shape and insertion changes of the *adductor mandibularis*, *levator arcus palatini* and *adductor arcus palatini*. Remarkably, *Catoprion* exhibits several adaptations distinctive among the Serrasalminae, which led the genus to be allocated in several taxonomic groups. The genus has been included in Serrasalmoninae (Eigenmann & Eigenmann, 1891), Mylinae (*sic.*) (Eigenmann, 1912; 1915), closely related to *Serrasalmus* and *Pygopristis* (Gosline, 1951), *Catoprioninae* (Géry, 1972, 1976, 1977), or related to the other piranhas (Machado-Allison, 1982; Jégu, 2004; Freeman *et al.*, 2007; Thompson *et al.*, 2014; Mateussi *et al.* in review). The latter hypothesis was corroborated by all phylogenetic studies using morphological, multilocus and phylogenomic data but with conflicting internal relationships.

3.2.2 | *Catoprion mento* (Cuvier, 1819)

urn:lsid:zoobank.org:act:CCC3B4C6-AAD5-4A06-B644-49956D63727A.

Figures 4–7; Table 2.

Serrasalmus mento Cuvier, 1819: 369, pl.28 (original description; type-locality “Brésil”).

Catoprion mento. Kner, 1859: 26 (description). Eigenmann, 1910: 442 (*partim*; listed). Géry, 1972: 207 (brief description). Géry, 1976:

54 (checklist). Britski *et al.*, 1999: 58, 2007: 78 (Pantanal; brief description). Ota *et al.*, 2013: 17 (Madeira basin, Brazil; brief description, photo).



FIGURE 5 *Catoprion mento*. LBP 7556, Brazil, Mato Grosso, Barão de Melgaço, lake at margin of rio Cuiabá, rio Paraguai basin: (a) male, 74.0 mm L_S ; (b) female, 65.0 mm L_S

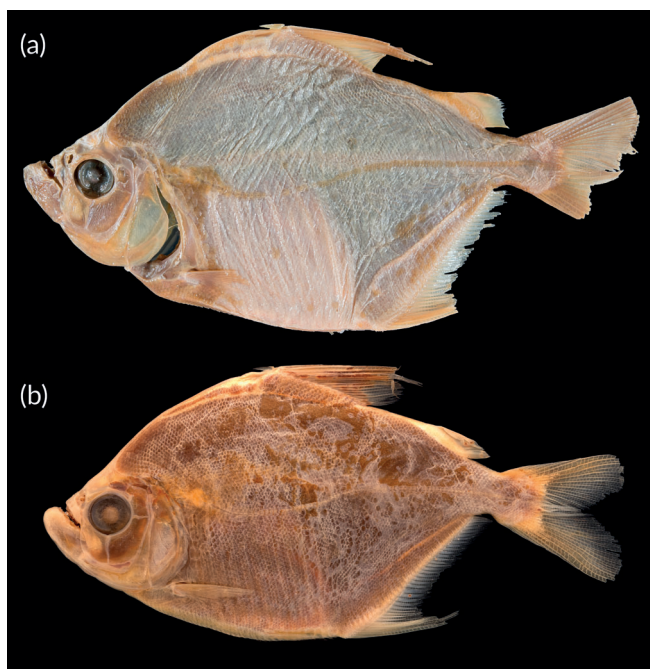


FIGURE 4 (a) Holotype of *Serrasalmus mento* (= *Catoprion mento*), MNHN A.9869, 79.8 mm L_S , Cabinet d'Ajuda (see Remarks for type locality). Photo by MNHN: L. Randrihasipara. (b) Holotype of *Mylesinus macropterus*, CUMV 3267, 74 mm L_S , Brazil. Photo by Casey B. Dillman

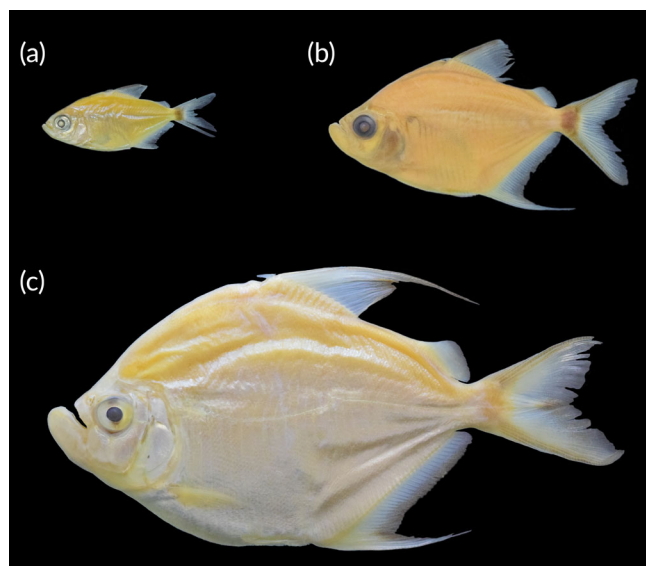


FIGURE 6 *Catoprion mento*. (a) LBP 11127, 24.3 mm L_S , rio Purus basin. (b) NUP 1044, 37.7 mm L_S , Reservatório Manso, rio Paraguai basin. (c) LBP 7556, 74.0 mm L_S , rio Cuiabá, rio Paraguai basin

Mylesinus macropterus Ulrey, 1894: 612 (original description; type-locality: "Brazil"). Ulrey, 1895: 296 (description).

Amended diagnosis

Catoprimon mento differs from *C. absconditus* sp. nov. by presenting 65–86 perforated scales in the lateral line (vs. 85–94 scales) and 29–34 circumpeduncular scales (vs. 35–40 scales).

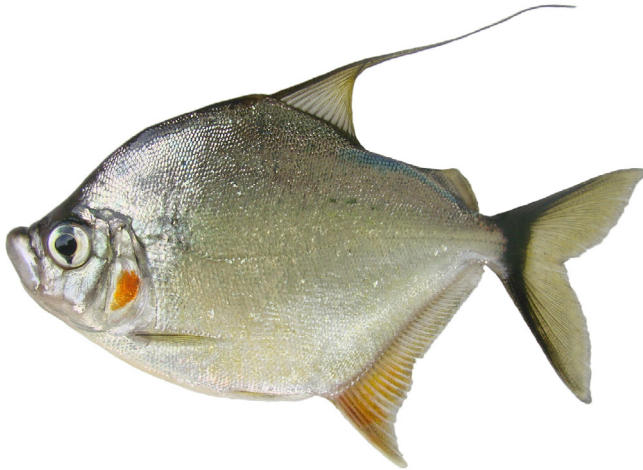


FIGURE 7 *Catoprimon mento*, male, LBP 3820, 55 mm L_S , rio Negro, Aquidauana, Mato Grosso do Sul, Brazil. Photo by Claudio Oliveira

Description

Morphometric data presented in Table 2. Body deep, compressed laterally; general shape rhomboid. Highest body depth at vertical through dorsal-fin origin. Dorsal profile slightly concave along head and convex between head and dorsal-fin origin. Dorsal profile of body fairly sloping at base of dorsal and adipose fins, and straight at interval between these two fins. Ventral profile convex from isthmus to end of anal fin. Ventral keel with serra of spines. Pre-pelvic spines 17 (2), 18 (1), 19 (7), 20 (9), 21 (17), 22 (21), 23* (12), 24 (7) or 25 (2). Post-pelvic spines 7 (1), 8 (2), 9 (34), 10* (34) or 11 (4). Anal spines 1 (3), 2 (60), 3* (13) or 4 (1). Caudal peduncle deeper than long.

Eye positioned laterally at middle of head; upper margin of eye above longitudinal line of first lateral line scale. Frontal and parietal fontanels expanded laterally. Snout very short and slightly pointed in lateral view. Nostrils dorso-laterally positioned, at longitudinal axis through dorsal margin of eye. Mouth upturned. Jaw strongly prognathous. Lower jaw longer and projecting past the upper jaw. Premaxillary and dentary teeth mamilliform, with a round base and narrower tip. Outer premaxillary row with two large, antrorse teeth; inner row with three small, vertically directed teeth. Dentary with a single row of six teeth; the fourth tooth smaller than others. Maxilla edentulous.

Body completely covered by small cycloid scales. Lateral line complete, with 65 (1), 66 (1), 68 (1), 69 (1), 71 (2), 72 (1), 73 (2), 74 (2), 75 (2), 76 (4), 77 (5), 78 (6), 79 (5), 80 (5), 81 (5), 82 (4), 83 (7), 84 (5), 85 (2) or 86 (2) perforated scales; first to tenth scale larger than posterior scales. Scale series above lateral line 24 (1), 27 (1), 29 (1), 30 (2), 31

TABLE 2 Morphometric data of *Catoprimon mento*

	H	N	Range	Mean	S.D.
Standard length (mm)	79.8	65	24.3–119.5	64.1	–
Percentages of standard length					
Body depth	64.6	74	42.3–72.4	62.6	6.43
Postdorsal length	60.9	68	48.9–61.8	57.0	2.47
Predorsal length	55.4	68	53.8–60.9	57.0	1.42
Caudal-peduncle depth	10.5	68	8.0–11.3	10.0	0.63
Caudal-peduncle length	10.1	68	5.7–9.0	7.5	0.77
Head length	29.6	68	27.1–37.1	30.6	1.77
Dorsal-fin base	22.0	67	17.8–26.1	22.1	1.63
Dorsal-fin length	32.6	62	23.9–74.2	45.1	13.35
Interdorsal length	16.6	68	12.6–19.4	15.3	1.58
Adipose-fin base	10.9	68	7.2–12.6	10.4	1.21
Pectoral-fin length	–	68	14.7–23.6	20.3	2.15
Pelvic-fin length	12.6	67	12.2–17.3	14.9	1.23
Anal-fin base	39.3	68	32.9–46.9	41.5	3.20
Anal-fin length	–	61	18.1–60.8	32.5	9.82
Percentages of head length					
Interorbital width	34.5	68	20.5–40.7	32.7	4.62
Orbital diameter	31.6	68	25.4–40.5	33.0	2.76
Snout length	20.4	68	14.2–28.8	22.6	2.78
Maxilla length	39.7	67	25.2–43.9	36.4	3.67

Abbreviations: H: holotype; N: number of specimens; S.D.: standard deviation.

(1), 32 (7), 33 (7), 34 (1), 36 (2) or 37 (1). Scales below lateral line 21 (1), 24 (3), 25 (1), 26 (5), 27 (3), 28 (2), 29 (2), 30 (4) or 31 (1). Circumpeduncular scales 29 (1), 30 (6), 31 (5), 32 (13), 33 (4) or 34 (5).

Dorsal fin preceded by strong pointed spine, previously directed, separated from first unbranched ray, with origin approximately equidistant from tip of snout to end of hypural plate. First dorsal-fin rays prolonged; in some specimens surpassing caudal-fin base. Branched dorsal-fin rays gradually decreasing in size, branched dorsal-fin rays 13 (1), 14 (31), 15* (36) or 16 (9). Adipose fin short, longer than deep. Pectoral fin falcate, with $i + 11$ (7), 12* (27), 13 (19), 14 (12) or 15 (1) rays. Pelvic fin small, with $i, 6^*$ (61) branched rays. First anal-fin rays prolonged; surpassing caudal-fin base in some specimens. Branched anal-fin rays gradually decreasing in size; branched anal-fin rays 30 (1), 32 (5), 33* (15), 34 (28), 35 (24), 36 (6) or 37 (2). Caudal fin bifurcated, lobes of similar size, with 17 (55) branched rays.

First gill arch with elongated gill rakers, almost as long as filaments, decreasing in size towards the extremities; 8 (14), 9 (17), 10 (7) or 11 (1) gill rakers on upper limb, 9 (1), 10 (3), 11 (14), 12 (20) or 13 (5) gill rakers on lower limb. Lower gill rakers longer than upper. Vertebrae 36 (7), 37* (18) or 38 (2). Supraneurals 4* (29).

Molecular polymorphisms

In the final COI matrix, 33 variable sites were detected between sequences of *Catoprion mento* and *C. absconditus* sp. nov. In addition to the morphological diagnoses, the two species showed 6.9% of genetic divergence (Min Dist = 6.4%; Max Dist = 7.7%) and had the species groups delimited by the four applied methods (i.e., BIN, PTP, ABGD and GMYC).

Colour in alcohol

Vertical dark band through the eye. General body colour brown to yellowish, darker in dorsal portion of the body. Humeral blotch black or brown, vertically elongated, sometimes inconspicuous or absent, larger in mature males, when it may join other blotchs or spots spreading through region below the pectoral fins to anal fin, as typically found for male serrasalmids. Fins hyaline to yellowish. First rays of dorsal fin often dark. First rays and distal margin of anal fin often dark. Conspicuous dark band extending from the posterior portion of the caudal peduncle, reaching the median procurrent of the caudal fin and most external rays, forming a V-shape with the apex directed towards the head (Figure 5). This pattern in caudal peduncle advancing through caudal fin gets darker and larger during ontogeny. Juvenile specimens under about 30 mm L_S present the caudal peduncle dark brown and base of caudal-fin hyaline; at about 40 mm L_S the base of caudal-fin begins to get darker, including a pale V-shape which becomes darker and in larger specimens (Figure 6).

Colour in life

Vertical dark band through the eye. General body colour silvery, darker dorsally. Conspicuous orange blotch on the opercle. Dorsal, pectoral, pelvic and adipose fins hyaline. First ray of dorsal and pectoral fins often dark grey. Anal fin yellow to orange, mainly on first rays, gradually turning to hyaline on last rays. Caudal-fin base black, in V-

shape with the apex directed towards the head, advancing through the caudal peduncle (Figure 7).

Geographic distribution

Catoprion mento occurs in the río Orinoco, upper río Paraguay and tributaries of the Amazon basin, including the upper río Araguaia, rio Madeira, rio Purus and the lower rio Negro (Figure 1).

Sexual dimorphism

Catoprion mento presents anterior lobe developed from the elongation of distal borders of the anal fin, between about the 7th and 13th branched rays, in males (Figures 5a and 7), whereas females present elongation restricted at the first anterior rays of the anal fin (Figure 5b). The prolongation of the first dorsal and anal-fin rays was observed in both males and females and, thus, is not associated with sexual dimorphism. In addition, the vertically elongated humeral blotch becomes larger in males during the reproductive period. It may join other blotchs or spots spreading through region below the pectoral fins to anal fin, as typically found in serrasalmid males.

Ecological notes

Catoprion mento feeds primarily on fish scales, whereas aquatic insect larvae, fish flesh and fins and plants are reported as rare items (Nico & Taphorn, 1988; Sazima, 1983). Feeding behaviour involves stalking preys, using vegetation as covers to ambush, linger around the prey and attack from close quarters (Sazima, 1983) or yet attacking fish momentarily disoriented by the dashes of another predator (e.g., other piranhas) (Sazima & Machado, 1990). Generally solitary (Nico et al., 2017), it is a territorial species, responding agonistically to conspecifics that approach its clump of vegetation (Sazima, 1988). In the Orinoco basin, it is considered uncommon, with preferences of dark water with abundant vegetation and clear water (Taphorn, 2003). Spawning is reported at the beginning of the rainy season, with eggs dispersed the aquatic vegetation (Taphorn, 2003). The species is reported as ornamental (Colombia, 2006; Prang, 2007; Taphorn, 2003).

Conservation status

Catoprion mento is relatively common throughout the area of occurrence and widespread along large drainage basins of central and north-western portions of South America. No specific threats were detected. Accordingly, it is suggested that the species remains classified as Least Concern (LC) according to IUCN criteria (IUCN, 2018) following the last evaluation performed by the ICMBio.

Remarks

In the original description of *Serrasalmus mento*, the type locality was assigned as Brazil although brought from Lisbon ("venu de Lisbonne, paroît aussi originaire du Brésil" – Cuvier, 1819). Both the muséum national d'histoire naturelle (MNHN) database and the label of the type assign the specimens to "Cabinet d'Ajuda," a collection from Museu da Ajuda in Lisbon, Portugal, known for having been ransacked during the Napoleonic era (Myers, 1950; Vanzolini, 2004). The

collection, made by Alexandre Rodrigues Ferreira during his travel to Brazil at the behest of the Portuguese Crown, presents severe doubts about the exact source of specimens, which did not have its origins indicated by the drawings or records at the Museu d'Ajuda (Vanzolini, 2004). Finding the type locality is difficult because no other record have been discovered. Nonetheless, meristic data taken by NTBM directly from the holotype of *S. mento* (MNHN A.9869) indicate about 80–85 perforated scales in the lateral line (approximated counting because of poor conditions of the type), which match the counts of specimens from the upper Paraguay, Araguaia and tributaries of the Amazon basin (65–86 scales). Thus, the authors conclude that *S. mento* Cuvier, 1819 was most likely collected in one of these aforementioned drainages, and thus the other species requires a new name.

In the "Poissons Characoides des Guyanes," Géry (1972) did not use any *Catoprion* specimen from the Guianas, so the counts and measures were taken from specimens from the Bolivian Amazon. His counting confirms the identification of *C. mento* (80 perforated scales in the lateral line), so that species from the Guianas belongs actually to *C. absconditus*. Although it was not possible to examine specimens from the Bolivian Amazon, the species found there was considered as *C. mento* based on Géry's (1972) counting, on checklists from that region (Chernoff *et al.*, 2000; Chernoff & Willink, 1999) and based on the confirmed occurrence of the species in middle portions of the Madeira and Purus Rivers.

Mylesinus macropterus was described based on a single specimen by Ulrey (1894), and then supplemented by two specimens 1 year later (Ulrey, 1895), with both papers assigning it to "Brazil." The Ulrey (1895)'s paper was based on fishes collected by Charles Frederick Hartt in Brazil, during the "Thayer Expedition," which encompassed the area of occurrence of both *Catoprion mento* and *C. absconditus* (Agassiz, 1868; Hartt, 1870). The counts present in the original description indicate about 83 perforated scales in the lateral line (Ulrey, 1894) and the type has been considered as "whereabouts unknown" by Fricke *et al.* (2020). Although the authors could not analyse the specimens by themselves, the curator of the Cornell University Museum of Vertebrates (CUMV), Casey B. Dillman, found and examined the type material and performed the counting on the behalf of authors. The "lost status" of the type can now be corrected and, according to his counting, the holotype of *M. macropterus*, CUMV 3267, presents 79 perforated scales in the lateral line and 32 circumpeduncular scales. Therefore, *M. macropterus* Ulrey, 1894 must remain a junior synonym of *C. mento* (Cuvier, 1819).

Material examined

Types. MNHN A.9869, 1 (rd), 79.8 mm L_S , holotype of *Serrasalmus mento*, Brazil. CUMV 3267, 1 (rd), 74 mm L_S , holotype of *Mylesinus macropterus*, Brazil, Jan 1860, C. Hartt (examined by C. Dillman). **Non-types.** **Brazil. Amazon basin. Amazonas.** MZUSP 9570, 2, 90.0–102.0 mm L_S , fish market, Manaus, 17 Sep 1968, Expedição Permanente da Amazônia. **Rio Araguaia basin. Goiás.** MZUSP 54525, 1, 76.7 mm L_S , rio Araguaia, 1997–1998, Coleção rio Araguaia. MZUSP 89136, 1 (rd), 50.3 mm L_S , Aruanã, lake at margin of Araguaia river,

14°39'23"S 50°54'03"W, 25 Jul 2005, CBE team. **Pará.** MZUSP 20574, 2, 57.0–70.9 mm L_S , Jurunundéua lake, tributary of rio Capim, 19 Aug 1970, Expedição Permanente da Amazônia. **Rio Madeira basin. Amazonas.** INPA 33717, 1, 92.3 mm L_S , Apuí, rio Guariba, tributary rio Aripuanã, 08°42'42"S 60°25'53"W, Pedroza WS *et al.* **Mato Grosso.** MZUSP 37511, 2, 46.4–104.2 mm L_S , Vila Bela da Santíssima Trindade, rio Guaporé (trib. Rio Mamoré), 28 Sep 1984, Garavelo JC & Polonoroeste team. MZUSP 37664, 2, 27.7–28.6 mm L_S , Vila Bela da Santíssima Trindade, rio Guaporé (trib. rio Mamoré), 10 Oct 1984, Garavelo JC & Polonoroeste team. MZUSP 64951, 1, 97.5 mm L_S , Vila Bela da Santíssima Trindade, rio Guaporé (trib. Rio Mamoré), 15°01'17"S 59°58'30"W, Oct 1997, Machado FA *et al.* MZUSP 77203, 2, 84.7–106.5 mm L_S , Panelas, rio Roosevelt, 17 Jul 1997, Machado FA *et al.* MZUSP 95321, 1, 83.9 mm L_S , Vila Bela da Santíssima Trindade, rio Guaporé (trib. Rio Mamoré), 15°01'37"S 59°49'09"W, 13 Oct 2006, Machado FA *et al.* MZUSP 115655, 1, 40.9 mm L_S , Vila Bela da Santíssima Trindade, rio Guaporé (trib. rio Mamoré), 15°00'18"S 59°57'19"W, 28 Aug 2013, Oyakawa O *et al.* **Rondônia.** UFRO-ICT 7501, 2, 87.3–119.5 mm L_S , Jaciparaná, Madalena lake (trib. rio Madeira), 09°17'03"S 64°23'43"W, 25 Nov 2011, Matsuzaki A. **Rio Negro basin. Amazonas.** MZUSP 6717, 5, 64.8–68.6 mm L_S , Manaus, rio Negro, 23 Nov 1967, Expedição Permanente da Amazônia. MZUSP 43350, 1, 90.9 mm L_S , Paricatuba, lake at margin of rio Negro, 11 Nov 1972, Expedição Permanente da Amazônia. MZUSP 54517, 2, 43.4–57.2 mm L_S , Paricatuba, lake at margin of rio Negro, 11 Nov 1972, Expedição Permanente da Amazônia. **Rio Paraguay basin. Mato Grosso.** LBP 7556, 4, 57.4–74.0 mm L_S , Barão de Melgaço, lake at margin of rio Cuiabá, 16°11'39"S 55°48'25"W, 29 Jan 2009, Oliveira C *et al.* LBP 26133, 4 (rd), 30.1–30.8 mm L_S , Pantanal, rio Paraguay, 16°27'02.6" S 55°19'12.6" W, Flausino Jr. N *et al.* MZUSP 19941, 1, 64.9 mm L_S , Itiquira, baía Grande, rio Itiquira (trib. rio Piquiri), 29 Oct 1978, Oliveira JC. MZUSP 27274, 6 (1 cs), 50.9–64.9 mm L_S , Poconé, rio Paraguay, 11 May 1983, Sazima I *et al.* MZUSP 35874, 1, 42.1 mm L_S , Itiquira, rio Itiquira, 30 Sep 1979, Medeiros JHB & Oliveira, JC. MZUSP 90217, 1, 39.0 mm L_S , Cáceres, rio Sepotuba, 15°47'33"S 57°39'20"W, 2 Mar 2002, Britski HA *et al.* MZUSP 75237, 1, 48.0 mm L_S , Itiquira, lake between rivers Piquira and Itiquira, Oct 1984, Medeiros JHB & Oliveira, JC. MZUSP 90282, 4, 26.8–38.4 mm L_S , Cáceres, rio Sepotuba, 15°46'07"S 57°38'54"W, 4 Mar 2002, Britski HA *et al.* MZUSP 95079, 1 (rd), 60.6 mm L_S , Barão de Melgaço, rio Mutum, 16°19'30"S 55°49'59"W, 30 Sep 2006, Machado FA & Lima FCT. MZUSP 96679, 1, 54.5 mm L_S , Barão de Melgaço, Pantanal de Paiaguás, 16°17'00"S 55°48'00"W, 30 Sep 2006, Machado FA & Lima FCT. NUP 1044, 5, 37.6–108.2 mm L_S , Chapada dos Guimarães, Reservatório Manso, 14°52'S 55°47'W, 2000–2004, Nupélia. **Mato Grosso do Sul.** LBP 3820, 1 (rd), 55 mm L_S , Aquidauana, rio Negro, 19°34'33"S 56°14'49"W, 1 Aug 2006, Oliveira C. *et al.* MZUSP 36412, 2, 60.6–74.9 mm L_S , Nhecolândia, Corumbá, baía dos Búfalos, Mar 1985, Mourão GM & Bastos EK. MZUSP 36417, 1, 42.4 mm L_S , Nhecolândia, Corumbá, faz. Nhumirim, 24 May 1985, Bastos EK. MZUSP 36418, 4, 29.6–38.1 mm L_S , Nhecolândia, Corumbá, farm Nhumirim, May 1985, Mourão GM & Bastos EK. MZUSP 48306, 2, 39.7–51.8 mm L_S , Pantanal de Paiaguás,

Farm Santo Antônio, Liparelli T. **Rio Purus basin. Amazonas.** LBP 11127, 13 (rd), 24.2–41.0 mm L_S , Lábrea, rio Purus, 07°29'34"S 63°35'03"W, 24 Aug 2010, Oliveira C *et al.* **Rio Solimões basin. Amazonas.** MZUSP 5878, 1, 97.1 mm L_S , Manacapuru, Manacapuru lake (trib. Rio Solimões), 27 Mar 1967, Expedição Permanente da Amazônia. MZUSP 6884, 2, 67.1–106.3 mm L_S , Manaus, Januari lake (trib. Rio Solimões), 20 Nov 1967, Expedição Permanente da Amazônia. **Colombia. Río Orinoco basin. Casanare.** CZUT-IC 9675, 1 (rd), 36.5 mm L_S , rio Meta, 05°15'31"N 70°43'27"W. **Meta.** MNHN 2007 0229, 1, 78.6 mm L_S , Puerto López, Caño estero (trib. Río Meta), 04°15'00"N 72°30'00"W, 04 Apr 1995, Pedreros SP. **Vichada.** CZUT-IC 8982, 3 (2) (rd), 30.3–30.4 mm L_S , Santa Rosalia, Laguna La Portuguesa (trib. Río Vichada), 05°11'49"N 70°44'09"W. **Venezuela. Río Orinoco basin.** MNHN 87792, 1, 45.7 mm L_S , rio Orinoco, Chaffanjon. MNHN 87793, 1, 50.9 mm L_S , rio Orinoco, Chaffanjon. USNM 310392, 2, 57.3–63.7 mm L_S , rio Orinoco, Quiribana, May 1925, Ternetz. **Amazonas.** AUM 41461, 1, 47.9 mm L_S , 14 km northwest of San Juan de Manapiare, rio Manapiare at mouth of Caño Yutaje, 05°26'12"N 66°06'45"W, 11 Apr 2004. **Apure.** AUM 22539, 1, 35.4 mm L_S , 38 km south of Bruzual, Caño Guarico, 07°42'47"N 69°19'50"W, 29 Dec 1999. AUM 22575, 1, 28.1 mm L_S , rio Cinaruco, 06°32'44"N 67°30'24"W, 25 Dec 1999. **Guarico.** USNM, 4, 97.2–111.4 mm L_S , Government Reserve east-southeast of Calabozo, rio Guariquito, 08°35'N 67°15'W, 27 Jan 1983, Machado A.

3.2.3 | *Catoprión absconditus* Mateussi, Melo & Oliveira sp. nov.

urn:lsid:zoobank.org:act:468D890B-78C9-4677-92EF-E02210766192.

Figures 8–12; Table 3.

Catoprión mento (non Cuvier, 1819). Müller & Troschel, 1844: 96 (description). Müller & Troschel, 1845: 22 (description). Eigenmann, 1910: 442 (*partim*; listed). Eigenmann, 1912: 387 (British Guiana; brief description). Fowler, 1914: 251 (Rupununi river, British Guiana; listed). Lowe-McConnell, 1964: 142 (Rupununi River, British Guiana; listed). Ferreira *et al.*, 2007: 126 (rio Branco). Vari *et al.*, 2009: 33 (Guiana Shield). Machado *et al.*, 2018: 7 (Barcoding of Serrasalminidae).

Holotype

MZUSP 125764, 78.3 mm L_S , Caracará, igarapé do Campo, rio Jufari, rio Branco, 01°03'54"S 62°07'46"W, 4 Sep 2011, Oyakawa OT *et al.* (Figure 8).

Paratypes

Brazil. Rio Branco basin. Roraima. LBP 4342, 1, 75.0 mm L_S , Boa Vista, igarapé do Cajual, rio Uraricoera, 03°11'00"N 60°33'20"W, 11 Nov 2006, Devidé R *et al.* LBP 15582, 1, 109.1 mm L_S , Bonfim, igarapé Chidaua, rio Takutu, Rio Branco, 03°18'28"N 59°53'19"W, 23 Apr 2012, Britzke R & Melo BF. MZUSP 113015, 1 (rd), 70.3–78.3 mm L_S , Caracará, igarapé do Campo, rio Jufari, rio Branco,

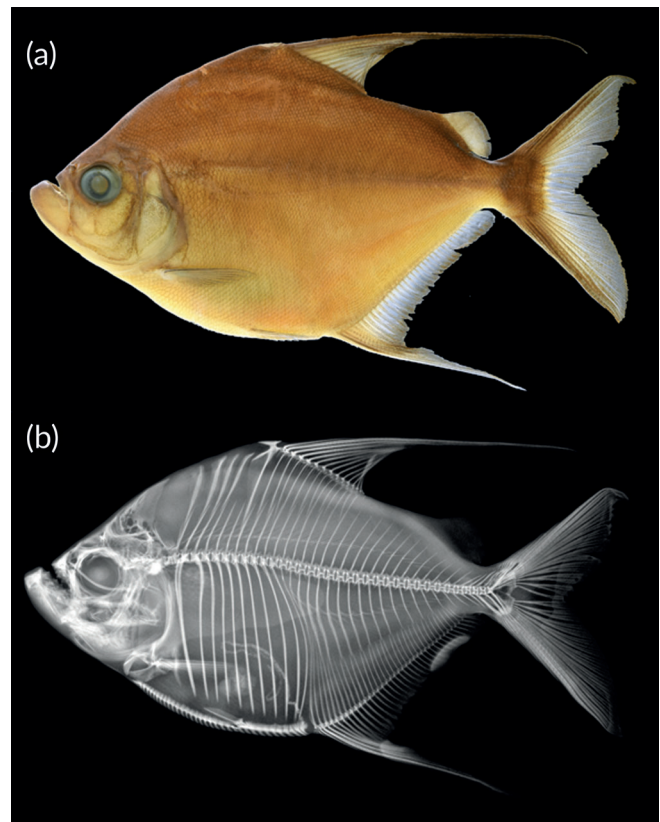


FIGURE 8 *Catoprión absconditus*, MZUSP 125764, holotype, 78.3 mm L_S , Brazil, Roraima, Caracará, igarapé do Campo, tributary of rio Jufari, rio Branco, Amazon basin. (a) Preserved specimen; (b) radiography



FIGURE 9 *Catoprión absconditus*, MZUSP 50015, paratype, male, 93.7 mm L_S , Brazil, Amazonas, Presidente Figueiredo, rio Uatumã, about 500 m downstream UHE Balbina

01°03'54"S 62°07'46"W, 4 Sep 2011, Oyakawa OT *et al.* **Rio Negro basin. Amazonas.** INPA 37862, 1, 100.3 mm L_S , Santa Isabel do rio Negro, rio Aiuanã, 00°35'24"S 64°55'10"W, 04 Apr 2012, Silva R *et al.* **Rio Nhamundá basin. Amazonas.** INPA 46313, 1, 131.2 mm L_S , Nhamundá, rio Nhamundá, 01°40'30"S 57°28'36"W, 13 Nov 2013, Machado V. *et al.* INPA 46314, 2, 124.3–125.6 mm L_S , Nhamundá, rio

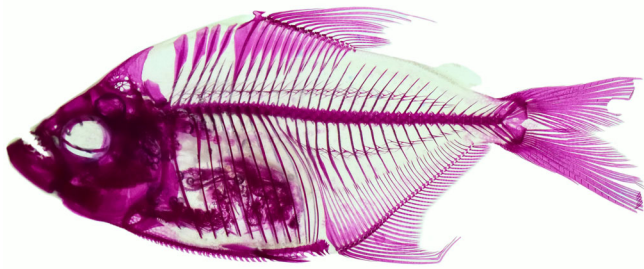


FIGURE 10 *Catoprion absconditus*, LBP 15534, cleared and stained, rio Takutu, Amazon basin. Lepidophagy evidenced by the presence of scales in the stomach



FIGURE 12 *Catoprion absconditus*, INPA 37246, 121 mm L_S , live coloration, rio Jatapu, Amazonas. Photo by Valéria Machado

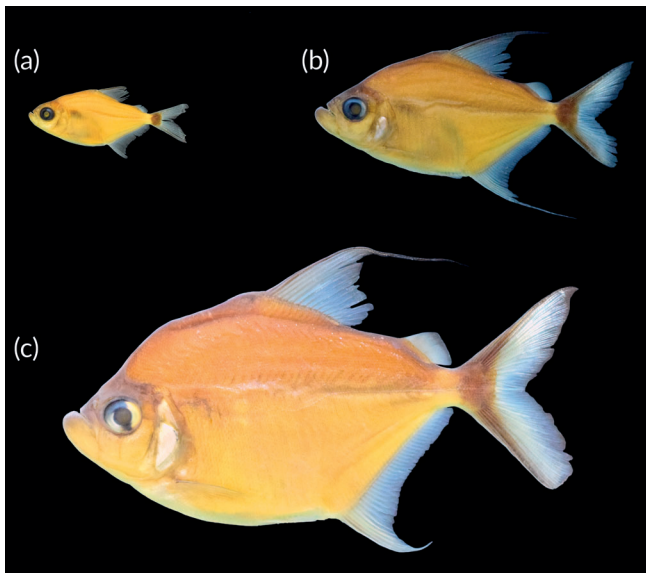


FIGURE 11 Ontogenetic variation of *Catoprion absconditus*. AUM 36146, rio Rupununi, Essequibo basin, Guyana: (a) 20.1 mm L_S ; (b) 44.7 mm L_S ; (c) 81.8 mm L_S

Nhamundá, 01°41'27"S 57°25'20"W, 11 Nov 2013, Machado V. *et al.* **Rio Uatumã basin. Amazonas.** INPA 37246, 5 (1), 123.5 mm L_S , São Sebastião do Uatumã, rio Jatapu, 02°01'03"S 58°10'26"W, 01 Oct 2011, Rapp Py-Daniel L. *et al.* MZUSP 50015, 93.7 mm L_S , male, Brazil, Amazonas, Presidente Figueiredo, rio Uatumã, about 500 m downstream UHE Balbina, 01°55'12"S 59°28'22"W, 21 Jul 1995, Lima FCT & UHE Balbina team. **Rio Xingu basin. Pará.** ANSP 198245, 1, 112.5 mm L_S , Porto de Moz, rio Xingu, 01°46'30"S 52°12'57"W, Sabaj M *et al.* INPA 47302 (rd), 1, 113.1 mm L_S , Porto de Moz, rio Xingu, 01°46'30"S 52°12'57"W, Sabaj M *et al.* **Guyana. Rio Branco basin. Region 9.** AUM 44757, 1, 63.5 mm L_S , Manari Pond, rio Takutu, 3°29'20"N 59°47'21"W, 28 Nov 2005.

Non-types

Brazil. Rio Amazonas basin. Amazonas. MZUSP 7328, 1, 75.2 mm L_S , Maués, Igarapé at rio Marau, 03 Dec 1967, Expedição Permanente da Amazônia. **Pará.** MZUSP 9178, 3, 82.5–94.5 mm L_S , Santarém, rio

TABLE 3 Morphometric data of *Catoprion absconditus*

	H	N	Range	Mean	S.D.
Standard length (mm)	78.3	72	30.2–144.7	72.5	–
Percentages of standard length					
Body depth	68.8	83	46.3–75.4	59.9	7.62
Postdorsal length	59.3	83	50.2–63.7	56.3	3.17
Predorsal length	59.3	83	53.2–61.0	56.8	1.78
Caudal-peduncle depth	10.5	83	8.3–11.3	9.6	0.63
Caudal-peduncle length	8.0	83	6.0–10.2	8.0	0.77
Head length	33.1	83	27.2–33.2	29.9	1.17
Dorsal-fin base	23.6	83	17.3–24.9	21.5	1.73
Dorsal-fin length	50.7	82	23.5–71.0	42.3	12.55
Interdorsal length	16.8	83	10.1–18.9	15.4	1.83
Adipose-fin base	11.0	83	6.1–12.9	10.2	1.27
Pectoral-fin length	20.2	81	13.5–24.8	19.5	2.29
Pelvic-fin length	15.0	79	11.7–17.7	14.4	1.21
Anal-fin base	44.5	83	33.8–45.9	40.0	2.84
Anal-fin length	56.1	71	17.4–56.6	33.2	9.51
Percentages of head length					
Interorbital width	32.3	83	24.2–41.0	33.6	4.57
Orbital diameter	30.4	67	27.1–39.5	32.8	3.31
Snout length	22.7	83	18.1–27.7	22.9	1.79
Maxilla length	29.4	83	27.8–47.6	37.6	4.15

Note: Range includes the holotype.

Abbreviations: H: holotype; N: number of specimens; S.D.: standard deviation.

Maicá, 19 Oct 1971, Expedição Permanente da Amazônia. MZUSP 9507, 2, 99.1–100.1 mm L_S , Monte Alegre, rio Amazonas, 14 Aug 1968, Expedição Permanente da Amazônia. **Rio Branco basin. Roraima.** INPA 35670, 2 (rd), 102.6–102.7 mm L_S , Caracarái, rio Anaua, rio Jauari, 00°57'12"N 61°06'49"W, 16 Apr 2007. LBP 15148, 3 (rd), 30.2–37.1 mm L_S , Boa Vista, rio Branco, 03°08'16"N

60°16'33"W, 20 Apr 2012, Britzke R & Melo BF. LBP 15534, 22 (21 rd, 1 cs), 31.6–54.3 mm L_S , Bonfim, Lago Fazenda Romer, Rio Takutu, 03°22'55"N 59°51'28"W, 22 Apr 2012, Britzke R & Melo BF. LBP 21608, 1 (rd), 47.0 mm L_S , same data as LBP 15534 LBP 21615, 5, 19.9–47.0 mm L_S , Boa Vista, Igarapé Au-Au, 02°56'19"N 61°03'06"W, 26 Apr 2012, Britzke R & Melo BF. MZUSP 20246, 11, 24.4–79.0 mm L_S , Boa Vista, lake at Tepequem road, 10 Feb 1969, Roberts T. **Rio Japurá basin. Amazonas.** MZUSP 36162, 1, 110.7 mm L_S , Igarapé Cacar, lago Amanã near mouth of rio Japurá, 06 Sep 1979, Barthem R. **Rio Negro basin. Amazonas.** INPA 52533, 1, 96.2 mm L_S , São Gabriel da Cachoeira, 00°07'13"S 67°06'07"W, 02 Feb 2014, Machado V. *et al.* **Roraima.** MZUSP 112544, 1, 126.6 mm L_S , Caracará, igarapé do Campo, rio Jufari, 01°04'01"S 62°07'40"W, 28 Aug 2011, Oyakawa O *et al.* MZUSP 113085, 1, 112.1 mm L_S , Caracará, igarapé Santa Fé, rio Jufari, 01°00'34"S 62°13'04"W, 01 Sep 2011, Oyakawa O *et al.* MZUSP 113599, 1, 34.9 mm L_S , Caracará, praia do Paricá, rio Jufari, 01°08'41"S 61°59'57"W, 10 Sep 2011, Oyakawa O *et al.* **Rio Tapajós basin. Pará.** LBP 15054, 1, 97.7 mm L_S , Itaituba, rio Tapajós, 04°34'07"S 56°18'49"W, 10 Jun 2012, Britzke R. *et al.* MZUSP 8451, 8 (1 cs), 44.3–102.5 mm L_S , Alter do Chão, igarapé Jacundá, 02°30'00"S 54°57'00"W, Expedição Permanente da Amazônia. MZUSP 57576, 1, 111.9 mm L_S , Santarém, lake near Alter do Chão, 02°28'05"S 54°55'34"W, Westneat M. *et al.* **Rio Trombetas basin. Pará.** INPA 46254, 2 (1), 119.6 mm L_S , Porto Trombetas, igarapé Água Fria, 01°27'56"S 56°49'42"W, 16 Nov 2013 Soares I. *et al.* MZUSP 5439, 2, 95.7–98.4 mm L_S , Oriximiná, rio Trombetas, Feb 1967, Expedição Permanente da Amazônia. MZUSP 5512, 1, 99.2 mm L_S , Oriximiná, lago Jacupã, Feb 1967, Expedição Permanente da Amazônia. MZUSP 8210, 1, 100.0 mm L_S , Oriximiná, lake Jacupã, 17 Dec 1967, Expedição Permanente da Amazônia. **Rio Uatumã basin. Amazonas.** INPA 37419, 1, 144.7 mm L_S , São Sebastião do Uatumã, igarapé Três, rio Jatapu, 02°00'07"S 58°11'35"W, 27 Sep 2011, Rapp Py-Daniel L. *et al.* MZUSP 9546, 1, 70.5 mm L_S , São Sebastião do Uatumã, 08 Sep 1968, Expedição Permanente da Amazônia. **Guyana. Rio Essequibo basin. Region 9.** AUM 48680, 13 (4), 46.7–52.6 mm L_S , creek between Lake Amuku and Pirara creek, rio Takutu, 3°39'14"N 59°31'43"W, 20 Nov 2007. AUM 36146, 10 (4), 20.1–81.8 mm L_S , dam pond 5.4 km northwest Karanambo, rio Rupununi, 03°46'77"N 59°20'59"W, 28 Oct 2002. AUM 45023, 1, 60.2 mm L_S , Pond at Yukupari, rio Rupununi, 03°39'33"N 59°21'38"W, 29 Nov 2005. AUM 48761, 1, 38.5 mm L_S , Lake Amuku, rio Rupununi, 03°43'20"N 59°26'49"W, 22 Nov 2007.

Diagnosis

C. absconditus differs from *C. mento* by presenting 85–94 perforated scales in the lateral line (vs. 65–86 scales) and 35–40 circumpeduncular scales (vs. 29–34 scales).

Description

Morphometric data presented in Table 3. Body deep, compressed laterally; general shape rhomboid. Highest body depth at vertical line through dorsal-fin origin. Dorsal profile slightly concave along head and convex between head and dorsal-fin origin. Dorsal profile of the

body fairly sloping at base of dorsal and adipose fins, and straight at interval between these two fins. Ventral profile convex from isthmus to end of anal fin. Ventral keel with a serra of spines (Figures 8 and 10). Pre-pelvic spines 19 (4), 20 (3), 21 (13), 22* (13), 23 (22), 24 (17), 25 (6), 26 (2) or 27 (1). Post-pelvic spines 8 (3), 9 (28), 10 (33), 11* (15) or 12 (3). Anal spines 1 (9), 2* (61) or 3 (11). Caudal peduncle deeper than long.

Eye positioned laterally at middle of head; upper margin of eye above longitudinal line of first lateral-line scale. Frontal and parietal fontanelles expanded laterally. Snout very short and slightly pointed in lateral view. Nostrils dorso-laterally positioned, at longitudinal axis through dorsal margin of eye. Mouth upturned. Jaw strongly prognathous. Lower jaw longer and projecting past the upper jaw. Premaxillary and dentary teeth mamilliforms, with a round base and narrower tip. Outer premaxillary row with two large, antrorse teeth; inner row with three small, vertically directed teeth (Figure 3b). Dentary with a single row of six teeth; the fourth tooth smaller than others (Figure 3a). Maxilla edentulous (Figure 3a).

Body completely covered by small cycloid scales. Lateral line complete, with 85 (3), 86 (6), 87 (7), 88 (8), 89 (11), 90* (8), 91 (9), 92 (6), 93 (7) or 94 (2) perforated scales; first to tenth scale larger than remaining. Scale series above lateral line 32 (1), 34 (1), 35 (2), 36 (6), 37 (7), 38 (9), 39 (7), 40* (4) or 41 (1). Scales below lateral line 26 (1), 27 (1), 28 (3), 29 (7), 30 (3), 31 (7), 32* (9) or 33 (4). Circumpeduncular scales 35 (5), 36 (12), 37 (12), 38* (19), 39 (6) or 40 (3).

Dorsal fin preceded by strong pointed spine, previously directed, separated from first unbranched ray (Figures 8 and 10), with origin approximately equidistant from tip of snout to end of hypural plate. First dorsal-fin rays prolonged; in some specimens surpassing caudal-fin base. Branched dorsal-fin rays gradually decreasing in size, branched dorsal-fin rays 13 (6), 14 (29), 15* (34) or 16 (13). Adipose fin short, longer than deep. Pectoral fin falcate, with $i + 11$ (6), 12 (21), 13 (30), 14* (20) or 15 (1) rays. Pelvic fin small, with $i, 6^*$ (62) branched rays. First anal-fin rays prolonged, surpassing caudal-fin base in some specimens. Branched anal-fin rays gradually decreasing in size; branched anal-fin rays 32 (4), 33 (21), 34* (29), 35 (15) or 36 (6). Caudal fin bifurcated, lobes of similar size, with 17* (70) branched rays.

First gill arch with elongated gill rakers, almost as long as filaments, decreasing in size towards the extremities; 6 (2), 8 (23), 9 (23) or 10* (4) gill rakers on upper limb, 11 (7), 12 (21), 13* (25) or 14 (2) gill rakers on lower limb. Lower gill rakers longer than upper. Vertebrae 36 (5), 37* (23) or 38 (2). Supraneurals 4* (29) or 5 (1) (Figures 8 and 10).

Colour in alcohol

C. absconditus presents a colour pattern very similar to that observed in *C. mento*. Vertical dark band through the eye. General body colour brown to yellowish, darker in the dorsal portion of the body. Humeral blotch black or brown, vertically elongated, sometimes inconspicuous or absent; larger in mature males, whose may have other smaller joint blotches or spots. Fins hyaline to yellowish. First rays of dorsal fin black or brown. First rays and distal margin of anal fin often dark. Conspicuous dark band extending from the posterior portion of the caudal peduncle, reaching the median procurrent of the caudal fin and most

external rays, and forming a V-shape with the apex directed towards the head (Figures 8 and 9). This pattern in the caudal peduncle advancing through the caudal fin gets darker and larger during ontogeny. Juvenile specimens under about 30 mm L_S present the caudal peduncle dark brown and the base of the caudal fin hyaline; at about 40 mm L_S , the base of the caudal fin begins to get darker, including a pale V-shape which becomes darker in larger specimens (more than 40 mm L_S) (Figure 11).

Colour in life

C. absconditus has a live coloration very similar to that observed in *C. mento*. Vertical dark band through the eye. General body colour silvery, darker dorsally. Conspicuous orange blotch over the ventral portion of the opercle. Dorsal, pectoral, pelvic and adipose fins with shades of orange, red and black, gradually turning hyaline posteriorly. Anal fin yellow to orange or red, mainly in the anterior rays although reaching the entire fin in some specimens, gradually turning to hyaline on posteriormost rays. Caudal fin base dark, in V-shape with the apex directed towards the head, advancing through the caudal peduncle (Figure 12).

Geographic distribution

C. absconditus occurs in the Amazon basin, including the Branco, Negro, Japurá, Uatumã, Nhamundá, Trombetas, Tapajós and lower Xingu Rivers, and in the Essequibo basin (Figure 2).

Sexual dimorphism

C. absconditus presents anterior lobe developed from the elongation of distal border of the anal fin, between about the 7th and the 13th branched rays, in males (Figure 9), whereas females present only the first rays of anal fin elongated. Vieira and Géry (1979) consider the prolongation of the first rays of the dorsal fin as exclusive to males. Here, both females and males with lengthy dorsal and anal fins extending to the caudal fin were analysed, and it is concluded that this character is not related to sexual dimorphism. Furthermore, the vertically elongated humeral blotch becomes larger in males during the reproductive period. It may join other blotches or spots spreading through the region around pectoral to anal fins, as typically found in serrasalmid males.

Ecological notes

C. absconditus shows lepidophagous behaviour, with adults preferentially feeding on scales (Figure 10) and juveniles additionally feeding on insects (Vieira & Géry, 1979).

Conservation status

C. absconditus is widespread throughout major drainages of the Amazon basin, where it is relatively common where it occurs. No specific threats were detected, which suggests the categorization as Least Concern (LC) according to IUCN criteria (IUCN, 2018).

Etymology

The epithet *absconditus* is from the Latin meaning "hidden." *C. absconditus* has been identified as *C. mento* in the Amazon basin for 201 years, since its original description (Cuvier, 1819).

Remarks

The new species *C. absconditus* is very similar to *C. mento* in body shape, colour pattern, sexual dimorphism and ecology, being the reason for why the two species were treated as conspecific for such a long time.

A single sequence attributed to rio Aripuanã of the rio Madeira basin (GenBank MG751928; Machado *et al.*, 2018) was identified here as *C. absconditus* through the analysis of DNA barcode, but the voucher specimen could not be analysed morphologically. All remaining specimens analysed from the rio Madeira basin, both morphologically and molecularly, were confidentially identified as *C. mento*. Therefore, more data are needed to confirm the occurrence of *C. absconditus* in the rio Aripuanã and the rio Madeira basin.

4 | DISCUSSION

An integrative approach was performed herein to investigate species diversity in *Catopriion*. This integrative analysis of morphological and molecular features has been highly informative and valuable to study different genera of Serrasalminae flagging new candidate species and improving the description and delimitation of species boundaries (Andrade *et al.*, 2017; Mateussi *et al.*, 2016, 2018).

Taphorn (2003) had already suggested that more than one species exists within the concept of *C. mento*, but a limited examination of specimens from a wide range of localities or a complete analysis of morphological features did not allow him to diagnose and describe such species. A previous molecular study (Machado *et al.*, 2018) sampled 19 *Catopriion* individuals from seven major Amazon tributaries, but did not include any *C. mento* individuals. Herein, the combined analysis of about 40 morphometric and meristic characters in 198 specimens of *Catopriion* from several basins, in combination with a molecular analysis of mitochondrial data in 49 specimens, allows the authors to unambiguously discriminate two distinct species: *C. mento* from Paraguay, Araguaia, Madeira, Purus and Orinoco river basins, and *C. absconditus* from Amazonas, Branco, Negro, Japurá, Uatumã, Nhamundá, Trombetas, Tapajós and Xingu Rivers and the Essequibo basin.

The disjunct distribution of populations of *C. mento* can be first explained by the lack of analysed specimens from western Amazon basin, more specifically in the Peruvian and Colombian Amazon (Figure 2). Assuming that the species also occurs in that region, and the occurrence in south-western Amazon tributaries (Madeira and Purus Rivers), the biogeographic pattern that best explains the distribution of *C. mento* is the Amazonas-Paraguay-Orinoco lowland, also represented by species occurring in the Tocantins-Araguaia basin, such as *Abramites hypselonotus* (Vari & Williams, 1987), *Curimatella dorsalis* (Vari, 1992), *Sorubim lima* (Littmann, 2007), among others (Dagosta & de Pinna, 2019). In the case of *C. absconditus*, the observed distribution best fits the eastern Amazon pattern, represented by taxa isolated by the Purus Arch before the formation of the Amazon main channel by the Late Miocene (Albert *et al.*, 2018; Dagosta & de Pinna, 2019); other examples of the eastern Amazon pattern are

Curimatopsis cryptica (Vari, 1982), *Synaptolaemus latofasciatus* (Britski et al., 2011), *Aphanothorulus emarginatus* (Ray & Armbruster, 2016), among others (Dagosta & de Pinna, 2019).

C. mento and *C. absconditus* have a similar body shape, coloration and the lepidophagous behaviour, but they differ in the number of scales in the lateral line and around caudal peduncle, which are slightly larger (thus fewer) in *C. mento* than those in *C. absconditus*. Moreover, molecular data strongly support the existence of two species based on four species delimitation analyses: BIN, PTP, ABGD and GMYC, in addition to the 6.97.3% pairwise K2P mean genetic distance (Min Dist = 6.4%; Max Dist = 7.7%). Traditionally, a 2% cut-off of interspecific distance has been used, at least initially, in species delimitation studies based on the K2P genetic distance (Carvalho et al., 2011; Pereira et al., 2013). This mean value is concordant with mean values found in other serrasalmids, e.g., 1.4%–9.0% in *Mylossoma* (Mateussi et al., 2016), 2.7%–6.2% in *Pygocentrus* (Mateussi et al., 2019) and 1.6%–9.3% in *Tometes* (Andrade et al., 2017).

4.1 | Comparative material examined

Acnodon senai, MNHN 1989 312, paratypes, 4, 45–82 mm L_S , rio Jari, Pará, Brazil. *Colossoma macropomum*, UFRO-ICT 11118, 1, 152 mm L_S , rio Jaciparaná, Jaciparaná, Rondônia, Brazil. *Metynnis guaporensis*, UFRO-ICT 5396, 1, 111 mm L_S , Igarapé Jatuarana, Porto Velho, Rondônia, Brazil. *Metynnis maculatus*, 1, UFRO-ICT 7528, 1, 122 mm L_S , lake Cuniã, Porto Velho, Rondônia, Brazil. *Mylesinus paraschomburgkii*, MNHN 1987 1403, paratypes, 2, 270–295 mm L_S , rio Cachorro, rio Trombetas, Pará, Brazil. *Myleus setiger*, LBP 24509, 4, 171–174 mm L_S , rio Jamaxim, Tapajós, Novo Progresso, Pará, Brazil. *Myloplus arnoldi*, MNHN 2017 0251, 2, 127–151 mm L_S , rio Xingu, Altamira market place, Pará, Brazil. *Myloplus planquettei*, MNHN 2001 1226, paratype, 400 mm L_S , riv. Litany, Saut Loue, French Guyana. *Mylossoma aureum*, LBP 21832, 2, 103–109 mm L_S , Catalão, rio Negro, Manaus, Amazonas, Brazil. *Mylossoma albiscopum*, LBP 18175, 3 (rd), 59–71 mm L_S , rio Solimões, Manacapuru, Amazonas, Brazil. *Ossubtus xinguense*, MNHN 1992 0004, 2 paratypes, 149–164 mm L_S , rio Xingu, Altamira, Pará, Brazil. *Pristobrycon calmoni*, MNHN 2007 0225, 1, 196 mm L_S , Caño Laguna Catagena de Chaira, rio Caguán, Cartagena de Chaira, Caquetá, Colombia. *Pygocentrus cariba*, LBP 2229, 36–50 mm L_S , Punta Brava, río Orinoco, Caicara del Orinoco, Bolívar, Venezuela. *Pygocentrus nattereri*, LBP 7785, 3 (rd), 101–108 mm L_S , lake Boca Franca, rio Araguaia, Cocalinho, Mato Grosso, Brazil. *Pygopristis denticulata*, MNHN 2017 0242, 2, 171–187 mm L_S , Paraná–Maxiparaná, rio Xingu, Brazil. *Serrasalmus altispinnis*, MNHN 1997 113, 1 paratype, 133 mm L_S , rio Quarenta Ilhas, rio Uatumã, Amazonas, Brazil. *Serrasalmus compressus*, MNHN 1986 0615, holotype, 110 mm L_S , Laguna Mocovi, Bolivia. *Serrasalmus rhombeus*, UFRO-ICT 5498, 4, 83–90 mm L_S , Igarapé Jatuarana, rio Madeira, Porto Velho, Rondônia, Brazil. *Tometes lebaili*, MNHN 2001 1212, 1 paratype, 139 mm L_S , riv. Litany, village Antecume Pata, French Guyana. *Tometes makue*, MNHN 2001 1231, 2 paratypes, 157–159 mm L_S , fleuve Maroni, village Antecume Pata, French Guyana.

Utariitchthys sp. MNHN 1991 0704, 1, 193 mm L_S , fleuve Sinnamony, French Guyana.

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AUTHOR CONTRIBUTIONS

N.T.B.M. contributed ideas, generated and analysed data and prepared manuscript. B.F.M. and C.O. analysed data and prepared manuscript.

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REFERENCES

- Agassiz, L. (1868). *A journey in Brazil* (4th ed.). Boston: Ticknor and Fields.
- Albert, J. S., Val, P., & Hoorn, C. (2018). The changing course of the Amazon River in the Neogene: Center stage for Neotropical diversification. *Neotropical Ichthyology*, 16, e180033.
- Andrade, M. C., Machado, V. N., Jégu, M., Farias, I. P., & Giarrizzo, T. (2017). A new species of *Tometes* Valenciennes 1850 (Characiformes: Serrasalminidae) from Tocantins-Araguaia River Basin based on integrative analysis of molecular and morphological data. *PLoS One*, 12, e0170053.
- Britski, H. A., Birindelli, J. L., & Garavello, J. C. (2011). *Synaptolaemus latofasciatus*, a new combination for *Leporinus latofasciatus* Steindachner, 1910 and its junior synonym *Synaptolaemus cingulatus* Myers and Fernández-Yépez, 1950 (Characiformes: Anostomidae). *Zootaxa*, 3018, 59–65.
- Britski, H. A., Silimon, K. Z., & Lopes, B. A. (1999). *Peixes do Pantanal: Manual de identificação*. Brasília, DF: Embrapa Informação Tecnológica.
- Britski, H. A., Silimon, K. Z., & Lopes, B. S. (2007). *Peixes do Pantanal: Manual de identificação* (2nd ed.). Brasília, DF: Embrapa Informação Tecnológica.
- Carvalho, D. C., Oliveira, D. A. A., Pompeu, P. S., Leal, C. G., Oliveira, C., & Hanner, R. (2011). Deep barcode divergence in Brazilian freshwater fishes: The case of the São Francisco River basin. *Mitochondrial DNA*, 22, 80–86.
- Chernoff, B., Machado-Allison, A., Willink, P., Sarmiento, J., Barrera, S., Menezes, N., & Ortega, H. (2000). Fishes of three Bolivian rivers: Diversity, distribution and conservation. *Interiencia*, 25, 273–283.
- Chernoff, B., & Willink, W. (1999). *A biological assessment of the aquatic ecosystem of the upper rio Orthon basin, Pando, Bolivia*. Washington DC: Conservation International Center for Applied Biodiversity Science.

- Cione, A. L., Dahdul, W. M., Lundberg, J. G., & Machado-Allison, A. (2009). *Megapiranha paranensis*, a new genus and species of Serrasalminae (Characiformes, Teleostei) from the upper Miocene of Argentina. *Journal of Vertebrate Paleontology*, 29, 350–358.
- Colombia, W. W. F. (2006). *Aspectos socioeconómicos y de manejo sostenible del comercio internacional de pexes ornamentales de agua dulce em el Norte de Sudamérica: retos y perspectivas*. Bogotá, DC: Memorias Taller Internacional.
- Cuvier, G. (1819). Sur les poissons du sous-genre *Hydrocyn*, sur deux nouvelles espèces des *Clalceus*, sur trois nouvelles espèces du *Serrasalmes*, et sur l'*Argentina glossodonta* de Forskahl, qui est l'*Albula gonorhynchus* de Bloch. *Mémoires du Muséum National d'Histoire Naturelle*, 5, 351–379.
- Dagosta, F. C., & De Pinna, M. (2019). The fishes of the Amazon: Distribution and biogeographical patterns, with a comprehensive list of species. *Bulletin of the American Museum of Natural History*, 2019, 1–163.
- Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUTI and the BEAST 1.7. *Molecular Biology and Evolution*, 29, 1969–1973.
- Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
- Eigenmann, C. H. (1910) Catalogue of the freshwater fishes of tropical and south temperate America. In *Reports of the Princeton University expeditions to Patagonia 1896–1899. Zoology. Fishes Patagonia* (Vol. 3, pp. 375–511).
- Eigenmann, C. H. (1912) The freshwater fishes of British Guiana, including a study of the ecological grouping of species, and the relation of the fauna of the plateau to that of the lowlands. In *Memoirs of the Carnegie Museum* (Vol. 5, pp. 1–578). Pittsburgh: Carnegie Institute.
- Eigenmann, C. H., & Eigenmann, R. S. (1891) A catalogue of the freshwater fishes of South America. In *Proceedings of the United States National Museum* (Vol. 14, pp. 1–81).
- Ferreira, E., Zuanon, J., Forsberg, B., Goulding, M., & Briglia-Ferreira, R. (2007). *Rio Branco: Peixes, ecologia e conservação de Roraima*. Gráfica Biblos: Wust Ediciones.
- Fowler, H. W. (1914). Fishes from Rupununi river, British Guiana. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 66, 229–284.
- Freeman, B., Nico, L. G., Osentoski, M., Jelks, H. L., & Collins, T. M. (2007). Molecular systematics of Serrasalminae: Deciphering the identities of piranha species and unraveling their evolutionary histories. *Zootaxa*, 38, 1–38.
- Fricke, R., Eschmeyer, W. N., & Fong J. D. (2020) *Eschmeyer's catalog of fishes: Species by family/subfamily*. Retrieved from <http://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp>.
- Fujisawa, T., & Barraclough, T. G. (2013). Delimiting species using single-locus data and the Generalized Mixed Yule Coalescent (GMYC) approach: A revised method and evaluation on simulated data sets. *Systematic Biology*, 62, 707–724.
- Géry, J. (1972). Poissons Characoïdes des Guyanes. I. Généralités. II. Famille des Serrasalminae. *Zoologische Verhandlungen*, 122, 1–250.
- Géry, J. (1976). Les genres de Serrasalminae (Pisces, Characoïdei). *Bulletin Zoologisch Museum*, 5, 47–54.
- Géry, J. (1977). *Characoids of the world*. Neptune City, NJ: T.F.H. Publications, Inc.
- Gosline, W. A. (1951). Notes on the characid fishes of the subfamily Serrasalminae. *Proceedings of the California Academy of Sciences*, 27, 17–64.
- Goulding, M. (1980). *The fishes and the forest: Explorations in Amazonian natural history*. Berkeley and Los Angeles, CA: University of California Press.
- Hartt, C. F. (1870). *Thayer expedition*. Boston: Fields, Osgood & Co.
- IUCN (2018). *The IUCN red list of threatened species*. Version 2018–1. Retrieved from <http://www.iucnredlist.org>.
- Jégu, M. (2003). Subfamily Serrasalminae. In R. E. Reis, S. O. Kullander, & C. J. Ferraris (Eds.), *Check list of the freshwater fishes of south and Central America* (pp. 185–199). Porto Alegre, RD: EDIPUCRS.
- Jégu, M. (2004). *Taxonomie des Serrasalminae phytophages et Phylogenie des Serrasalminae (Teleostei: Characiformes: Characidae)*, Paris, France: . Museum National d'Histoire Naturelle.
- Jégu, M., & Ingenito, L. F. S. (2007). Família Characidae: Serrasalminae. In P. A. Buckup, N. A. Menezes, & M. S. Ghazzi (Eds.), *Catálogo das espécies de peixes de água doce do Brasil* (pp. 40–43). Rio de Janeiro, RJ: Museu Nacional.
- Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., ... Drummond, A. (2012). Geneious basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28, 1647–1649.
- Kimura, M. (1980). A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16, 111–120.
- Kner, R. (1859). Zur Familie der Characinen. III. Folge der Ichthyologischen Beiträge. In *Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Classe* (Vol. 17, pp. 137–182). Vienna, Austria: Kaiserlichen Akademie der Wissenschaften in Wien.
- Lanfear, R., Calcott, B., Ho, S. Y. W., & Guindon, S. (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701.
- Littmann, M. W. (2007). Systematic review of the Neotropical shovelnose catfish genus *Sorubim* Cuvier (Siluriformes: Pimelodidae). *Zootaxa*, 1422, 1–29.
- Lowe-McConnell, R. H. (1964). The fishes of the Rupununi savanna district of British Guiana, South America. Part 1. Ecological groupings of fish species and effects of the seasonal cycle on the fish. *Journal of Linnean Society (Zoology)*, 45, 103–144.
- Machado, V. N., Collins, R. A., Ota, R. P., Andrade, M. C., Farias, I. P., & Hrbeek, T. (2018). One thousand DNA barcodes of piranhas and pacus reveal geographic structure and unrecognised diversity in the Amazon. *Scientific Reports*, 8, 1–12.
- Machado-Allison, A. (1982). *Studies on the systematics of the Subfamily Serrasalminae (Pisces - Characidae)*. Washington, DC: The George Washington University.
- Mateussi, N. T. B., Melo, B. F., Foresti, F., & Oliveira, C. (2019). Molecular data reveal multiple lineages in piranhas of the genus *Pygocentrus* (Teleostei, Characiformes). *Genes*, 10, 371.
- Mateussi, N. T. B., Oliveira, C., & Pavanelli, C. S. (2018). Taxonomic revision of the Cis-Andean species of *Mylossoma* Eigenmann & Kennedy, 1903 (Teleostei: Characiformes: Serrasalminae). *Zootaxa*, 4387, 275–309.
- Mateussi, N. T. B., Pavanelli, C. S., & Oliveira, C. (2016). Molecular identification of cryptic diversity in species of cis-Andean *Mylossoma* (Characiformes: Serrasalminae). *Mitochondrial DNA Part A: DNA Mapping, Sequencing, and Analysis*, 28, 778–780.
- Müller, J., & Troschel, F. H. (1844). Synopsis generum et specierum familiae Characinarum (Prodomus descriptionis novorum generum et specierum). *Archiv für Naturgeschichte*, 10, 81–99.
- Müller, J., & Troschel, F. H. (1845). Beschreibung und Abbildung neuer Fische Die Familie der Characinen. *Horae Ichthyologicae*, 1, 1–40.
- Myers, G. S. (1950). On the characid fishes called *Hydrocinus* and *Hydrocynon* by Cuvier. *Proceedings of the California Zoological Club*, 1, 45–47.
- Nelson, E. M. (1961). The swin bladder in the Serrasalminae: with notes on additional morphologica features. *Fieldiana Zoology*, 39, 603–624.
- Nico, L. G., Jégu, M., & Andrade, M. C. (2017). Family Serrasalminae – piranhas and pacus. In P. van der Sleen & J. Albert (Eds.), *Field guide to the fishes of the Amazon, Orinoco & Guianas* (pp. 172–195). Princeton and Oxford: Princeton University Press.

- Nico, L. G., & Taphorn, D. C. (1988). Food habits of piranhas in the low llanos of Venezuela. *Biotropica*, 20, 311–321.
- Ortí, G., Petry, P., Porto, J. I. R., Jégu, M., & Meyer, A. (1996). Patterns of nucleotide change in mitochondrial ribosomal RNA genes and the phylogeny of piranhas. *Journal of Molecular Evolution*, 42, 169–182.
- Ortí, G., Sivasundar, A., Dietz, K., & Jégu, M. (2008). Phylogeny of the Serrasalminae (Characiformes) based on mitochondrial DNA sequences. *Genetics and Molecular Biology*, 31, 343–351.
- Ota, R. P., Röpke, C. P., Zuanon, J., & Jégu, M. (2013). Serrasalminae. In L. J. Queiroz, G. Torrente-Vilara, W. M. Ohara, T. H. S. Pires, J. Zuanon, & C. R. C. Doria (Eds.), *Peixes do rio Madeira v.II* (pp. 14–48). São Paulo, Brasil: Santo Antônio Energia.
- Pattengale, N. D., Alipour, M., Bininda-Emonds, O. R., Mored, B. M., & Stamatakis, A. (2010). How many bootstrap replicates are necessary. *Journal of Computational Biology*, 17, 337–354.
- Pereira, L. H. G., Hanner, R., Foresti, F., & Oliveira, C. (2013). Can DNA barcoding accurately discriminate megadiverse Neotropical freshwater fish fauna? *BMC Genetics*, 14, 1–14.
- Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., ... Vogler, A. P. (2006). Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology*, 55, 595–609.
- Prang, G. (2007). An industry analysis of the freshwater ornamental fishery with particular reference to the supply of Brazilian freshwater ornamentals to the UK market. *Scientific Magazine UAKARI*, 3, 7–51.
- Puillandre, N., Lambert, A., Brouillet, S., & Achaz, G. (2012). ABGD, automatic gap discovery for primary species delimitation. *Molecular Ecology*, 21, 1864–1877.
- QGIS Development Team (2019) QGIS Geographic Information System. Open Source Geospatial Foundation Project. Retrieved from <http://qgis.osgeo.org>
- Rambaut, A., Drummond, A. J., Xie, D., Baele, G., & Suchard, M. A. (2018). Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, 67, 901–904.
- Ratnasingham, S., & Hebert, P. D. N. (2013). A DNA-based registry for all animal species: The Barcode Index Number (BIN) System. *PLoS One*, 8, e66213.
- Ray, C. K., & Armbruster, J. W. (2016). The genera *Isorineloricaria* and *Aphanotorulus* (Siluriformes: Loricariidae) with description of a new species. *Zootaxa*, 407, 501–539.
- Roberts, T. R. (1970). Scale-eating American characoid fishes, with special reference to *Probolodus heterostomus*. In *Proceedings of the California Academy of Sciences* (Vol. 38, pp. 383–390).
- Sabaj, M. H. (2019) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: An online reference. Version 7.1. Retrieved from <http://www.asih.org>.
- Sazima, I. (1983). Scale-eating in characoids and other fishes. *Environmental Biology of Fishes*, 9, 87–101.
- Sazima, I., & Machado, F. A. (1990). Underwater observations of piranhas in western Brazil. *Environmental Biology of Fishes*, 28, 17–31.
- Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30, 1312–1313.
- Taphorn, D. C. (1990) *The characiform fishes of the Apure river drainage, Venezuela* (Doctoral thesis), University of Florida.
- Taphorn, D. C. (2003). *Manual de Identificación y Biología de los Peces Characiformes de la Cuenca del Río Apure en Venezuela*. Guanare, Venezuela: BioCentro, Universidad Nacional Experimental de los Llanos Occidentales 'Ezequiel Zamora'.
- Taylor, W., & VanDyke, G. (1985). Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9, 107–119.
- Thompson, A. W., Betancur, R., López-Fernández, H., & Ortí, G. (2014). A time-calibrated, multi-locus phylogeny of piranhas and pacus (Characiformes: Serrasalminae) and a comparison of species tree methods. *Molecular Phylogenetics and Evolution*, 81, 242–257.
- Ulrey, A. B. (1894). Preliminary descriptions of some new South American Characinidae. *American Naturalist*, 28, 608–615.
- Ulrey, A. B. (1895). The South American Characinidae collected by Charles Frederick Hartt. *Annals of the New York Academy of Sciences*, 8, 257–300.
- Vanzolini, P. E. (2004). *Episódios da zoologia brasileira*. São Paulo, SP: Editora Hucitec.
- Vari, R. P. (1982). Systematics of the Neotropical characoid genus *Curimatopsis* (Pisces: Characoidei). *Smithsonian Contributions to Zoology*, 373, 1–28.
- Vari, R. P. (1992). Systematics of the Characiform genus *Curimatella* Eigenmann and Eigenmann (Pisces, Ostariophysi) with summary comment on the Curimatidae. *Smithsonian Contribution to Zoology*, 553, 1–48.
- Vari, R. P., Ferraris, C. J., Jr., Radosavljevic, A., & Funk, V. A. (2009). Checklist of freshwater fishes of the Guiana Shield. *Bulletin of the Biological Society of Washington*, 17, 93.
- Vari, R. P., & Williams, A. M. (1987). Headstanders of the Neotropical anostomid genus *Abramites* (Pisces: Characiformes: Anostomidae). *Proceedings of the Biological Society of Washington*, 100, 89–103.
- Vieira, I., & Géry, J. (1979). Crescimento diferencial e nutrição em *Catoprion mento* (Characoidei). Peixe lepidófago da Amazônia. *Acta Amazonica*, 9, 143–146.
- Ward, R. D., Zemlak, T. S., Innes, B. H., Last, P. R., & Hebert, P. D. N. (2005). DNA barcoding Australia's fish species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 360, 1847–1857.
- Zhang, J., Kapli, P., Pavlidis, P., & Stamatakis, A. (2013). A general species delimitation method with applications to phylogenetic placements. *Bioinformatics*, 29, 2869–2876.

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