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ARTICLE

Two new, remarkably colored species of the Neotropical catfish genus *Cetopsorhamdia* Eigenmann & Fisher, 1916 (Siluriformes, Heptapteridae) from Chapada dos Parecis, western Brazil, with an assessment of the morphological characters bearing on their phylogenetic relationships

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Abstract. Two new species of heptapterid catfish genus *Cetopsorhamdia* are described from close localities in western Brazil, at Chapada dos Parecis, an area with extremely high level of endemism. One species is from the upper Rio Madeira system, Rondônia State, and the other from the upper Rio Tapajós system, Mato Grosso State. The two species are diagnosed, among several other features, by their markedly distinctive color patterns, with the former having well-defined quadrangular marks in trunk flanks while the latter bearing irregular, vertical bars along the trunk. The monophyly of *Cetopsorhamdia* is discussed, with two putative synapomorphies being proposed to support the genus. Potentially informative morphological characters to resolve the internal relationships of the genus are presented and discussed. Despite the striking external differences between the two species herein described, they are found to likely form a clade.

Keywords. Systematics; Ichthyology; Taxonomy; South America.

INTRODUCTION

One of the most diversified and widely distributed Neotropical catfish families is Heptapteridae, currently totaling 23 valid genera and 228 valid species (*Phreatobius* Göldi, 1905 has been excluded and assigned to its own family – Sullivan *et al.,* 2013; Lundberg *et al.,* 2014). Heptapterids inhabit freshwater water bodies draining into the Atlantic Ocean from northern Mexico to southern Argentina and to the Pacific Ocean from northern Mexico to southern Peru (Bockmann & Guazzelli, 2003; Bockmann & Ferraris-Jr., 2005; Fricke *et al.,* 2021). Fishes of this family are generally small to medium-sized and prefer small rivers with shallow, fast waters although there are forms living in deep channels of large rivers and in calm waters inside caves (Heptapteridae bears the second largest diversity of troglomorphic fishes in the Neotropics) (Bockmann & Guazzelli, 2003; Bockmann & Castro, 2010).

Among heptapterids, the genus *Cetopsorhamdia* was erected by Eigenmann & Fisher *in* Eigenmann (1916: 83) for a single species, *C. nasus,* described in the same paper and originally designed as its type species (Eigenmann & Fisher *in* Eigenmann, 1916). The type locality established for *C. nasus* is "Honda, Colombia" [= Honda, Colombia, Magdalena River System] (Eigenmann & Fisher *in* Eigenmann, 1916: 83), but the species is presently known to occur in the upper and mid courses of the Río Magdalena basin, including in the upper Río Cauca, in Colombia (Ortega-Lara, 2004, 2012; Mojica *et al.,* 2006; Ortega-Lara *et al.,* 2006; Villa-Navarro *et al.,* 2006). In addition to its type species, nine other nominal species have been described for *Cetopsorhamdia,* namely: *C. boquillae* Eigenmann & Fisher *in*

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Eigenmann, 1922, from the Río Cauca basin of Colombia; *C. filamentosa* Fowler, 1945, from the Río Tulumayo basin, upper Ucayali drainage of Peru; *C. iheringi* Schubart & Gomes, 1959, from the upper reaches of the Rio Paraná and Rio São Francisco of Brazil; *C. molinae* Miles, 1943, from the Río Magdalena basin of Colombia; *C. orinoco* Schultz, 1944, from the Río Orinoco basin of Venezuela; *C. phantasia* Stewart, 1985, from the Río Napo basin of Ecuador and Rio Madeira of Brazil; *C. picklei* Schultz, 1944, from the Lago Maracaibo basin, Venezuela; *C. pijpersi* Hoedeman, 1961, from the Corantijn River basin of Suriname; and *C. shermani* Schultz, 1944, from the Río Magdalena basin of Colombia, Río Orinoco basin of Venezuela, and Rio Tocantins of Brazil (Eigenmann & Fisher *in* Eigenmann, 1922; Miles, 1943; Schultz, 1944; Fowler, 1945; Schubart & Gomes, 1959; Hoedeman, 1961; Stewart, 1985; Bockmann & Guazzelli, 2003; Ruiz-C. & Román-Valencia, 2006; Bockmann & Slobodian, 2013).

Schultz (1944) recombined four additional species formerly described in other heptapterid genera into *Cetopsorhamdia* (their geographic distributions are cited according to Bockmann & Guazzelli, 2003), namely: *Chasmocranus rosae* Eigenmann, 1919, from the Río Meta basin of Colombia; *Imparfinis hasemani* Steindachner, 1915, from the Rio Branco and Rio Tapajós basins of Brazil; *Imparfinis insidiosus* Steindachner, 1915, from the Rio Branco of Brazil; and *Imparfinis mirini* Haseman, 1911, from the upper Rio Araguaia and upper Rio Paraná basins of Brazil [the placement of *I. hasemani, I. insidiosus,* and *I. mirini* in *Cetopsorhamdia* had been previously suggested by Gosline (1941) but not formally implemented by him] (Haseman, 1911; Steindachner, 1915; Eigenmann, 1919; Bockmann & Guazzelli, 2003).

Based on the phylogenetic analysis of the family performed by Bockmann (1998), a stricter definition of the genus *Cetopsorhamdia* has been proposed. Consequently, several of these species must have been assigned to different genera of Heptapteridae, some yet to be described (*cf.* Bockmann, 1998; Zuanon *et al.,* 2006; Bockmann & Slobodian, 2018). Therefore, five nominal species are currently recognized as belonging to *Cetopsorhamdia: C. boquillae, C. iheringi, C. insidiosa, C. nasus,* and *C. picklei.*

As is the case for the whole family Heptapteridae (Bockmann, 1998; Bockmann & Guazzelli, 2003), the alpha diversity of *Cetopsorhamdia* is considerably underestimated, containing at least eight species pending description, some of which have already been listed in catalogs and faunistic works (*cf.* Bockmann & Slobodian, 2013; Ohara & Lima, 2015; Ohara & Loeb, 2016; Ohara & Marinho, 2016; Ohara *et al.,* 2016). During the Brazilian leg of the Transcontinental Catfish Expedition, funded by the All Catfish Species Inventory Project, carried out mainly across the upper Paraguay, upper Tapajós, upper and middle Madeira and Purus, at least 38 new catfishes have been unveiled (Reis, 2005). About one-third of all new species are heptapterids and, among them, there were two beautifully colored species that were putatively assigned to *Cetopsorhamdia.* Furthermore, in the last 15 years, collections carried out by the teams of the ichthyology laboratories of the Federal University of Rondônia and Museu de Zoologia da Universidade de São Paulo have brought to light additional material of these two species. In order to help fill the taxonomic gap of the family Heptapteridae (Dubois, 2010; Raposo *et al.,* 2020) and, in particular, of the genus *Cetopsorhamdia,* in this work we describe these two new forms. As a basis for the observations made, comments on potentially informative morphological characters are presented to diagnose the genus and elucidate its internal relationships.

MATERIAL AND METHODS

Measurements and counts were made on the left side of specimen whenever possible. All measurements were taken point-to-point with digital calipers and expressed to the nearest 0.1 mm. Methodology and terminology for measurements followed Bockmann & de Pinna (2004) and Bockmann & Castro (2010), excluding the nasal barbel length which is inapplicable due to the absence of that structure. Subunits of the head were presented as proportions of head length (HL), except for measurements of barbels, which were converted to proportions of standard length (SL). Head length and measurements of trunk parts were given as proportions of SL.

Methodology and terminology for taking meristic data and fin position followed Bockmann & de Pinna (2004) and Bockmann & Castro (2010). All anal-fin rays were counted individually, including the anterior splints and the two most posterior rays inserted in the same base. When a ray is distally broken or ill-formed, this element is counted and its branching pattern is, whenever possible, presumed according to the adjacent rays. Vertebral counts encompassed all vertebrae, including the first five modified into the complex vertebrae and the compound caudal centrum (PU1+U1) counted as a single element – *cf.* Lundberg & Baskin (1969). Counts of serial elements (branchiostegal rays, basal radials, pleural ribs, rays associated to caudal skeleton, procurrent rays, and vertebrae), and records of the first vertebra bearing a complete hemal spine and of fin positions (in relation to vertebral number) were taken from cleared and stained preparations and radiographs. The landmarks of the fin origin and terminus are always the total vertebrae (*i.e.,* the first five vertebrae associated with the Weberian complex are considered). Numbers of fin rays and branchiostegal rays were also verified in alcohol-preserved specimens with aid of transmitted illumination. In the descriptions, holotype counts are followed by an asterisk.

Cleared and counterstained specimens were prepared according to Taylor & Van Dyke (1985). Radiographs were obtained at FMNH, LIRP, MZUSP, and USNM (see list of institutional acronyms below). Most radiographs were obtained using a digital radiography cabinet-x-ray equipment Faxitron, model LX-60-DC12, hosted at the Laboratório de Ictiologia de Ribeirão Preto (LIRP), belonging to the Center for Biodiversity Documentation, Department of Biology, FFCLRP/University of São Paulo, Ribeirão Preto, SP, Brazil. All radiographs were stored at

LIRP and digital copies were sent to each institution holding radiographed specimens. Notations cited throughout the text are 'c&s' for cleared and stained specimens, 'ms' for measured specimens, 'SL' for standard length, and 'xr' for x-rayed specimens.

In addition, for further examination of the skeleton, the holotypes of the two species herein described were scanned by using a GE high-resolution X-ray CT, model Phoenix V|TOME|X S 240, housed at the Center for Biodiversity Documentation. The scans were taken from the snout tip through the fifth post-Weberian centrum, using a nanofocal X-ray source. CT-Scan details are presented in Supplementary information. Vizualization of the CT data was performed using the software package VGStudioMax, version 3.0 (64-bit) (https://www.volumegraphics.com/en/products/vgstudio.html; Volume Graphics, Heidelberg, Germany).

Osteological terminology follows Bockmann & Miquelarena (2008). The general nomenclature for cephalic laterosensory canals herein employed considers ontogenies and homologies of their components, as summarized by Pastana *et al.* (2020). Especifically for siluriforms, homologies for supraorbital and infraorbital laterosensory canal systems, and resulting terminology, follow Arratia & Huaquín (1995); and for preoperculomandibular laterosensory canal system follow Bockmann & Miquelarena (2008). The nomenclature of foramina in the mandibular suspensorium for the branches of the trigeminal and facial nerves follows Herrick (1899, 1901).

It has not been possible to borrow any specimen of *Cetopsorhamdia nasus,* the type species of the genus *Cetopsorhamdia,* from Colombian collections, so that the holotype was the only representative of this species we have directly examined. Fortunately, a redescription of *C. nasus* by Ortega-Lara (2012), including its skeleton, has confidently provided all the necessary information for comparative analyses herein undertaken. The conservation status of the new species was assessed following the categories and criteria of the International Union for Conservation of Nature (IUCN Standards and Petitions Sub-Committee, 2019).

Institutional abbreviations: AMNH, American Museum of Natural History, New York; **ANSP**, Academy of Natural Sciences of Drexel University, Philadelphia; **CAS**, California Academy of Sciences, San Francisco; **CM**, Carnegie Museum of Natural History, Pittsburgh; **CZUEL**, Museu de Zoologia da Universidade Estadual de Londrina, Londrina; **FMNH**, Field Museum of Natural History, Chicago; **INPA**, Instituto Nacional de Pesquisas da Amazônia, Manaus; **IU**, Indiana University, Bloomington; **LIRP**, Laboratório de Ictiologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto; **MCP**, Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; **MNRJ**, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; **MZUSP**, Museu de Zoologia da Universidade de São Paulo, São Paulo; **NMW**, Naturhistorisches Museum Wien, Wien; **NUP**, Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura, Universidade Estadual de Maringá, Maringá; **UFRJ**, Laboratório de Sistemática e Evolução de Peixes Teleósteos, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro; **UFRO-I**, Universidade Federal de Rondônia, Laboratório de Ictiologia e Pesca, Porto Velho; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Anatomical abbreviations in figures: AC, anterior ceratohyal; **AF**, anterior fontanel; **AN**, antorbital; **AP**, autopalatine; **AT**, antorbital tubule; **BB2-3**, basibranchials 2 and 3; **BL,** Baudelot's ligament; **BO**, basiooccipital; **BR**, branchiostegal rays; **CB1-5**, ceratobranchials 1 to 5; **EB1-4**, epibranchials 1 to 4, **EN**, entopterygoid; **EP**, epioccipital; **ES**, extrascapula; **EX**, exoccipital; **FR**, frontal; **HB1-2**, hypobranchials 1 and 2; **HF**, hyomandibular facet; **HFen**, foramen for entrance of the *ramus hyoideus facialis;* **HFex**, foramen for exit of the *ramus hyoideus facialis;* **HK**, hyomandibular keel; **HMen**, foramen for entrance of hyodeomandibular nerve trunk; **HY**, hyomandibula; **i1**, infraorbital laterosensory branch 1; **i3-6**, infraorbital laterosensory branches 3 to 6; **IH**, interhyal; **IO**, interopercle; **LE**, lateral ethmoid; **ll1-4**, lateral line sensory branches 1 to 4; **ME**, mesethmoid; **MFen**, foramen for entrance of the *ramus mandibularis VII;* **MFex**, foramen for exit of the *ramus mandibularis VII;* **MT**, metapterygoid; **MX**, maxilla; **NA**, nasal; **OF**, optic foramen; **OP**, opercle; **OS**, orbitosphenoid; **PA**, parasphenoid; **PB3-4**, pharyngobranchials 3 and 4; **PC**, posterior ceratohyal; **PF**, posterior fontanel; **PM**, premaxilla; **pm1-10**, preoperculomandibular laterosensory branches 1 to 10; **PO**, prootic; **po1+pm11**, postotic-preoperculomandibular complex laterosensory branch (postotic laterosensory branch 1+ preoperculomandibular laterosensory branch 11); **po2**, postotic laterosensory branch 2 (pterotic or temporal branch); **po3**, postotic laterosensory branch 3; **PR**, preopercle; **PS**, pterosphenoid; **PT**, pterotic; **QU**, quadrate; **RPR1**, rigid part of the first pectoral-fin ray; **s1-3**, supraorbital laterosensory branches 1 to 3; **s2+i2**, supraorbital-infraorbital complex sensory branch (supraorbital sensory branch 2+ infraorbital sensory branch 2); **s6+s6**, supraorbital complex laterosensory branch 6 (left and right epiphyseal branches 6 fused); **s8**, supraorbital laterosensory branch 8 (parietal branch); **SB**, subpreopercle; **SC**, supracleithrum; **SP**, sphenotic; **SPR1**, soft part of the first pectoral-fin ray; **ST1-4**, suborbital tubules 1 to 4; **SU**, supraoccipital; **TF**, trigeminofacial foramen; **TP**, tooth plate; **UH**, urohyal; **VH**, ventral hypohyal; **VL**, ventrolateral limb of supracleithrum; **VM**, ventromedial limb of supracleithrum; and **VO**, vomer.

RESULTS

Cetopsorhamdia clathrata sp. nov.
http://zoobank.org/03CD1517-2543-4698-BDF0-9212BDEBDF4A
(Figs. 1-4, Table 1)

Cetopsorhamdia new species 1. – Bockmann & Reis, 2011 [distribution – upper Rio Madeira basin, in State of Rondônia: unnumb. p.; brief characterization based

Table 1. Morphometric features of *Cetopsorhamdia clathrata,* taken from the holotype MCP 36064, and the paratypes in ANSP 188921, LIRP 10032, MCP 36063, MNRJ 35877, UFRO-I 10968, UFRO-I 10979, UFRO-I 22921, and UFRO-I 23004. Morphometric data 1-34 are expressed as percent of Standard Length and 35-45 as percent of Head Length. Abbreviations: H = holotype; Min = minimum value; Max = maximum value; N = number of specimens; SD = standard deviation.

	Rio Ji-Paraná (or Machado) basin						Rio Roosevelt basin					TOTAL				
	H	Range		Mean	SD	N	Range		Mean	SD	N	Range		Mean	SD	N
		Min	Max				Min	Max				Min	Max			
Total length (mm)	62.7	25.6	76.4	—	—	13	45.4	93.8	—	—	3	25.6	93.8	—	—	16
Standard length (mm)	50.8	20.3	61.2	—	—	13	35.5	72.7	—	—	3	20.3	72.7	—	—	16
1. Predorsal length	45.6	43.8	48.5	45.7	1.6	13	43.5	44.8	44.2	0.6	3	43.8	48.5	45.4	1.6	16
2. Preanal length	67.5	66.8	71.9	69.2	1.8	13	67.2	71.5	69.0	2.2	3	66.8	71.9	69.1	1.8	16
3. Prepelvic length	44.5	43.1	49.2	46.3	1.9	13	43.6	46.5	45.5	1.7	3	43.1	49.2	46.1	1.8	16
4. Preadipose length	72.9	69.5	75.4	72.4	1.9	13	69.2	73.3	71.3	2.1	3	69.2	75.4	72.2	1.9	16
5. Caudal-peduncle length	20.7	16.7	20.7	18.8	1.2	13	18.9	20.8	19.5	1.1	3	16.7	20.8	18.9	1.2	16
6. Caudal-peduncle depth	9.2	8.5	10.5	9.3	0.5	13	9.3	10.1	9.7	0.4	3	8.5	10.5	9.4	0.5	16
7. Adipose-fin length	14.4	13.7	16.2	15.2	0.7	13	15.3	17.1	16.4	1.0	3	13.7	17.1	15.4	0.9	16
8. Adipose-fin depth	3.9	3.4	5.7	4.4	0.6	13	4.4	4.6	4.6	0.1	3	3.4	5.7	4.4	0.6	16
9. Dorsal fin to adipose fin	18.8	13.0	18.8	16.5	1.5	13	15.6	18.6	17.2	1.5	3	13.0	18.8	16.6	1.5	16
10. Anal-fin base	12.3	12.3	15.3	13.7	1.1	13	12.8	13.5	13.1	0.4	3	12.3	15.3	13.6	1.0	16
11. Snout-anus distance	51.0	49.4	55.8	52.5	2.0	13	50.7	52.5	51.6	0.9	3	49.4	55.8	52.3	1.8	16
12. Snout-urogenital papilla distance	52.8	50.6	56.5	54.1	2.1	13	52.0	54.1	53.4	1.2	3	50.6	56.5	54.0	2.0	16
13. Anus-urogenital papilla distance	1.7	0.8	1.7	1.3	0.3	13	1.3	1.9	1.5	0.3	3	0.8	1.9	1.3	0.3	16
14. Length of first dorsal-fin ray (unbranched)	13.4	12.6	16.9	15.0	1.5	13	14.3	16.8	15.2	1.4	3	12.6	16.9	15.0	1.4	16
15. Length of rigid part of first dorsal-fin ray	4.8	4.0	6.9	5.7	0.8	13	5.5	6.2	6.0	0.4	3	4.0	6.9	5.7	0.7	16
16. Length of second dorsal-fin ray (first branched)	16.2	15.0	19.3	17.2	1.3	12	15.7	18.1	17.2	1.3	3	15.0	19.3	17.2	1.3	15
17. Length of third dorsal-fin ray (second branched)	15.4	15.1	19.2	17.1	1.6	13	17.0	17.5	17.3	0.3	2	15.1	19.2	17.1	1.5	15
18. Dorsal-fin base	10.2	9.5	11.6	10.7	0.7	13	10.1	11.3	10.7	0.6	3	9.5	11.6	10.7	0.6	16
19. Length of first pectoral-fin ray (unbranched)	14.1	12.4	15.1	13.7	0.9	13	13.6	14.5	14.1	0.4	3	12.4	15.1	13.7	0.9	16
20. Length of rigid part of first pectoral-fin ray	5.1	3.4	5.2	4.4	0.5	13	5.1	6.2	5.6	0.6	3	3.4	6.2	4.6	0.7	16
21. Length of second pectoral-fin ray (first branched)	15.5	13.7	16.1	15.1	0.7	13	15.4	16.6	16.1	0.7	3	13.7	16.6	15.3	0.8	16
22. Length of third pectoral-fin ray (second branched)	15.5	13.9	16.4	15.1	0.8	13	15.1	16.0	15.5	0.5	3	13.9	16.4	15.2	0.8	16
23. Length of first pelvic-fin ray (unbranched)	11.2	11.0	13.8	12.3	1.1	12	10.9	12.0	11.5	0.6	3	10.9	13.8	12.2	1.0	15
24. Length of second pelvic-fin ray (first branched)	13.1	12.8	15.3	14.3	0.8	12	13.9	15.0	14.4	0.6	3	12.8	15.3	14.3	0.7	15
25. Length of third pelvic-fin ray (second branched)	14.0	13.0	15.4	14.2	0.7	11	13.1	13.5	13.4	0.3	3	13.0	15.4	14.0	0.7	14
26. Length of dorsal caudal-fin lobe	23.0	19.8	24.3	22.8	1.3	13	22.6	26.2	24.0	1.9	3	19.8	26.2	23.1	1.4	16
27. Length of ventral caudal-fin lobe	26.2	20.3	27.9	24.8	1.7	13	25.7	29.6	27.4	2.0	3	20.3	29.6	25.3	2.0	16
28. Body depth	16.6	12.8	16.6	15.3	1.3	13	13.4	15.1	14.3	0.9	3	12.8	16.6	15.1	1.2	16
29. Body width	12.8	10.4	12.8	11.5	0.7	13	11.1	11.7	11.4	0.3	3	10.4	12.8	11.5	0.6	16
30. Cleithral width	17.8	16.2	18.2	17.2	0.6	13	17.2	18.3	17.6	0.6	3	16.2	18.3	17.3	0.6	16

		Rio Ji-Paraná (or Machado) basin					Rio Roosevelt basin					TOTAL				
	H	Range		Mean	SD	N	Range		Mean	SD	N	Range		Mean	SD	N
		Min	Max				Min	Max				Min	Max			
31. Maxillary-barbel length	16.6	16.6	25.6	21.9	3.2	13	20.9	21.6	21.3	0.4	3	16.6	25.6	21.8	2.8	16
32. Outer mental-barbel length	12.3	12.3	20.4	16.5	2.6	12	16.3	17.3	16.9	0.5	3	12.3	20.4	16.6	2.3	15
33. Inner mental-barbel length	9.7	9.7	15.6	12.9	1.7	13	13.1	13.4	13.3	0.2	3	9.7	15.6	13.0	1.5	16
34. Head length	25.8	24.5	29.2	27.0	1.7	13	25.8	28.1	26.8	1.2	3	24.5	29.2	26.9	1.5	16
35. Head depth	50.2	46.4	55.8	50.5	2.9	13	44.3	46.7	45.7	1.2	3	44.3	55.8	49.6	3.3	16
36. Head width	71.4	67.1	75.4	70.3	2.2	13	68.8	71.5	70.0	1.4	3	67.1	75.4	70.2	2.1	16
37. Fleshy interorbital	26.3	25.0	31.6	28.3	2.6	13	24.2	26.7	25.5	1.2	3	24.2	31.6	27.8	2.6	16
38. Bony interorbital	19.6	17.4	24.6	20.8	2.3	13	18.1	19.2	18.5	0.6	3	17.4	24.6	20.4	2.2	16
39. Eye diameter	10.8	10.1	13.5	11.9	1.0	13	8.8	12.6	11.1	2.0	3	8.8	13.5	11.7	1.2	16
40. Snout length	40.9	38.1	43.6	39.8	1.5	13	38.4	39.7	39.0	0.7	3	38.1	43.6	39.6	1.4	16
41. Distance between snout tip and posterior nare	27.7	24.4	30.2	26.9	1.7	13	25.0	27.1	26.3	1.2	3	24.4	30.2	26.8	1.6	16
42. Intranarial length	14.5	12.2	16.8	13.8	1.2	13	12.3	12.8	12.6	0.3	2	12.2	16.8	13.6	1.2	15
43. Anterior internarial width	10.3	10.3	13.9	12.2	1.2	13	11.3	13.3	12.1	1.0	3	10.3	13.9	12.2	1.2	16
44. Posterior internarial width	13.7	13.7	17.9	15.5	1.2	13	13.9	14.8	14.4	0.5	3	13.7	17.9	15.3	1.1	16
45. Mouth gape	33.8	33.8	41.5	38.6	2.6	13	35.5	39.8	38.3	2.4	3	33.8	41.5	38.5	2.5	16

on body coloration: unnumb. p.; phylogenetic relationships: unnumb. p.].

Cetopsorhamdia sp. n. 3. – Bockmann & Slobodian, 2013 [likely endemic of part of the Rio Madeira system: 19; photograph in left lateral view: 24 (UFRO-I 10968, 72.7 mm SL); distribution – Rio Machado and Roosevelt, Brazil: 25; material cited – UFRO-I 10869 (misspelled catalog number; actually UFRO-I 10968; part of lot currently at LIRP 10032): 25; brief description: 25; in key of identification of heptapterids of Rio Madeira basin: 72; in list of heptapterids reported to the Mamoré/Beni/Madre de Díos/Madeira system – geographic distribution; additional material (MCP 36063, MCP 36064): 74, unnumb. tab.]; Ohara & Lima, 2015 [ecological notes of the collecting site – Brazil, Rondônia, Vilhena, rio Madeira basin, upper rio Machado, tributary of igarapé Piracolina, near road BR-364, 12°48′56.5″S, 60°06′37.6″W – UFRO-I 22918: 566]; Ohara & Marinho, 2016 [ecological notes of the collecting site – Brazil, Rondônia, Vilhena, rio Madeira basin, upper rio Machado, tributary of igarapé Piracolina, near road BR-364, 12°48′56.5″S, 60°06′37.6″W – UFRO-I 22918: 41]; Ohara *et al.*, 2016 [ecological notes of the collecting site – Brazil, Rondônia, Vilhena, rio Madeira basin, upper rio Machado, tributary of igarapé Piracolina, near road BR-364, 12°48′56″S, 60°06′37″W – UFRO-I 22918: 547].

Undescribed species of *Cetopsorhamdia*. – Ohara *et al.*, 2016 [endemic to the Rio Madeira basin: 549].

Holotype: MCP 36064, 50.8 mm SL in ethyl alcohol (ms and xr), Brazil, Rondônia State, Vilhena, Igarapé Piracolina, Rio Ji-Paraná (or Machado) basin, Rio Madeira drainage, *ca.* 6 km W of Vilhena, near highway BR-364, at Chapada dos Parecis, 12°43′33″S, 60°11′34″W, coll. R.E. Reis, P.A. Buckup, A.R. Cardoso, E.H.L. Pereira, 14 Jul 2004.

Paratypes: All specimens from Brazil, Rondônia State, Vilhena: ANSP 188921, 2 ex. in ethyl alcohol (21.3-55.0 mm SL, ms and xr), collected with holotype; LIRP 10032 (ex UFRO-I 10968), 2 ex. in ethyl alcohol (35.5-40.1 m SL, ms and xr), unnamed igarapé affluent of Rio Roosevelt, Rio Madeira drainage, at Chapada dos Parecis, 12°24′33.6″S, 59°58′31.5″W, coll. Laboratório de Ictiologia e Pesca/UNIR team, 4 Sep 2011; MCP 36063, 5 ex. in ethyl alcohol (20.3-27.8 mm SL, all ms and xr), 1 ex. c&s (49.2 mm SL); MNRJ 35877, 1 ex. in ethyl alcohol (40.9 mm SL, ms and xr), collected with holotype; MZUSP 115512, 9 ex. in ethyl alcohol (15.5-52.4 mm SL), unnamed igarapé affluent of Igarapé Piracolina, Rio Ji-Paraná (or Machado) basin, Rio Madeira drainage, *ca.* 3 km from the border between the states of Mato Grosso and Rondônia, at Chapada dos Parecis, 12°48′58″S, 60°06′43″W, coll. W.M. Ohara, 3 Sep 2014; MZUSP 117063, 1 ex. in ethyl alcohol (31.0 mm SL), unnamed igarapé affluent of Igarapé Piracolina, Rio Ji-Paraná (or Machado) basin, Rio Madeira drainage, at Chapada dos Parecis, 12°48′58″S, 60°06′43″W, coll. W.M. Ohara, 12 Nov 2014; UFRO-I 10968, 1 ex. in ethyl alcohol (72.7 mm SL, ms and xr), same data as LIRP 10032; UFRO-I

10979, 2 ex. in ethyl alcohol (24.7-53.9 mm SL, ms and xr), unnamed igarapé affluent of Rio Ji-Paraná (or Machado), Rio Madeira drainage, near Vilhena, towards Porto Velho, at Chapada dos Parecis, 12°42′54.1″S, 60°21′35.6″W, coll. Laboratório de Ictiologia e Pesca/UNIR team, 3 Sep 2011; UFRO-I 22918, 12 ex. in ethyl alcohol (21.7-34.0 mm SL), unnamed igarapé affluent of Igarapé Piracolina, Rio Ji-Paraná (or Machado) basin, Rio Madeira drainage, at Chapada dos Parecis, 12°48′56.5″S, 60°06′37.6″W, coll. W.M. Ohara, D.B. Hungria, B.S. Barros, 14 Sep 2013; UFRO-I 22921, 1 ex. in ethyl alcohol (61.2 mm SL, ms and xr), unnamed igarapé affluent of Igarapé Piracolina, Rio Ji-Paraná (or Machado) basin, Rio Madeira drainage, at Chapada dos Parecis, 12°40′04″S, 60°15′58″W, 29 July 2013, coll. I.D. Costa; UFRO-I 23004, 1 ex. in ethyl alcohol (28.3 m SL, ms and xr), unnamed stream affluent of Igarapé Piracolina, where crossed by highway BR-364, in the road next to the telecom tower, at Chapada dos Parecis, 12°40′51″S, 60°13′36.9″W, coll. Laboratório de Ictiologia e Pesca/UNIR team, 14 Sep 2013.

Diagnosis

Cetopsorhamdia clathrata differs from its congeners, and all other heptapterids, by a unique color pattern of trunk constituted by two longitudinal rows of 10-12 quadrangular marks which gives the fish a crisscross appearance (evident in specimens 27.8 mm SL and larger). Such a color pattern is produced by two presumably independent features: 9-11 transverse bars of interrupted pigmentation and an unpigmented stripe along the mid-lateral portion of trunk (*vs.* body homogeneously darkly pigmented or with different color pattern). Specimens of all sizes of *C. clathrata* are further distinguished from

Figure 1. *Cetopsorhamdia clathrata,* MCP 36064, 50.8 mm SL, holotype; Brazil, Rondônia State, Vilhena: Igarapé Piracolina, Rio Madeira basin, at Chapada dos Parecis.

Figure 2. *Cetopsorhamdia clathrata,* UFRO-I 10979, 53.9 mm SL, paratype (right after collection); Brazil, Rondônia State, Vilhena: unnamed igarapé affluent of Rio Ji-Paraná (or Machado), Rio Madeira drainage, near Vilhena, towards Porto Velho, at Chapada dos Parecis. Photograph by W.M. Ohara.

Figure 3. Developmental series of *Cetopsorhamdia clathrata,* lateral view, paratypes, showing ontogenetic color pattern changes; Brazil, Rondônia State, Vilhena: Igarapé Piracolina, Rio Madeira basin: MCP 36063, (A) 21.5 mm SL, (B) 22.1 mm SL, (C) 22.4 mm SL, (D) 27.8 mm SL; and MNRJ 35877, (E) 40.9 mm SL.

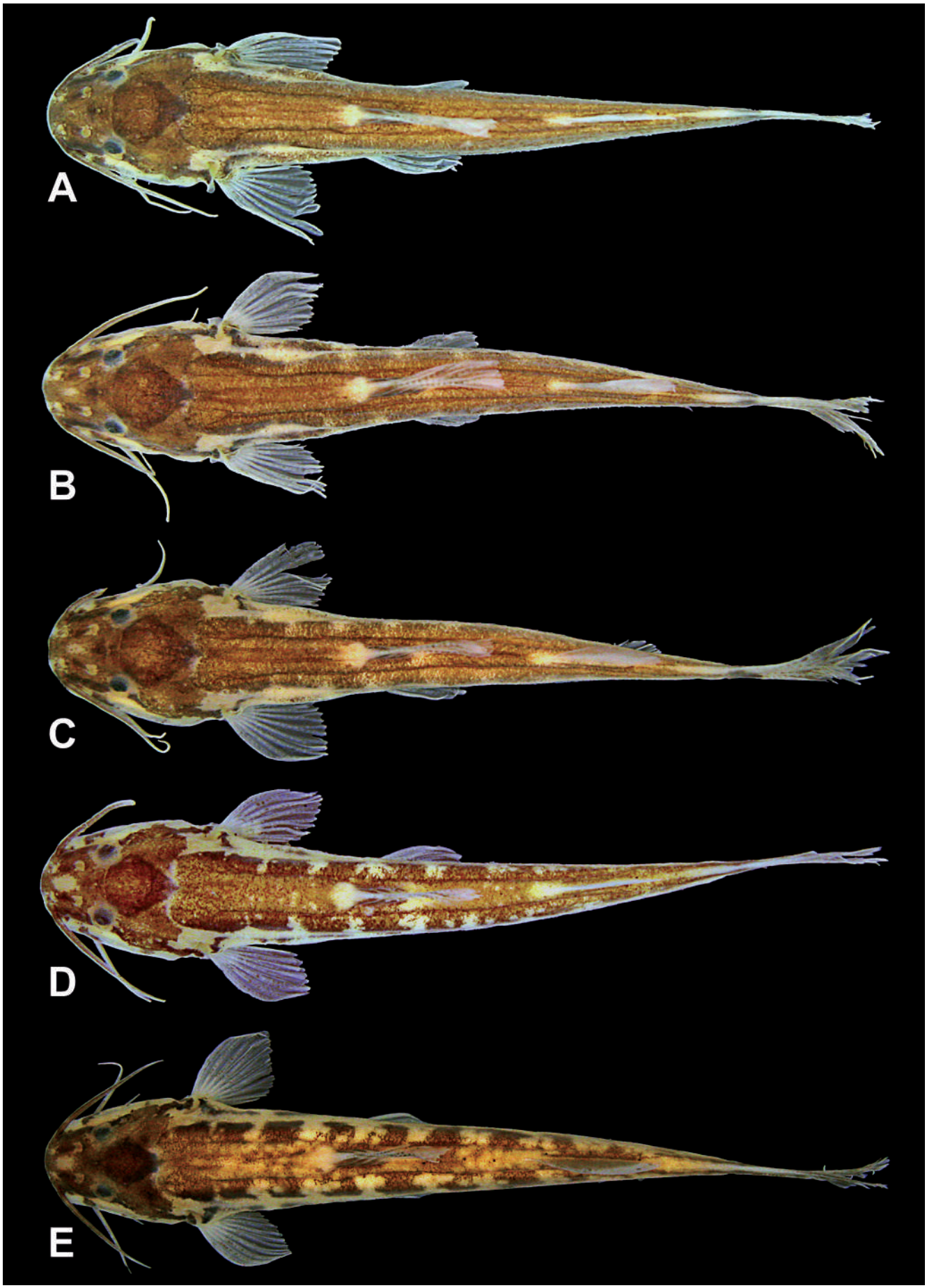

Figure 4. Developmental series of *Cetopsorhamdia clathrata,* dorsal view, paratypes, showing ontogenetic color pattern changes; Brazil, Rondônia State, Vilhena: Igarapé Piracolina, Rio Madeira basin: MCP 36063, (A) 21.5 mm SL, (B) 22.1 mm SL, (C) 22.4 mm SL, (D) 27.8 mm SL; and MNRJ 35877, (E) 40.9 mm SL.

other species of *Cetopsorhamdia* by possessing a higher number of vertebrae, 40-42, usually 41 (*vs.* 37 in *C. boquillae;* 37-39, usually 37-38, in *C. iheringi;* 35-38, usually 36-37 in *C. insidiosa, C. nasus,* and *C. picklei;* 39-40 in *C. spilopleura*). It can be distinguished from most species of *Cetopsorhamdia,* except *C. spilopleura,* by having: very short maxillary barbel, not reaching posterior margin of opercle in specimens 22.4 mm SL or longer (*vs.* reaching the first third of pectoral fin in *C. insidosa* and *C. nasus;* reaching the second third of pectoral fin in *C. iheringi* and *C. picklei;* and surpassing the posterior margin of pectoral fin in *C. boquillae*); dorsal fin more posteriorly located, with first basal radial articulated with the bifid dorsal process of vertebrae 11-12 (*vs.* 8-9 in *C. boquillae, C. iheringi, C. insidiosa, C. nasus,* and *C. picklei*); anal fin situated more posteriorly, with its first basal radial normally articulated between hemal spines of vertebrae 23-25 (*vs.* 21-22 in *C. boquillae* and *C. insidiosa,* 21-23 in *C. iheringi* and *C. nasus;* and 20-23, usually 20-22, in *C. picklei*); and whitish ovoid areas on both caudal-fin lobes (*vs.* caudal fin lobes homogeneously dark in other species). *Cetopsorhamdia clathrata* is further distinguished from *C. spilopleura* by having fins narrow, with marked concave posterior margins (*vs.* fins broad, with convex posterior profiles); a long and complete lateral line, extending to slightly beyond the caudal-fin base (*vs.* lateral line fragmented as isolated patches behind the level of the adipose-fin origin, reaching the level of the anterior portion of the caudal plate); and the laterodorsal and lateroventral regions of the trunk with continuous dark pigmentation (not forming two unpigmented lateral streaks), except for the intervals between the squares (*vs.* laterodorsal and lateroventral regions of trunk devoid of dark pigmentation).

Description

Morphometrics of holotype and some paratypes in Table 1. See Figs. 1-4 for general body shape. Body relatively elongated, its cross-section oval predorsally, becoming gradually more compressed caudally. Anterior dorsal profile of body gently convex, with sometimes discrete hump at posterior limit of head. Dorsal profile of head gently convex, continuous with dorsal profile of trunk. Dorsal profile of trunk posterior to dorsal-fin base approximately straight to base of caudal fin. Ventral profile of head approximately straight and continuous with abdominal region. Ventral trunk contour slightly convex or straight from pelvic-fin origin to end of anal-fin base, and straight to base of caudal fin. Posterior body depth gradually decreasing caudally. Axillary pore minute, just dorsal to pectoral-fin base, and ventral to first pore of lateral line. Urogenital and anal openings adjacent to each other; anal opening approximately on vertical through middle of pelvic fin.

Head longer than broad, depressed, and subtriangular to trapezoidal in dorsal view (Figs. 1-5). Anterior and posterior cranial fontanels short, separated from each other by broad bridge, about two times longer than each fontanel (Fig. 6B). Eye small, laterodorsally located, approximately equidistant from snout tip and supraoccipital end, and without free orbital rim except for shallow ventral invagination. Deep longitudinal facial ridge marking dorsal limit of *adductor mandibulae* muscle, extending from dorsal base of maxillary barbel to or just anterior of eye. Cheek distinctly swollen below eye forming groove to maxillary barbel. Anterior intranarial width and posterior intranarial width approximately equal. Anterior and posterior nares far apart from each other; internarial length slightly greater than distance between each pair of nares. Anterior naris surrounded by fleshy tubular flap of integument, with anterior margin slightly raised. Base of anterior nostril shallow, not sunk in conspicuous trench. Posterior naris wide, elliptical, with transversal axis longest. Posterior naris surrounded by low fleshy flap anteriorly, mesially and laterally; posterior margin devoid of flap. Mouth distinctly subinferior; gape gently convex anteriorly, slightly downturned at corners. Skin of lips with fleshy rictal fold at corner of gape. Rictal fold ventrally subtended by submandibular groove that extends anteriorly to point approximately adjacent to third or fourth preoperculomandibular pores (pm3 and pm4, respectively).

Premaxilla with 8-9 and dentary with 4-5 irregular rows of small, villiform teeth (Fig. 6C). Anteriormost tooth row of premaxilla with 15-18 teeth; anteriormost tooth row of dentary with 23-26 teeth. Palate and vomer edentulous.

Gular fold distinct, fleshy, and broadly V-shaped. Branchiostegal membranes well-developed, free, united to isthmus only at medial apex, and not connected to each other anteriorly (Fig. 5C). Branchiostegal rays 8 (13*) or 9 (4), posteriormost two wider and more laminar than anterior ones (Fig. 7). Ceratobranchials 1-2, and 5 with rakers along lateral margin only; ceratobranchials 3-4 with rakers along both lateral and mesial margins (Fig. 8). Branchial rakers short and straight, 6/6 (4), 6/7 (2), 7/6 (1), 7/7 (9*), or 8/8 (1) on first ceratobranchial (including one on angle formed with epibranchial), and 0/0 (16*) or 1/0 (1) on first epibranchial.

Barbels relatively short and flattened dorso-ventrally, and progressively tapering distally (Figs. 1-5). Tip of maxillary barbel barely reaching posterior limit of opercle and rarely surpassing posterior margin of branchiostegal membrane (only in 22.1 mm SL or smaller specimens), when adpressed against body. Outer mental barbel longer than inner barbel. Inner and outer mental barbels inserted at approximately same line. Tip of outer mental barbel slightly beyond posterior border of branchiostegal membrane when parallel to main body axis, sometimes reaching level of pectoral-fin base, in 40.9 mm SL or smaller specimens; barely reaching posterior border of branchiostegal membrane of 50.8 mm SL or larger specimens. Tip of inner mental barbel slightly beyond to just reaching posterior border of branchiostegal membrane when papallel to main body axis in 27.8 mm SL or smaller specimens; barely reaching posterior border of branchiostegal membrane of specimens 50.8 mm SL or larger.

Dorsal fin approximately triangular in lateral profile, not reaching to adipose fin when adpressed (Figs. 1-3).

Dorsal fin with i,6 (17*) rays. First dorsal-fin ray (spinelet) absent. Second dorsal-fin ray unbranched, with basal third stiffened and unsegmented and distal two thirds flexible and segmented. Second dorsal-fin ray slightly shorter than third and fourth rays (first and second branched rays, respectively). Origin of dorsal fin slightly anterior to vertical through pelvic-fin origin. Dorsal fin with 7 (17*) basal radials. Anteriormost dorsal-fin basal radial on neural spine of vertebra 11 (3), on space between neural spines of vertebrae 11 and 12 (2), or on neural spine of vertebra 12 (12*). Posteriormost dorsal-fin basal radial on space between neural spines of vertebrae 15 and 16 (10), on neural spine of vertebra 16 (3), or between neural spines of vertebrae 16 and 17 (4*).

Pectoral fin with distal margin straight to slightly convex (Figs. 1-4), with i,7 (2) or i,8 (15*) rays. First pectoral-fin ray with basal third rigid and unsegmented and distal two thirds flexible and segmented (Fig. 9). First pectoral-fin ray slightly shorter than second (first branched) and third (second branched) rays, whose tips project slightly beyond tip of first ray. Pectoral fin lying parallel to main body axis when expanded and slightly directed upwards when adpressed to body.

Pelvic fin wide, with distal border straight to slightly rounded (Figs. 1-3), with i,5 (17*) rays. Origin of pelvic-fin base slightly posterior to vertical through dorsal-fin origin, on vertical through space between insertions of first (unbranched) and second (first branched) dorsal-fin

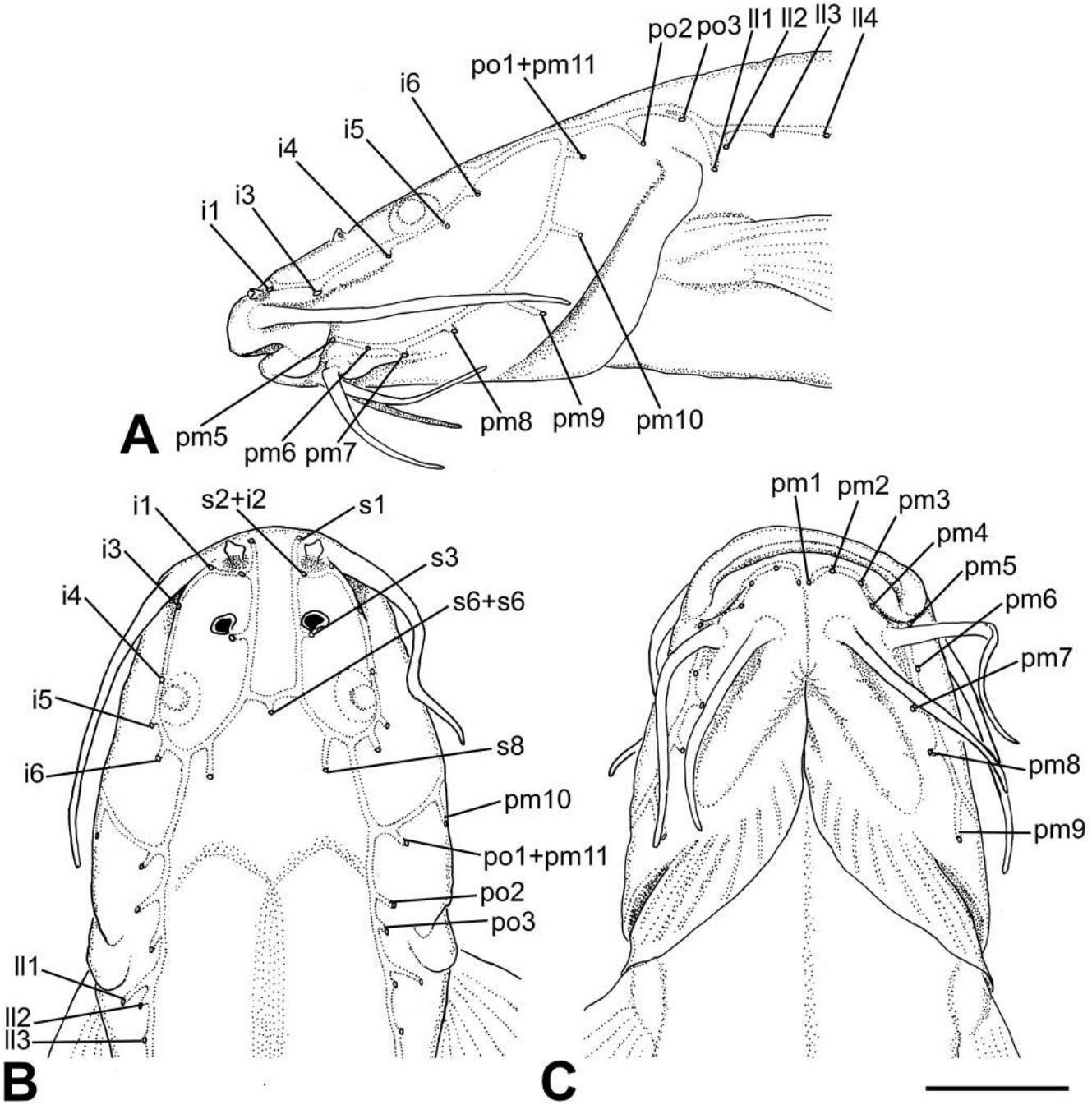

Figure 5. Anterior portion of the body of *Cetopsorhamdia clathrata,* ANSP 188921, 55.0 mm SL, paratype, showing laterosensory canal system. (A) left lateral view; (B) dorsal view; (C) ventral view. Scale bar = 4 mm.

rays (8*), or on vertical through insertion of second (first branched) dorsal-fin ray (9). Inner margins of pelvic-fin bases apart from each other. Tip of adpressed pelvic fin falling at mid distance between pelvic- and anal-fin origins. Lateralmost ray unbranched, completely flexible, segmented, and with tip distinctly falling short of tips of second and third rays (first and second branched rays, respectively). Origin of pelvic fin on vertical through region between centra 13 and 14 (1), on vertical through vertebral centrum 14 (5), on vertical through region between centra 14 and 15 (7), or on vertical through vertebral centrum 15 (4*).

Anal fin deeper than adipose fin, with short base and distal border slightly rounded (Figs. 1-3), with 12 (9*), 13 (7), or 14 (1) total rays, including 7 (3), 8 (12*), or 9 (2) branched rays. Anal-fin rays with following branching pattern: iv,8 (6*), iv,9 (2), v,7 (3), or v,8 (6). Two anteriormost anal-fin rays vestigial, unsegmented, embedded

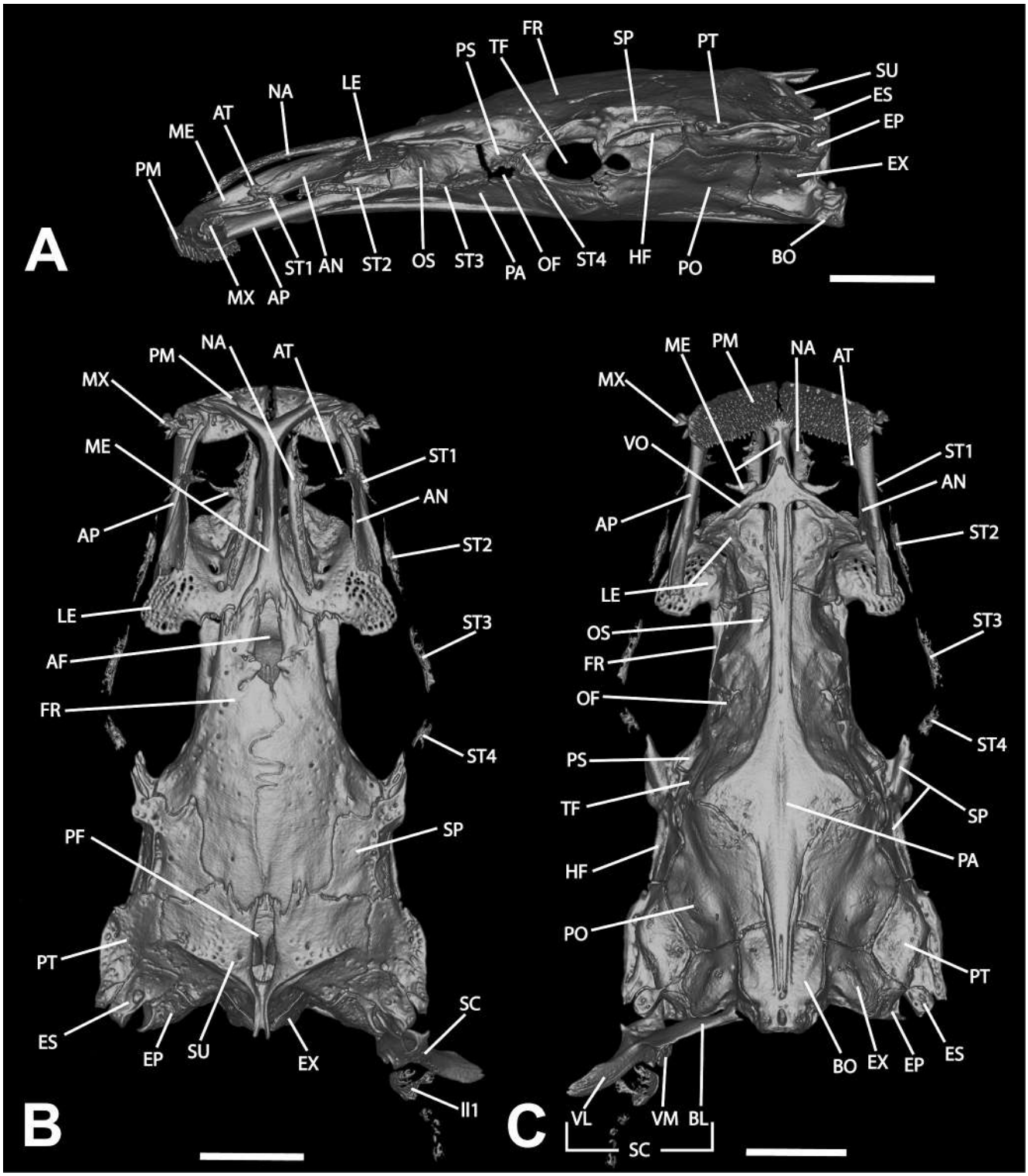

Figure 6. Neuroranium and associated structures of *Cetopsorhamdia clathrata,* MCP 36064, 50.8 mm SL, holotype (CT reconstructions). (A) left lateral view; (B) dorsal view; (C) ventral view. Cartilage not represented. Scale bars = 2 mm.

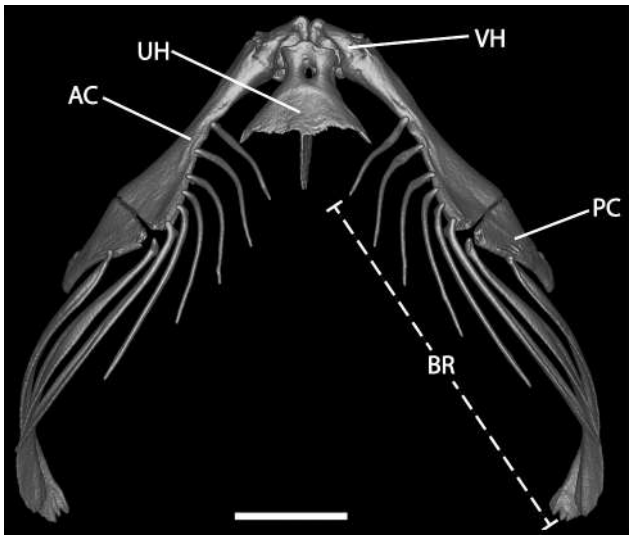

Figure 7. Hyoid arches of *Cetopsorhamdia clathrata,* MCP 36064, 50.8 mm SL, holotype (CT reconstruction). Ventral view. Cartilage not represented. Scale bar = 2 mm.

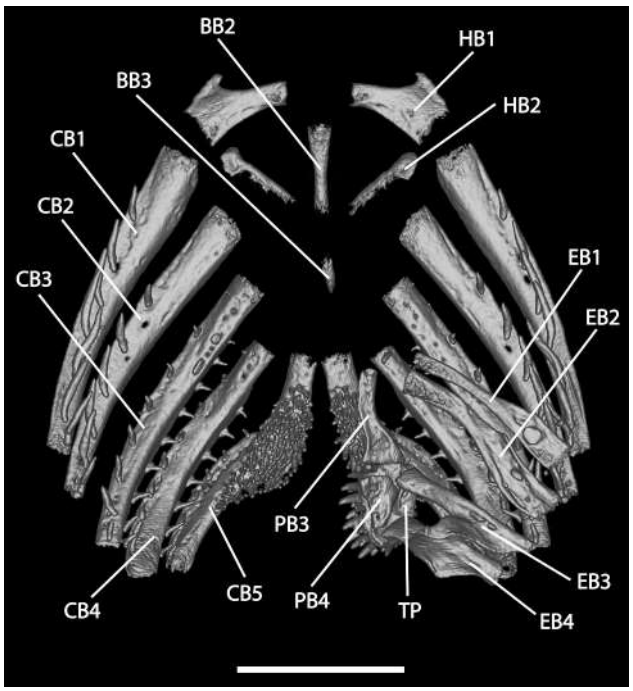

Figure 8. Branchial arches of *Cetopsorhamdia clathrata,* MCP 36064, 50.8 mm SL, holotype (CT reconstruction). Dorsal view. Dorsal elements of left arches not shown. Cartilage not represented. Scale bar = 2 mm.

into thick anterior fold. Origin of anal-fin base just anterior to vertical through origin of adipose fin. End of anal-fin base at or slightly posterior to vertical through middle of adipose-fin base. Anal fin with 10 (10), 11 (6*), or 12 (1) basal radials. Anteriormost anal-fin basal radial on space between hemal spines of vertebrae 22 and 23 (3), on space between hemal spines of vertebrae 23 and 24 (10), or on space between hemal spines of vertebrae 24 and 25 (4*). Posteriormost anal-fin basal radial on space between hemal spines of vertebrae 28 and 29 (9*), on space between hemal spines of vertebrae 29 and 30 (7), or on space between hemal spines of vertebrae 30 and 31 (1).

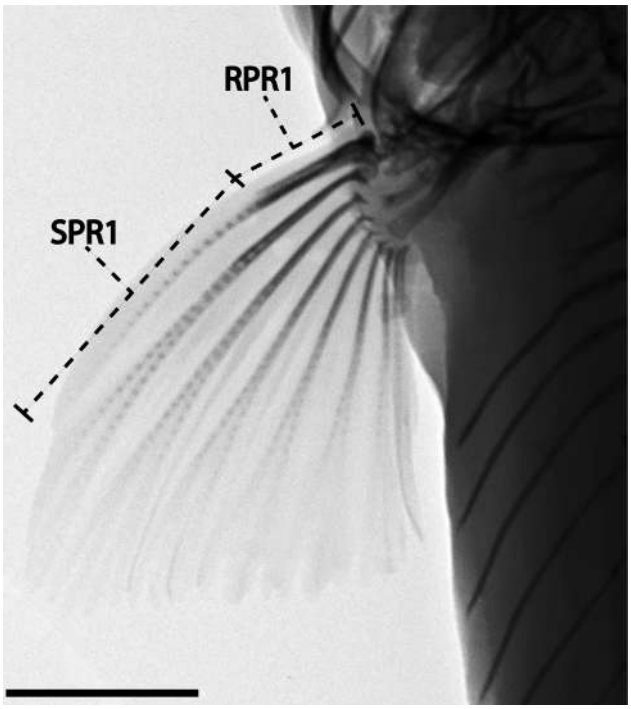

Figure 9. Left pectoral fin of *Cetopsorhamdia clathrata,* UFRO-I 10979, 53.9 mm SL, paratype (radiograph). Dorsal view. Scale bar = 3 mm.

Adipose fin moderately deep and short, highest approximately at midpoint (Figs. 1-3). Adipose fin merging gradually with back anteriorly, with imprecise origin. Distance from dorsal-fin base to adipose fin approximately twice length of dorsal-fin base. Origin of adipose fin slightly posterior to origin of anal fin, on vertical through insertion of last unbranched anal-fin ray (5), on vertical through insertion of first branched anal-fin ray (9), or second branched anal-fin ray (2*). Posterior limit of adipose fin well-defined, with distinct free, rounded lobe. Vertical through end of adipose-fin base at or slightly posterior to tip of posteriormost anal-fin ray. Origin of adipose fin on vertical through vertebral centrum 26 (5), on vertical through region between centra 26 and 27 (3), on vertical through vertebral centrum 27 (7), or on vertical through region between centra 27 and 28 (2*). End of adipose-fin base on vertical through vertebral centrum 34 (1), on vertical through region between centra 34 and 35 (4), on vertical through vertebral centrum 35 (9*), on vertical through region between centra 35 and 36 (2), or on vertical through centrum 36 (1).

Caudal fin forked, with ventral lobe longer than dorsal lobe (Figs. 1-3). Dorsal lobe with 7 (17*) branched rays; ventral lobe with 8 (16*) branched rays, rarely 7 (1). Total caudal fin-rays 39 (1), 40 (1), 41 (4), 42 (1), 43 (2), 44 (5*), 45 (1), 46 (1), or 47 (1), being 18 (1), 20 (6), 21 (4*), 22 (4), or 23 (2) rays in dorsal lobe, and 20 (1), 21 (6), 22 (4), 23 (5*), or 24 (1) rays in ventral lobe. Dorsal caudal plate (uroneural and hypurals 3, 4, and 5) with 8 (17*) rays, arranged as follows: 6 rays on hypural 3+4 and 2 rays on hypural 5 (16*), or 8 rays on hypural 3+4+5 (1). Ventral caudal plate (parhypural plus hypurals 1 and 2) with 8 (16*), rarely 9 (1) rays, arranged as follows: 1 ray on parhypural and 7 rays on hypural 1+2 (6), 2 rays on parhypural and 6 rays on hypural 1+2 (9*), 8 rays on parhypural + hypural

1+2 (1), or 2 rays on parhypural and 7 rays on hypural 1+2 (1).

Number of vertebrae 40 (6), 41 (10*) or 42 (1); first completely formed hemal spine on centrum 16 (6) or 17 (11*); and ribs 8/8 (10) or 9/9 (7*). Last four (4*), five (7), or six (6) precaudal vertebrae with discrete neural processes. Last precaudal vertebra (1), or last two (5), three (6), or four (5*) precaudal vertebrae with very discrete, almost imperceptible, neural processes.

Laterosensory system

Head laterosensory canals with simple (non-dendritic) tubes ending in single pores (Fig. 5). Supraorbital laterosensory canal continuous and connected to optic and infraorbital laterosensory canals posteriorly. Supraorbital laterosensory canal usually with 5 branches and pores: s1, s2, s3, s6 (epiphyseal branch), and s8 (parietal branch and pore). Contralateral epiphyseal branches (s6) fused to each other, bearing single symphyseal pore (s6+s6) (Fig. 5B). S4, s5, and s7 (postorbital) branches and pores absent. Supraorbital and infraorbital laterosensory canals anteriorly connected to each other through s2 and i2 branches (forming complex s2+i2 pore) (Fig. 5B). Otic laterosensory canal short, without pores, and continuous with posterior limits of supra- and infraorbital laterosensory canals, anteriorly, and with anterior limit of postotic laterosensory canal, posteriorly. Postotic (or temporal) laterosensory canal extends from posterior limit of otic laterosensory canals to anterior limit of lateral line, with 3 branches and pores (po1, po2, and po3) (Fig. 5A-B). Infraorbital laterosensory canal with 6 branches and pores, with s2 fused to i2 (see above). Preoperculomandibular laterosensory canal with 11 branches and pores (Fig. 5A-C); anteriormost preoperculomandibular laterosensory branch (pm1) independent from its symmetrical; posteriormost preoperculomandibular laterosensory branch (pm11) fused to po1 branch forming complex po1+pm11 branch and pore (Fig. 5A-B). Lateral line sensory canal continuous with postotic laterosensory canal anteriorly and not interrupted posteriorly (Fig. 5A-B). Lateral line sensory canal long, with posterior limit extending to vertical through anterior half of caudal plate in smaller specimens and to origin of caudal-fin rays in larger specimens (27.8 mm SL or larger). First lateral line pore ventral to level of adjacent pores of lateral line. One pair of short, anteriorly convergent, lines of neuromasts, with two neuromasts each, between anterior and posterior nostrils. One short neuromast line, with single neuromast, just posterior to each parietal branch (s8).

Pigmentation in alcohol and in life

Background body coloration withish pale or yellow. Body pigmented with brown melanophores dorsally and laterally, except for regions described below; ventral region mostly unpigmented except for few scattered melanophores (Figs. 1-4). Head mostly dark-brown dorsally and laterally. Cheeks (except for its anterior portion), ventral portion of opercle, and entire ventral surface of head unpigmented (Figs. 1-4). Anterior border of snout, anterior to anterior nares, with faint, unpigmented area (with milky hue) (Figs. 1, 4). Midportion of snout, between anterior and posterior nares, with faintly unpigmented area, more evident in juveniles (Fig. 4). Region between corner of mouth and cheek unpigmented, with milky tonality (Figs. 1-3). Maxillary barbel with brown melanophores dorsally, mental barbels yellow (Figs. 1-4). Dark stripe along region from base of maxillary barbel to region right posterior to eye (Figs. 1-4). Elongate, roughly rectangular white or yellow band ventral to eye (Figs. 1-3). Posterior portion of head, from posterodorsal region of opercle to posterior limit of branchiostegal membrane, with very dark mark extending ventrally along branchiostegal membrane (Figs. 1-3), reaching level of pectoral-fin base in larger specimens (50.8 mm SL or larger). Area immediately dorsal to terminus of opercular cleft with unpigmented, milky, oval spot (Figs. 1-4). Posterior border of supraoccipital of 22.1 mm SL or larger specimens with unpigmented (of milky hue), wide-angled "V" streak, extending laterally to about level of eyes (Figs. 1, 4); such unpigmented nuchal mark missing in 20.3 mm SL or smaller specimens and almost unperceivable in 21.5 mm SL specimen (Fig. 4A). Larger individuals with two longitudinal, wide rows (one laterodorsal and one lateroventral) of 10-12 brown, quadrangular marks on flanks, interspersed by 9-11 vertical unpigmented lines or bars and one unpigmented stripe along its midlateral region, giving criss-cross appearance (Figs. 1-2, 3D-E, 4D-E). Marks on both sides not perfectly symmetrical, meeting each other in midline dorsally (Figs. 1, 4). Quadrangular marks arranged as follows: three or four anterior to dorsal fin, one approximately below dorsal-fin base, two approximately between dorsal- and adipose-fin bases, three approximately below adipose-fin base, and one or two along caudal peduncle (Figs. 1-2, 3D-E, 4D-E). Trunk of small specimens (21.5 mm SL or smaller specimen) homogeneously brown colored, lacking unpigmented vertical bars (Figs. 3A, 4A), which become progressively more conspicuous in somewhat larger specimens (22.1 mm SL or larger specimen) (Figs. 3B-E, 4B-E). Larger specimens (50.8 mm SL or larger) with anteriormost quadrangular mark divided into two sections by extra vertical, unpigmented bar or lines (Figs. 1-2); also, quadrangular marks on caudal peduncle trend to subdivide in larger specimens, over ontogeny. Dark laterodorsal and lateroventral regions of trunk continuous or separated by narrow, short, unpigmented midlateral streak to adipose-fin origin, in small specimens (21.5 mm SL or smaller) (Fig. 3A); midlateral unpigmented stripe progressively wider and longer, reaching caudal region, over ontogeny (Figs. 3B-E). Anterior border of pseudotympanum wall, above pectoral-fin base, with dark brown, vertical mark (extending ventrally to level of pectoral-fin base); mark progressively darker and more defined in larger specimens (Fig. 3). Lateral wall of pseudotympanum densely pigmented, except for its central region in smaller specimens (21.5 mm SL or smaller), becoming progressive-

ly less pigmented in 22.1 mm SL and larger specimens (Fig. 3). Several small (one to half size of eye), rounded, unpigmented areas dispersed all over dorsal surface of trunk, fewer ventral to lateral line, in 27.8 mm SL and larger specimens (Figs. 1, 3-4); 22.4 mm SL and smaller specimens devoid of such unpigmented spots (Figs. 3-4). Middorsal region of trunk with three unpigmented, milky blotches (Figs. 1-4): one predorsal, rounded, and medium-sized mark (equal or slightly larger than eye size) just anterior to dorsal fin and around base of its first ray; one very discreet postdorsal mark just posterior to dorsal-fin base; and one inconspicuous preadipose mark; post-adipose and pre-caudal marks absent. First dorsal-fin ray light but proximal third of remaining rays and base of adipose fin brown. Base of dorsal fin darkly pigmented. Base of pectoral fin dark dorsally. Fin rays brown, fading distally, in larger individuals, with dark pigmentation restricted to their proximal thirds or almost absent, with few dark chromatophores, in smaller specimens; interradial membranes mostly hyaline. Muscular base of pectoral, dorsal, and anal fins dark brown. Caudal peduncle with dark-brown, blackened, vertical mark, extending posteriorly to limit of skin on base of caudal-fin rays and most evident at base of principal rays (Figs. 1-3); peduncular mark more conspicuous in smaller individuals (Fig. 3). Base of caudal fin lobes with large, oval or rounded unpigmented spots, with milky aspect (Figs. 1-3).

Etymology

The specific epithet is from the Latim "clathratus", meaning latticed, screened, or reticulate, in allusion to the network color pattern of its flanks. An adjective.

Geographic distribution and habitat

The species is known from the headwaters of the Rio Ji-Paraná (or Machado) and Rio Roosevelt basins, both belonging to the upper Madeira system, draining the northern slope of the Chapada dos Parecis, near Vilhena, Rondônia State, Brazil (Fig. 10). The body proportions of these two sets of geographically separated samples, both here assigned to *C. clathrata,* intermingle (Table 1), as well as the other morphological characteristics, such as color and meristic data, so that there is no reason to treat them as distinct species. The Igarapé Piracolina, where the holotype (MCP 36064) and several paratypes (ANSP 188921, MCP 36063, MNRJ 35877) of *C. clathrata* were caught, is a small river with sandy bottom, interspersed with sections of gravel and pebbles, and rich aquatic vegetation, with clear waters and moderate to strong current (Fig. 11). Similar habitat and environmental conditions have been reported by Ohara & Lima (2015) and Ohara & Marinho (2016) for *C. clathrata* (identified as *Cetopsorhamdia* sp. 3; UFRO-I 22918) in a

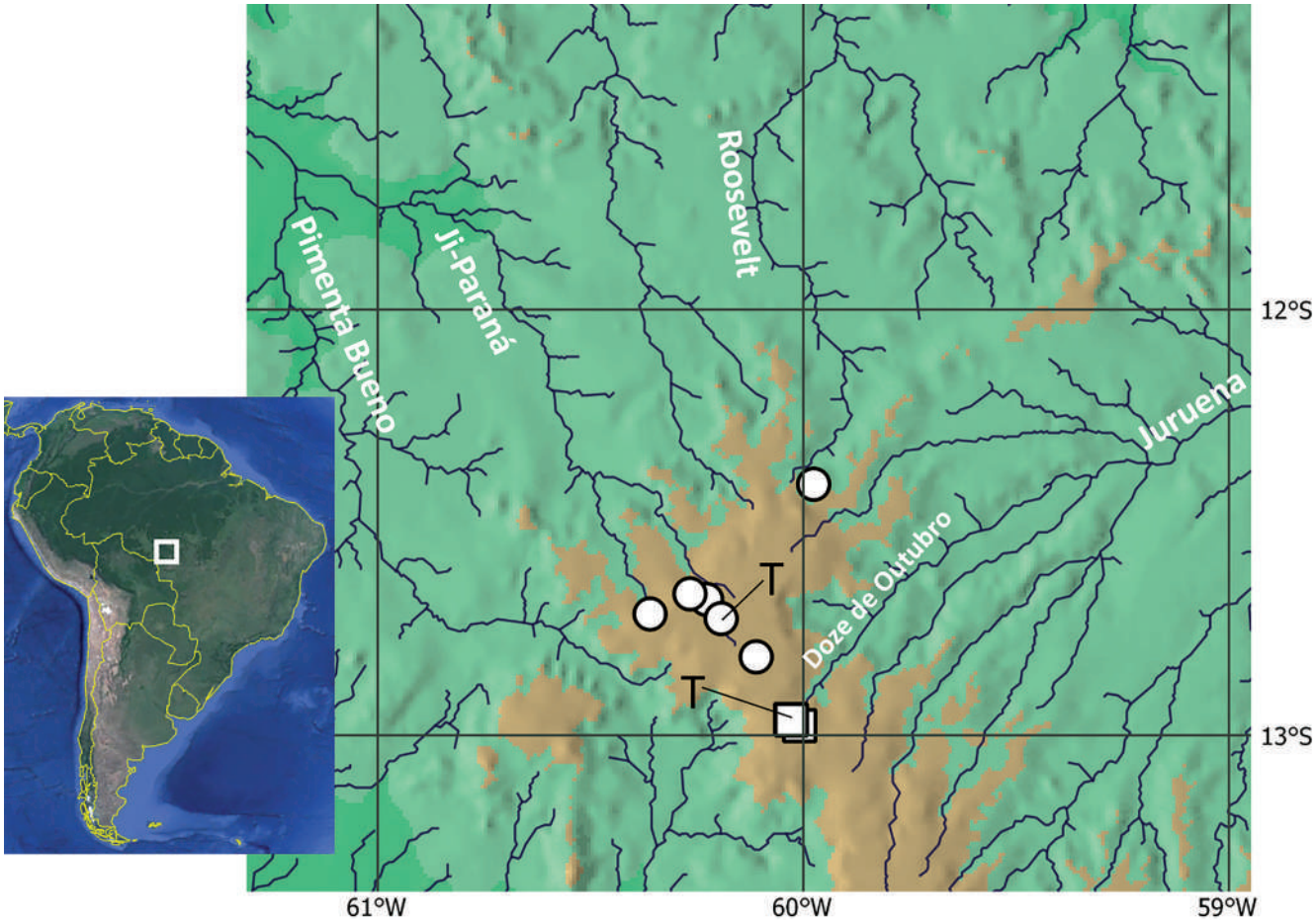

Figure 10. Drainage map of central western Brazil showing the localities of *Cetopsorhamdia clathrata* (white circle) and *C. spilopleura* (white squares). "T" indicates type-locality, each symbol may represent more than one lot or locality.

Figure 11. Igarapé Piracolina, Rio Madeira basin, at Chapada dos Parecis (12°24′36.6″S, 59°58′31.5″W), Brazil, Rondônia State, Vilhena, near to type locality of *Cetopsorhamdia clathrata.* Photograph by W.M. Ohara.

tributary of the Igarapé Piracolina, near highway BR-364 (12°48′56.5″S, 60°06′37.6″W), where it was collected together with *Ancistrus verecundus* Fisch-Muller, Cardoso, Silva & Bertaco, 2005, *Bryconops piracolina* Wingert & Malabarba, 2011, *Hyphessobrycon lucenorum* Ohara & Lima, 2015, *Hyphessobrycon* aff. *melonostichos* Carvalho & Bertaco, 2006, *Hyphessobrycon* sp., *Moenkhausia parecis* Ohara & Marinho, 2016, *Corydoras* sp. (= *C. hephaestus* Ohara, Tencatt & Britto, 2016) and *Pyrrhulina* sp. That tributary was categorized as a "terra-firme igarapé" (= highland creek), with its sampled stretch located at 585 m above sea level, described as being small, 1.5-2.5 m wide and 0.3-1.5 m deep, with clear and swift waters, and bottom composed of sand and dead leaves, with little preserved riparian vegetation and surrounded by large plantation fields (mostly soy and corn) (Ohara & Lima, 2015: fig. 4; Ohara & Marinho, 2016: fig. 4).

Conservation assessment

The extinction risk of *Cetopsorhamdia clathrata* is preliminarily assessed as high. The species is known from six localities in headwater streams of the upper Rio Ji-Paraná and one in a headwater creek of the Rio Roosevelt, both part of the Madeira Drainage, with an Extension of Occurrence (EOO) calculated by the convex polygon of 696 square kilometers. The area is severely converted and heavily impacted by deforestation, suffering effects from erosion, silting, and increased turbidity, with extensive agriculture of cotton, soybean, and other commodities that heavily rely on herbicides, pesticides, and fertilizers. There are no estimates of population size or population decline, and no rational can be used to determine the number of locations. For these reasons, *C. clathrata* is tentatively assessed as Near Threatened (NT) approaching Endangered by the criterion B1(biii), according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Sub-Committee, 2019).

***Cetopsorhamdia spilopleura* sp. nov.**
http://zoobank.org/AE5243DF-EEE7-4ED1-A0F5-4B7C10671F11
(Figs. 12-15, Table 2)

Cetopsorhamdia new species 2. – Bockmann & Reis, 2011 [distribution – upper Rio Tapajós drainage, in State of Mato Grosso: unnumb. p.; brief characterization based on body coloration: unnumb. p.; phylogenetic relationships: unnumb. p.].

Cetopsorhamdia sp. – Bertaco & Carvalho, 2005a [collected in Brazil, Mato Grosso, Comodoro, rio

Mutum on road BR-364 to cidade de Vilhena, tributary of rio Juruena, upper rio Tapajós drainage, 13°05′08″S, 59°53′32″W: 442]; Bertaco & Carvalho, 2005b [collected in the headwaters of the rio Tapajós drainage, in Chapada dos Parecis, Mato Grosso, Brazil: 145].

Cetopsorhamdia sp.3. – Ohara & Loeb, 2016 [Upper Rio Juruena on Chapada dos Parecis, Mato Grosso, Brazil, in sampling station 1 (igarapé Mutum located at BR-364, 13°05′08″S, 59°53′32″W – MZUSP 115478) and sampling station 4 (tributary of Rio Doze de Outubro located near BR-364, 12°57′50″S, 60°01′40″W – MZUSP 115498, part of specimens of this lot currently in MZUSP 121503 and LIRP 13992): 5, table 1].

Cetopsorhamdia sp. 3. – Ohara & Loeb, 2016 [photograph of live specimen in left lateral view: 5, fig. 4].

Table 2. Morphometric features of *Cetopsorhamdia spilopleura,* taken from the holotype MZUSP 121503, and the paratypes in LIRP 13992, MCP 35993, MCP 41057, MZUSP 115498, and MZUSP 118307. Morphometric data 1-34 are expressed as percent of Standard Length and 35-45 as percent of Head Length. Abbreviations: H = holotype; Min = minimum value; Max = maximum value; N = number of specimens; SD = standard deviation.

	H	Range		Mean	SD	N
		Min	Max			
Total length (mm)	58.2	30.1	71.9	—	—	8
Standard length (mm)	47.9	24.9	58.9	—	—	8
1. Predorsal length	46.3	42.7	46.3	44.8	1.4	8
2. Preanal length	69.4	68.1	71.2	69.5	1.1	8
3. Prepelvic length	46.0	46.0	47.5	46.6	0.6	8
4. Preadipose length	73.8	70.6	73.9	72.1	1.3	8
5. Caudal-peduncle length	19.6	18.7	19.6	19.2	0.3	8
6. Caudal-peduncle depth	10.3	9.2	10.9	10.0	0.7	8
7. Adipose-fin length	15.1	13.9	17.5	16.0	1.3	8
8. Adipose-fin depth	4.3	4.1	5.7	4.6	0.5	8
9. Dorsal fin to adipose fin	19.1	15.6	19.5	17.7	1.5	8
10. Anal-fin base	14.6	11.1	14.6	13.2	1.0	8
11. Snout-anus distance	52.7	52.6	54.9	53.2	1.0	8
12. Snout-urogenital papilla distance	54.7	54.1	56.2	55.1	0.7	8
13. Anus-urogenital papilla distance	1.5	0.9	1.8	1.5	0.3	8
14. Length of first dorsal-fin ray (unbranched)	12.9	12.8	15.5	13.5	1.0	8
15. Length of rigid part of first dorsal-fin ray	5.9	5.3	6.4	5.8	0.4	8
16. Length of second dorsal-fin ray (first branched)	15.4	14.2	17.4	15.8	1.1	8
17. Length of third dorsal-fin ray (second branched)	14.2	14.2	19.6	16.5	1.8	7
18. Dorsal-fin base	10.2	9.5	11.2	10.2	0.6	8
19. Length of first pectoral-fin ray (unbranched)	12.0	11.3	14.2	12.4	0.9	8
20. Length of rigid part of first pectoral-fin ray	4.2	4.1	5.1	4.4	0.3	8
21. Length of second pectoral-fin ray (first branched)	14.7	13.8	15.1	14.5	0.4	8
22. Length of third pectoral-fin ray (second branched)	14.6	13.9	15.2	14.5	0.4	8
23. Length of first pelvic-fin ray (unbranched)	9.8	9.8	11.9	10.5	0.7	8
24. Length of second pelvic-fin ray (first branched)	13.5	12.4	13.9	13.2	0.6	8
25. Length of third pelvic-fin ray (second branched)	13.4	12.7	14.7	13.6	0.8	7
26. Length of dorsal caudal-fin lobe	20.0	20.0	21.4	20.9	0.5	8
27. Length of ventral caudal-fin lobe	20.9	20.2	22.7	21.7	0.9	7
28. Body depth	17.5	14.9	17.6	16.1	1.0	8
29. Body width	13.0	10.9	13.5	12.3	0.9	8
30. Cleithral width	17.1	15.4	17.2	16.8	0.7	8
31. Maxillary-barbel length	20.2	18.0	21.1	19.5	1.0	8
32. Outer mental-barbel length	14.9	13.6	17.4	15.0	1.1	8
33. Inner mental-barbel length	12.4	8.6	12.9	11.5	1.4	8
34. Head length	25.5	24.9	27.2	26.1	0.9	8
35. Head depth	52.4	46.7	56.2	51.7	3.3	8
36. Head width	72.4	67.9	74.3	71.6	2.2	8
37. Fleshy interorbital	25.5	24.8	29.6	27.0	1.6	8
38. Bony interorbital	17.1	17.1	21.6	19.0	1.6	8
39. Eye diameter	11.1	9.1	11.8	11.1	0.9	8
40. Snout length	40.9	38.1	41.0	39.8	1.3	8
41. Distance between snout tip and posterior nare	28.3	26.8	30.9	29.1	1.3	8
42. Intranarial length	15.0	13.7	16.0	14.8	0.8	8
43. Anterior internarial width	12.5	12.5	14.0	13.3	0.6	8
44. Posterior internarial width	15.0	15.0	17.2	16.2	0.9	8
45. Mouth gape	40.5	38.1	42.9	39.9	1.5	8

Holotype: MZUSP 121503, 47.9 mm SL (ms and xr) in ethyl alcohol, Brazil, State of Mato Grosso, Comodoro, unnamed stream affluent of Rio Doze de Outubro, Rio Tapajós drainage, about 25 km from Vilhena (Rondônia State), on highway BR-364, at Chapada dos Parecis, 12°57′50″S, 60°01′40″W, coll. W. Ohara, 3 Sep 2014.

Paratypes: All specimens from Brazil, Mato Grosso State, Comodoro: LIRP 13992, 1 ex. in ethyl alcohol (50.9 mm SL, ms and xr), 1 ex. c&s (40.2 mm SL, ms and xr), collected with holotype; MZUSP 115498, 2 ex. (34.8-41.8 mm SL, ms and xr), collected with holotype; MCP 35993, 1 ex. in ethyl alcohol (24.9 mm SL, ms and xr), 1 ex. c&s (22.4 mm SL), Rio Doze de Outubro, between Comodoro and Vilhena, on highway BR-364, Rio Tapajós drainage, at Chapada dos Parecis, 12°58′39″S, 60°00′30″W, coll. R.E. Reis, P.A. Buckup, A.R. Cardoso, E.H.L. Pereira, 14 Jul 2004; MCP 41057, 1 ex. in ethyl alcohol (30.5 mm SL, ms and xr), collected with MCP 35993; MZUSP 118307, 1 ex. in ethyl alcohol (58.9 mm SL, ms and xr), unnamed stream affluent of Rio Doze de Outubro, Rio Tapajós drainage, at Luar do Sertão farm, between Comodoro and Vilhena, at Chapada dos Parecis, 12°57′46.60″S, 60°01′45.16″W, coll. F.C.P. Dagosta, W.M. Ohara, V. Giovanetti, 13 Nov 2014.

Diagnosis

Cetopsorhamdia spilopleura differs from its congeners, and all other heptapterids, by having a unique color pattern of trunk constituted by 18-22 irregular, vertical brown bars, sometimes resembling inverted "v", "y" or "x". In addition, it can be separated from other species of *Cetopsorhamdia* by having: 7 branched pectoral-fin rays (*vs.* 8 in *C. clathrata;* 8-9 in *C. boquillae;* 8-10, usually 9, in *C. iheringi, C. nasus,* and *C. picklei*); and lateral line fragmented as isolated patches posterior to vertical through the level of adipose-fin origin, reaching to anterior portion of caudal plate (*vs.* long and complete lateral line, extending to slightly beyond the caudal-fin base in all other species of *Cetopsorhamdia*). It is further distinguished from other *Cetopsorhamdia,* except *C. clathrata,* by having: very short maxillary barbel, not reaching posterior margin of opercle (*vs.* reaching the first third of pectoral fin in *C. insidosa* and *C. nasus;* reaching the second third of pectoral fin in *C. iheringi* and *C. picklei,* and surpassing the posterior margin of pectoral fin in *C. boquillae*); dorsal fin situated more posteriorly, with first basal radial normally

inserted on bifid dorsal process of vertebra 12 (*vs.* 8-9 in *C. boquillae, C. iheringi, C. insidiosa, C. nasus,* and *C. picklei*); a more posteriorly located anal fin, with first basal radial articulated between hemal spines of vertebrae 22-24 (*vs.* 21-22 in *C. boquillae* and *C. insidiosa,* 21-23 in *C. iheringi* and *C. nasus;* and 20-23, usually 20-22, in *C. picklei*); and whitish ovoid areas on both caudal-fin lobes (*vs.* caudal fin lobes homogeneously dark in other species). *Cetopsorhamdia spilopleura* differs further from *C. clathrata* by possessing: fins broad, with convex posterior profiles (*vs.* fins narrow, with marked concave posterior borders); the midlateral region of trunk darkly pigmented (*vs.* midlateral region devoid of pigmentation, forming a white stripe along the lateral line); and the laterodorsal and lateroventral regions of trunk devoid of dark pigmentation, forming unpigmented streaks (*vs.* laterodorsal and lateroventral regions of trunk with continuous dark pigmentation, except for the intervals between the squares).

Description

Morphometrics of holotype and paratypes in Table 2. See Figs. 12-14 for general body shape. Body relatively elongated, its cross-section round to vertically oval predorsally, becoming gradually more compressed caudally. Anterior dorsal profile of body gently convex, without noticeable hump at end of head. Dorsal profile of head gently convex, almost straight, continuous with dorsal profile of trunk. Dorsal profile of trunk posterior to dorsal-fin base approximately straight with slight elevation at origin of adipose fin. Ventral profile of head slightly convex and continuous with abdominal region, also slightly convex. Ventral trunk contour nearly straight from end of pelvic-fin base to caudal-fin base. Posterior body depth gradually decreasing caudally. Axillary pore minute, just dorsal to pectoral-fin base, and ventral to first pore of lateral line. Urogenital and anal openings adjacent to each other; anal opening approximately on vertical through middle of pelvic fin.

Head longer than broad, depressed, and subtriangular to trapezoidal in dorsal view (Figs. 12-15). Anterior and posterior cranial fontanels short, separated from each other by broad bridge, about two times longer than each fontanel (Fig. 16). Eye small, laterodorsally placed, approximately equidistant from snout tip and supraoccipital posterior end, and without free orbital rim except for shallow ventral invagination. Deep longitudinal facial ridge marking dorsal limit of *adductor mandibulae* muscle, extending from dorsal base of maxillary barbel to or just anterior of eye. Cheek distinctly swollen ventral to eye, forming groove to maxillary barbel. Anterior intranarial width and posterior intranarial width approximately equal. Anterior and posterior nares far apart from each other; with separation between them slightly greater than distance between each pair of nares. Anterior naris surrounded by fleshy tubular flap of integument, with anterior border slightly raised. Base of anterior nostril shallow, not sunk in conspicuous trench. Posterior naris wide, elliptical, with transversal axis longest. Posterior naris surrounded by low fleshy flap anteriorly, mesially

Figure 12. *Cetopsorhamdia spilopleura,* MZUSP 121503, 47.9 mm SL, holotype; Brazil, Mato Grosso State, Comodoro: unnamed stream affluent of Rio Doze de Outubro, Rio Tapajós basin.

Figure 13. *Cetopsorhamdia spilopleura,* MZUSP 121503, 47.9 mm SL, holotype (right after collection); Brazil, Mato Grosso State, Comodoro: unnamed stream affluent of Rio Doze de Outubro, Rio Tapajós basin. Image was flipped for comparative purposes. Photograph by W.M. Ohara.

Figure 14. *Cetopsorhamdia spilopleura,* juvenile, MCP 41057, 30.5 mm SL, paratype; Brazil, Mato Grosso State, Comodoro: Rio Doze de Outubro, Rio Tapajós basin.

and laterally; posterior border devoid of flap. Mouth distinctly subinferior; gape gently convex anteriorly, slightly downturned at corners. Skin of lips with fleshy rictal fold at corner of gape. Rictal fold ventrally subtended by submandibular groove that extends anteriorly to point approximately adjacent to third or fourth preoperculomandibular pores (pm3 and pm4, respectively).

Premaxilla with 5-7 and dentary with 3-4 irregular rows of small villiform teeth (Fig. 16C). Anteriormost tooth row of premaxilla with 14-16 teeth; anteriormost tooth row of dentary with 26-29 teeth. Palate and vomer edentulous.

Gular fold distinct, fleshy, and broadly V-shaped. Branchiostegal membranes well-developed, free, united to isthmus only at medial apex, and not connected to each other anteriorly (Fig. 15C). Branchiostegal rays 8 (9*), posteriormost two wider and more laminar than anterior ones (Fig. 17). Ceratobranchials 1-2, and 5 with rakers along lateral margin only; ceratobranchials 3-4 with rakers along both lateral and mesial margins (Fig. 18). Branchial rakers short and straight, 6/6 (2*), 6/7 (2), 7/7 (1), 7/8 (1), or 8/7 (2) on first ceratobranchial (including one on angle formed with epibranchial), and 0/0 (8*) on first epibranchial.

Barbels relatively short and depressed, and progressively tapering distally (Figs. 12-15). Tip of maxillary barbel almost reaching middle of opercle, usually to or short of posterior margin of bone, when adpressed against body. Tips of outer and inner mental barbels extending to or slightly surpassing outer border of branchiostegal membrane. Outer mental barbel longer than inner barbel. Inner and outer mental barbels inserted at approximately same line or origin of outer mental barbel slightly anterior to origin of inner mental barbel.

Dorsal fin approximately triangular in lateral profile, not reaching to adipose fin when adpressed (Figs. 12-14).

Dorsal fin with i,6 (9*) rays. First dorsal-fin ray (spinelet) absent. Second dorsal-fin ray unbranched, with basal third stiffened and distal two thirds flexible and segmented. Second dorsal-fin ray slightly shorter than third and fourth rays (first and second branched rays, respectively). Origin of dorsal fin at or slightly anterior to vertical through pelvic-fin origin. Dorsal fin with 7 (9*) basal radials. Anteriormost dorsal-fin basal radial on neural spines of vertebrae 11 (1) or 12 (8*). Posteriormost dorsal-fin basal radial on space between neural spines of vertebrae 14 and 15 (1) or between neural spines of vertebrae 15 and 16 (8*).

Pectoral fin with distal margin slightly convex, i,7 (8*) or i,8 (1) rays. First pectoral-fin ray with basal third rigid and unsegmented and distal two thirds flexible and segmented (Fig. 19). First pectoral-fin ray slightly shorter than second (first branched) and third (second branched) rays, whose tips project slightly beyond tip of first ray. Pectoral fin lying parallel to main body axis when expanded and slightly directed upwards when adpressed to body.

Pelvic fin wide, with distal border rounded (Figs. 12-14), i,5 (17*) rays. Origin of pelvic-fin base at or slightly posterior to vertical through dorsal-fin origin, on vertical through origin of first (unbranched) dorsal-fin ray (1), on vertical through space between origins of first (unbranched) and second (first branched) dorsal-fin rays (2*), on vertical through origin of second (first branched) dorsal-fin ray (4), or on vertical through space between origins of second (first branched) and third (second branched) dorsal-fin rays (2). Inner margins of pelvic-fin bases apart from each other. Tip of adpressed pelvic fin falling short of vertical through anal-fin

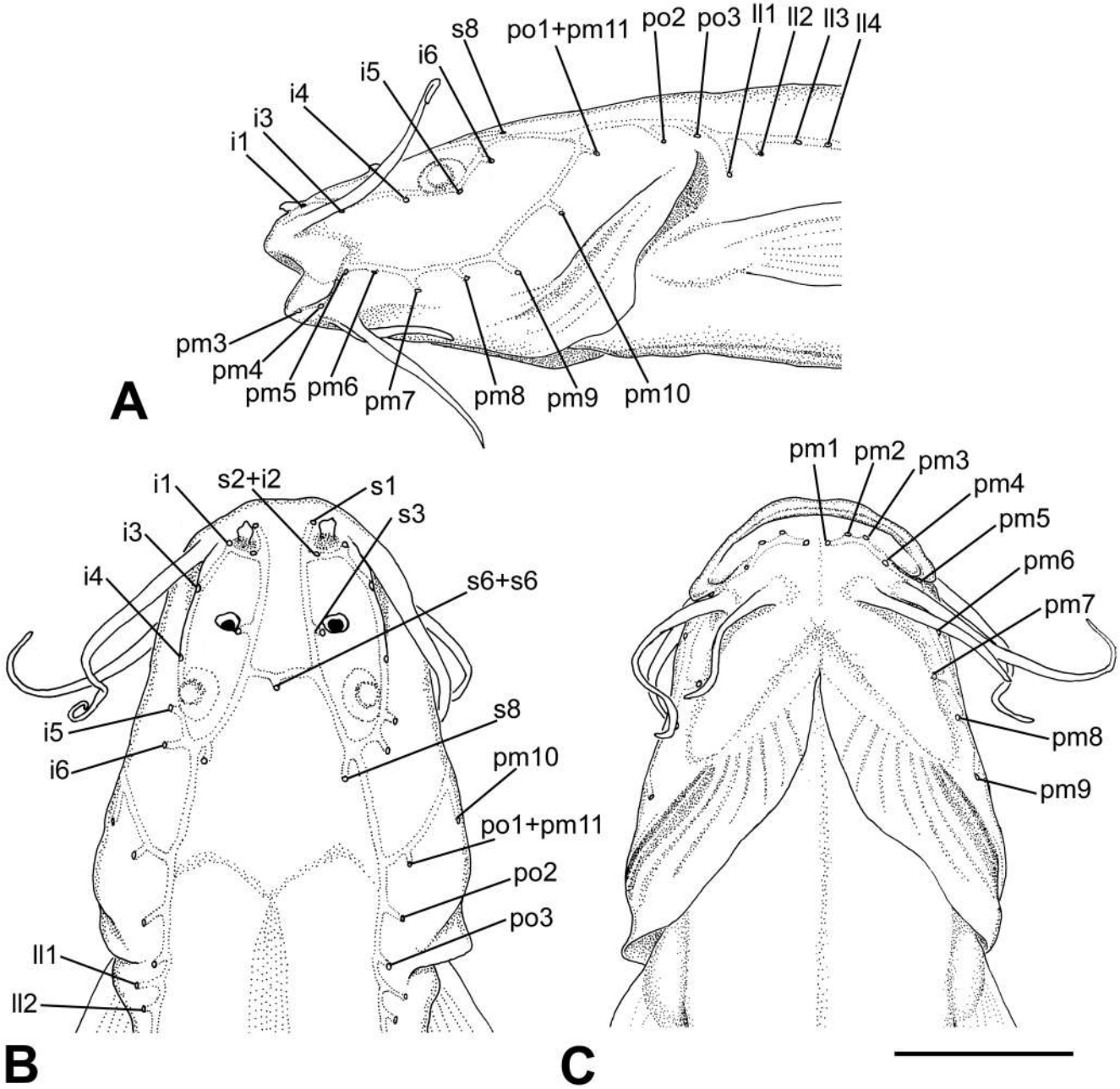

Figure 15. Anterior portion of the body of *Cetopsorhamdia spilopleura,* MCP 41057, 30.5 mm SL, paratype, showing laterosensory canal system. (A) letf lateral view; (B) dorsal view; (C) ventral view. Scale bar = 3 mm.

origin. Lateralmost ray unbranched, completely flexible, segmented, and with tip distinctly falling short of tips of second and third rays (first and second branched rays, respectively). Origin of pelvic fin on vertical through vertebral centrum 14 (3*) or on vertical through region between centra 14 and 15 (6).

Anal-fin deeper than adipose fin, with short base and posterior border slightly convex (Figs. 12-14), with 11 (1), 12 (6*), or 13 (2) total rays, including 7 (4) or 8 (5*) branched rays. Anal-fin rays with following branching pattern: iv, 7 (1), v, 7 (3), iv, 8 (3*), or v, 8 (2). Two or three anteriormost anal-fin rays vestigial, unsegmented, embedded into thick anterior fold. Origin of anal-fin base just anterior to vertical through adipose-fin origin. Anal-fin base terminus at or slightly posterior to vertical through middle of adipose-fin base. Anal-fin with 9 (4), 10 (3), or 11 (2*) basal radials. Anteriormost anal-fin basal radial on space between hemal spines of verte-

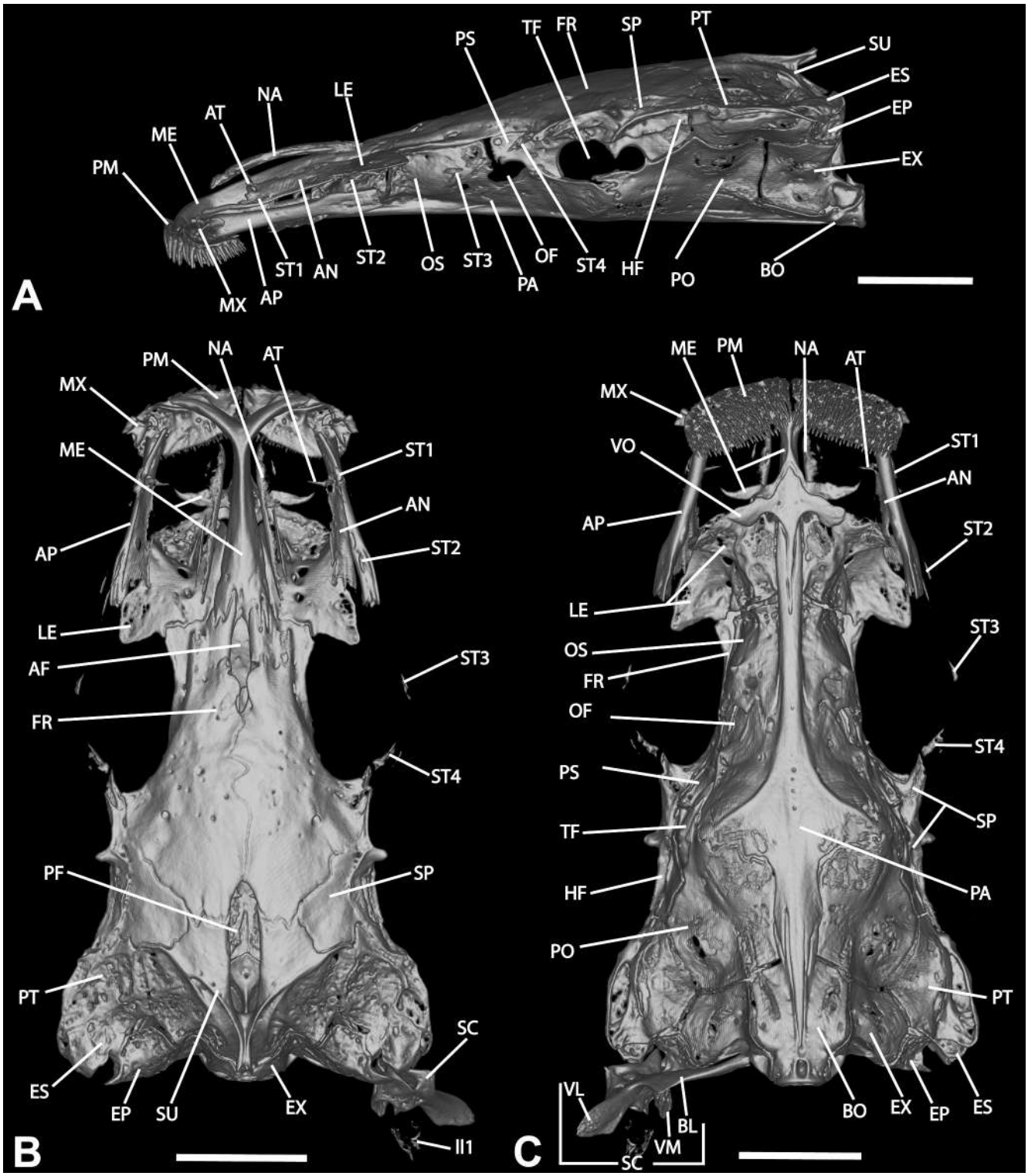

Figure 16. Neuroranium and associated structures of *Cetopsorhamdia spilopleura,* MZUSP 121503, 47.9 mm SL, holotype (CT reconstructions). (A) letf lateral view; (B) dorsal view; (C) ventral view. Cartilage not represented. Scale bars = 2 mm.

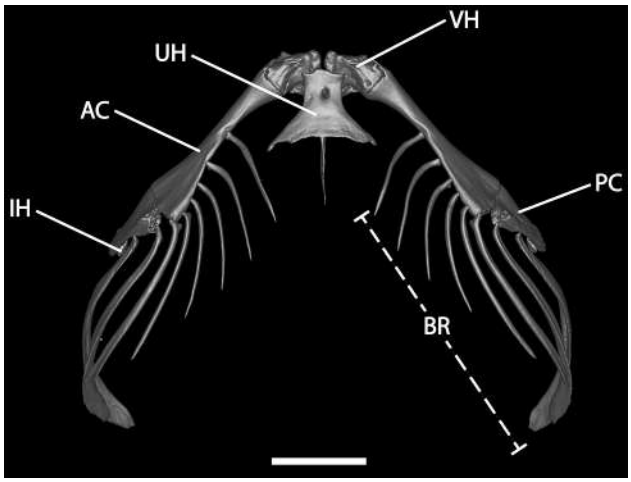

Figure 17. Hyoid arches of *Cetopsorhamdia spilopleura,* MZUSP 121503, 47.9 mm SL, holotype (CT reconstruction). Ventral view. Cartilage not represented. Scale bar = 2 mm.

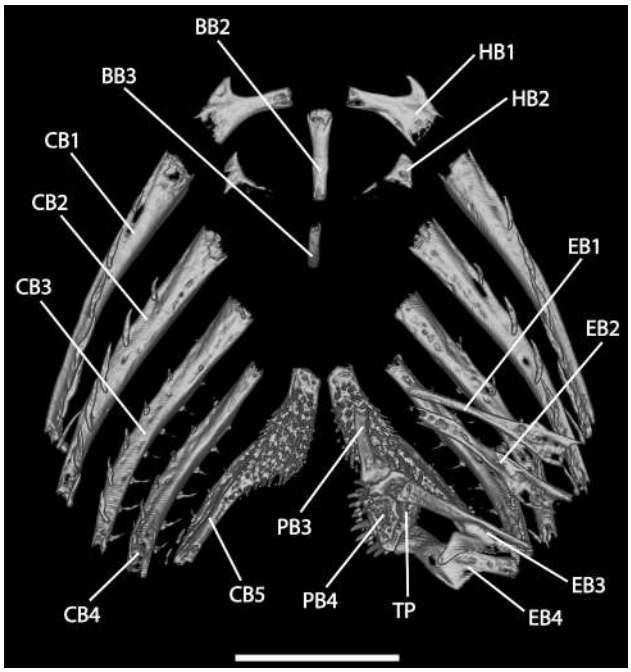

Figure 18. Branchial arches of *Cetopsorhamdia spilopleura,* MZUSP 121503, 47.9 mm SL, holotype (CT reconstruction). Dorsal view. Dorsal elements of left arches not shown. Cartilage not represented. Scale bar = 2 mm.

brae 22 and 23 (5*) or on space between hemal spines of vertebrae 23 and 24 (4). Posteriormost anal-fin basal radial on space between hemal spines of vertebrae 27 and 28 (2*) or on space between hemal spines of vertebrae 28 and 29 (7).

Adipose fin deep and short, with deepest point on second third of fin (Figs. 12-14). Distance from dorsal-fin base to adipose fin approximately twice length of dorsal-fin base. Origin of adipose fin slightly posterior to vertical through anal-fin origin, on vertical through insertion of first branched anal-fin ray (8), or second branched anal-fin ray (1*). Posterior limit of adipose fin well-defined, with free, conspicuous rounded lobe. Vertical through terminus of adipose-fin base slightly anterior to tip of posteriormost anal-fin ray. Origin of

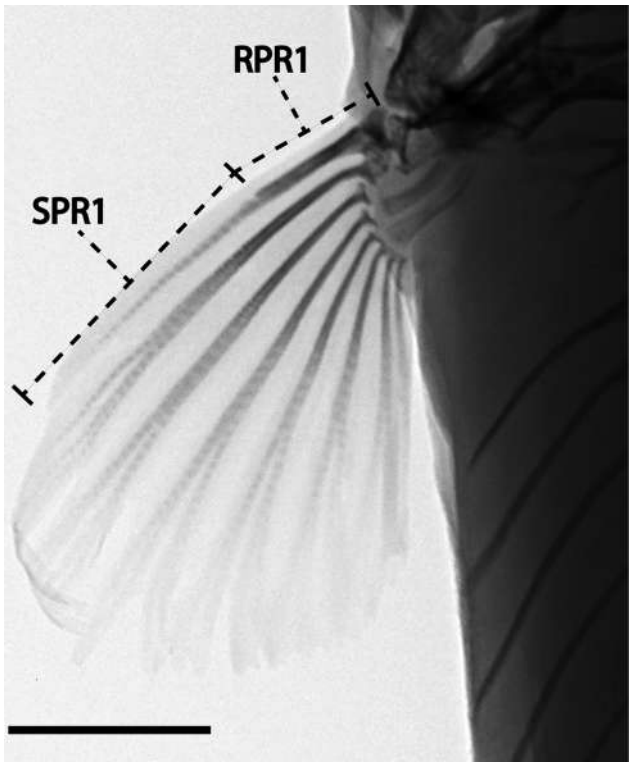

Figure 19. Left pectoral fin of *Cetopsorhamdia spilopleura,* MZUSP 118307, 58.9 mm SL, paratype (radiograph). Dorsal view. Scale bar = 3 mm.

adipose fin on vertical through vertebral centrum 25 (1), on vertical through region between centra 25 and 26 (1), on vertical through vertebral centrum 26 (4*), on vertical through region between centra 26 and 27 (2), or on vertical through vertebral centrum 27 (1). End of adipose-fin base on vertical through region between vertebral centra 33 and 34 (1), on vertical through vertebral centrum 34 (3*), on vertical through region between centra 34 and 35 (1), or on vertical through vertebral centrum 35 (4).

Caudal fin forked, with ventral lobe equal or slightly longer than dorsal lobe (Figs. 12-14). Dorsal lobe with 7 (9*) branched rays; ventral lobe with 8 (8*) branched rays. Total caudal fin-rays 39 (1), 41 (4*), 44 (1), or 45 (3), being with 19 (1), 20 (4*), or 22 (4) rays in dorsal lobe, and 20 (1), 21 (3), 22 (2*), or 23 (3) rays in ventral lobe. Dorsal caudal plate (uroneural and hypurals 3, 4, and 5) with 8 (9*) rays, arranged as follows: 5 rays on hypural 3+4 and 3 rays on hypural 5 (2*) or 6 rays on hypural 3+4 and 2 rays on hypural 5 (7). Ventral caudal plate (parhypural plus hypurals 1 and 2) with 9 (7*), less commonly 8 (2) rays, arranged as follows: 3 rays on parhypural and 6 rays on hypural 1+2 (5*), 2 rays on parhypural and 7 rays on hypural 1+2 (2), or 2 rays on parhypural and 6 rays on hypural 1+2 (2).

Number of vertebrae 39 (3*) or 40 (6); first completely formed hemal spine on centrum 16 (7*) or 17 (2); and pleural ribs 7/7 (3*), 7/8 (1), 8/7 (1), or 8/8 (4). Last precaudal vertebra (1), or last three (2), four (3*), five (1), or six (2) precaudal vertebrae with discrete neural processes. Last precaudal vertebra (6*), or last two (2), five (1) precaudal vertebrae with very discrete, almost imperceptible, neural processes.

Laterosensory system

Head laterosensory canals with simple (non-dendritic) tubes ending in single pores (Fig. 15). Supraorbital laterosensory canal continuous and connected to optic and infraorbital laterosensory canals posteriorly. Supraorbital laterosensory canal with 5 branches: s1, s2, s3, s6 (epiphyseal branch), and s8 (parietal branch). Contralateral epiphyseal branches (s6) fused to each other, bearing single symphyseal pore (s6+s6) (Fig. 15B). S4, s5, and s7 (postorbital) branches and pores absent. Supraorbital and infraorbital laterosensory canals anteriorly connected to each other through s2 and i2 branches (forming complex s2+i2 pore) (Fig. 15B). Otic laterosensory canal short, without pores, and continuous with posterior limits of supra- and infraorbital laterosensory canals, anteriorly, and with anterior limit of postotic laterosensory canal, posteriorly. Postotic (or temporal) laterosensory canal extends from posterior limit of otic laterosensory canals to anterior limit of lateral line, with 3 branches and pores (po1, po2, and po3) (Fig. 15A-B). Infraorbital laterosensory canal with 6 branches and pores, with s2 fused to i2 (see above). Preoperculomandibular laterosensory canal with 11 branches and pores (Fig. 15A-C); anteriormost preoperculomandibular laterosensory branch (pm1) independent from its symmetrical; posteriormost preoperculomandibular laterosensory branch (pm11) fused to po1 branch forming complex po1+pm11 branch and pore (Fig. 15A-B). Lateral line sensory canal continuous with postotic laterosensory canal anteriorly and interrupted posteriorly (Fig. 15A-B). Lateral line laterosensory canal long, with posterior limit extending to vertical through anterior half of caudal plate. First segment of lateral line long, with terminus at vertical through origin of anal fin to vertical through end of adipose-fin base, followed by 3-6 patches with 2-5 pores each. First lateral line pore ventral to level of adjacent pores of lateral line. One pair of short, anteriorly convergent, lines of neuromasts, with two neuromasts each, between anterior and posterior nostrils. Two vertical, short lines of neuromasts on face, just ventral to eye. One short neuromast line, with single neuromast, just posterior to each parietal branch (s8).

Pigmentation in alcohol and in life

Background body coloration withish pale or yellow. Body pigmented with brown melanophores dorsally and laterally, except for regions described below; lateroventral and ventral regions mostly unpigmented except for few scattered melanophores, slightly more concentrated dorsal to anal fin (Figs. 12-14). Head mostly dark-brown dorsally; lateral and ventral portions of head unpigmented. Anterior border of snout, anterior to each anterior nare, uniformly dark, lacking unpigmented area. Midportion of snout, between anterior and posterior nares, with two small, adjacent unpigmented areas in juveniles (30.5 mm SL or smaller) (Fig. 14). Region between corner of mouth and cheek unpigmented, with milky hue. Maxillary barbel dorsally with light-brown melanophores, mental barbels yellow. Region along base of maxillary barbel to just posterior to eye with dark stripe. Elongate, roughly rectangular white or yellow band ventral to eye (Figs. 12-14), less evident in larger specimens. Dark mark on posterior portion of head, from posterodorsal region of opercle to posterior limit of branchiostegal membrane, extending ventrally along branchiostegal membrane, reaching level of pectoral-fin base in larger specimens; such dark stripe fused with dark mark dorsal to pectoral-fin base (Figs. 12-14). Posterior border of supraoccipital with unpigmented (of milky hue), broad, M-shaped streak, extending laterally towards posterior extremity of opercle (Figs. 12-14). Trunk background bright yellow, with dark-brown to black marks in life and brownish in alcohol (Figs. 12-14). Dorsum mostly covered by dark-brown, marbled pigmentation (Figs. 12-14). Flanks with 18-22 irregular, vertical, dark bars, sometimes resembling inverted "v", "y", or "x" (Figs. 12-14). Anterior border of pseudotympanum wall, dorsal to pectoral-fin base, with dark brown, vertical mark, fusing dorsally with dark stripe across posterior region of opercle and branchiostegal membrane (Figs. 12-14). Lateral wall of pseudotympanum darkly pigmented, without any unpigmented region (Figs. 12-14). Laterodorsal region of trunk with whitish stripe (formed by absence of melanophores), extending posteriorly from level of pectoral-fin base up to approximately level of anal-fin origin (sometimes interrupting vertical bars), demarking midlateral, broad dark band (Figs. 12-14). Middorsal region of trunk with two unpigmented, milky blotches (Figs. 12-14): one predorsal, rounded, small mark (equal or slightly larger than eye size) just anterior to dorsal fin and around base of its first ray; and one diffuse, postdorsal unpigmented mark, just posterior to dorsal-fin base; preadipose, post-adipose, and precaudal white marks absent. Fin rays brown, fading distally, in larger individuals (40.2 mm SL or larger specimens) (Figs. 12-13), and with dark pigmentation restricted to their proximal thirds or almost absent, with few dark chromatophores, in smaller specimens (Fig. 14); interradial membranes mostly hyaline. Muscular base of pectoral, dorsal, and anal fins dark brown (Figs. 12-14). Adipose fin with ventral ⅔ light-brown and dorsal ⅓ translucent (Figs. 12-14). Caudal peduncle with dark-brown, blackened, vertical mark, extending posteriorly to limit of skin on base of caudal-fin rays and most evident at base of principal rays (Figs. 12-14); peduncular mark more conspicuous in smaller individuals. Base of caudal fin lobes with large, oval or rounded unpigmented spots, with milky appearance (Figs. 12-14), especially notable in life (Fig. 13).

Etymology

Cetopsorhamdia spilopleura, from the Greek "spilos", spot, stain, and "pleura", side, in allusion to the spotted pattern of the flanks. A noun in apposition.

Geographic distribution and habitat

Cetopsorhamdia spilopleura is only known from the Rio Doze de Outubro, a tributary of the upper Rio Juruena,

in the upper Rio Tapajós system, in Mato Grosso State, Brazil (Fig. 10). Ohara & Loeb (2016) found *C. spilopleura* (identified as *Cetopsorhamdia* sp. 3) in two collection sites, one in the Igarapé Mutum located near highway BR-364 (13°05′08″S, 59°53′32″W) (MZUSP 115478), described as 3-6 m wide and 0.5-2.5 m deep, with preserved riparian vegetation, swift current, and sand, pebbles, and dead leaves on the bottom (Ohara & Loeb, 2016: fig. 2a); and one in an unnamed stream affluent of Rio Doze de Outubro, also located near highway BR-364 (12°57′50″S, 60°01′40″W) (where the holotype, LIRP 13992, and MZUSP 115498 were caught), characterized as having 1-2 m wide and 0.5-1.7 m deep, with preserved riparian vegetation, swift current, subaquatic vegetation, and sand on the bottom (Ohara & Loeb, 2016: fig. 2c) (Fig. 20). Three other paratypes (MCP 35993, MCP 41057) were collected in a stretch of Rio Doze de Outubro where the river was small, with water clear and current moderate, sandy bottom and rich submersed and marginal vegetation.

Conservation assessment

The extinction risk of *Cetopsorhamdia spilopleura* is preliminarily assessed as low. The species is known from three localities very close together, in the headwaters of the Rio Doze de Outubro, a tributary to the Rio Juruena of the Rio Tapajós drainage. The three localities are very close and preclude the estimation of Extension of Occurrence. Instead, the Area of Occupation was estimated as eight square kilometers by the superposition of a 2×2 km grid. The three known collecting sites are located on the highway BR-364, and despite the area west of the road being heavily impacted by deforestation and agriculture, most of the Rio Doze de Outubro basin is located east of the road and is protected by the Nambikwara Indigenous Territory. As no specific threats to the species were detected and based on the inferred more widespread presence in the Rio Doze de Outubro basin, *C. spilopleura* is tentatively categorized as Least Concern (LC) according to the International Union for Conservation of Nature (IUCN) categories and criteria (IUCN Standards and Petitions Sub-Committee, 2019). Additional fish inventories should be conducted in the region in order reveal the real geographic distribution of this species.

DISCUSSION

Monophyly of *Cetopsorhamdia*

The genus *Cetopsorhamdia* is morphologically diagnosed by four synapomorphies (Bockmann, 1998:

Figure 20. Unnamed stream affluent of Rio Doze de Outubro, Rio Tapajós basin, about 25 km from Vilhena, on highway BR-174, at Chapada dos Parecis (12°57′50″S, 60°01′40″W), Comodoro, Mato Grosso State, Brazil, type locality of *Cetopsorhamdia spilopleura.* Photograph by W.M. Ohara.

clade 118): (1) presence of a medial ossification over the median portion of the skull, covering the epiphyseal bar and leaving reduced anterior and posterior fontanels; (2) orbital (= optic) foramen small; (3) mouth ventral; and (4) snout conical. The first character is notably present in both *Cetopsorhamdia clathrata* (Fig. 6B) and *C. spilopleura* (Fig. 16B). Plesiomorphically, the cranium of most catfishes has a dorsal fontanel divided into two by a narrow epiphyseal bridge. The anterior fontanel is delimited anteriorly by the mesethmoid and posterolaterally by the frontals, while the posterior fontanel is framed anteriorly and laterally by the frontals and posterolaterally by the supraoccipital. Among heptapterids, this generalized configuration has been illustrated for species of *Gladioglanis* Ferraris-Jr. & Mago-Leccia, 1989 (*cf.* Ferraris-Jr. & Mago-Leccia, 1989: fig. 5; Lundberg *et al.,* 1991: fig. 1), *Mastiglanis* Bockmann, 1994 (Bockmann, 1994: fig. 4), *Pimelodella* Eigenmann & Eigenmann, 1888 (Bockmann & Miquelarena, 2008: fig. 21; Slobodian & Pastana, 2018: fig. 3), *Rhamdella* Eigenmann & Eigenmann, 1888 (Miquelarena & Menni, 1999: fig. 7; Bockmann & Miquelarena, 2008: fig. 7), and *Rhamdiopsis* Haseman, 1911 (Bockmann & Castro, 2010: fig. 4A). We have found that all species of *Cetopsorhamdia* share the frontals with superficial outgrowths along their inner margins so as to obliterate the epiphyseal bar, the posterior half of anterior fontanel, and the anterior half of posterior fontanel. This condition has been noticed by Eigenmann (1916, 1922) for *C. nasus,* described as "a small frontal fontanel, far removed from the long parietal fontanel", and by Eigenmann (1922) for *C. boquillae,* described as "frontal fontanel and occipital fontanel […] shorter than the roofed space between them". Although we have not examined in detail the skeleton of *C. nasus* (only a radiograph of the holotype was available), the type species of the genus, that feature was illustrated for this species by Ortega-Lara (2012: fig. 6). Ruiz-C. & Román-Valencia (2006: fig. 4a) illustrated this condition for *C. boquillae,* but they were unaware about the presence of the epiphyseal bar, ignoring that it was indeed covered by the superficial ossifications along the medial margins of frontals. These authors also described and illustrated the anterior fontanel of a heptapterid identified as *C. nasus* as being wide and bifurcated (Ruiz-C. & Román-Valencia, 2006: fig. 4b). It is not clear what the authors mean by bifurcated, but their observation of a broad fontanel is probably owed to their inability in determining the correct limits of anterior fontanel in a poorly-calcified cleared and stained specimen (*cf.* Ruiz-C. & Román-Valencia, 2006: 129, fig. 4b). The weak calcification of that specimen is also indicated by the broadly cartilaginous composition of the anterior portion of the palatine, which was mistakenly recognized as a diagnostic characteristic for *C. nasus* by Ruiz-C. & Román-Valencia (2006). On the other hand, the limits of the posterior fontanel are well defined, and its shape represens the plesiomorphic configuration. This character, in addition to the presence of relatively large eyes, long maxillary barbel, fins with convex distal profile, long adipose-fin base, dorsal caudal-fin lobe longer than the ventral lobe, and total number of vertebrae indicate that the correct identification of *C. nasus* by Ruiz-C. & Román-Valencia (2006: fig. 2) is *Imparfinis usmai* Ortega-Lara, Milani, DoNascimiento, Villa-Navarro & Maldonado-Ocampo (*cf.* Ortega-Lara *et al.,* 2011). Among heptapterids, a state like that exhibited by *Cetopsorhamdia* is also present in *Taunayia* Miranda-Ribeiro, 1918, a condition thought to be homoplastic, considering that these genera are distantly related to each other (*cf.* Bockmann, 1998; Silva *et al.,* 2021). In members of *Brachyglanis* Eigenmann, 1912, *Brachyrhamdia* Myers, 1927, *Leptorhamdia* Eigenmann, 1918, and *Myoglanis* Eigenmann, 1912, and in *Rhamdella aymarae* Miquelarena & Menni, 1999, *Rhamdia enfurnada* Bichuette & Trajano, 2005, *Rhamdia guasarensis* DoNascimiento, Provenzano & Lundberg, 2004, and *Rhamdia quelen* (Quoy & Gaimard, 1824), the posterior cranial fontanel is totally or partially closed (*cf.* Lundberg & McDade, 1986; Bockmann, 1998; Silfvergrip, 1996; Miquelarena & Menni, 1999; DoNascimiento *et al.,* 2004; Bichuette & Trajano, 2005; Slobodian & Bockmann, 2013) but due to a non-homologous configuration. In those taxa the closure of the posterior fontanel is produced by the approximation of the internal borders of the posterior portion of the frontals and the anterior portion of the supraoccipital, at the region corresponding to the mid-portion of posterior fontanel.

Regarding the second character, the foramen for the optic nerve in *C. clathrata* (Figs. 6A, C) and *C. spilopleura* (Figs. 16A, C) is undoubtedly smaller than in those of most heptapterids (*cf.* Bockmann, 1998; Bockmann & Miquelarena, 2008), having approximately half the length of the trigeminofacial foramen. A further reduction in the foramen for the optic nerve to ¼ or less the length of the trigeminofacial foramen is observed in *C. boquillae, C. iheringi, C. insidiosa,* and *C. picklei.* Ortega-Lara (2012) did not describe or illustrate the foramen for the optic nerve in *C. nasus,* so that its state for this trait cannot be accessed.

The third and fourth synapomorphies proposed for *Cetopsorhamdia* by Bockmann (1998), *i.e.,* the ventral mouth and conical snout, are not derived characters for the genus. Instead, they are likely synapomophies for a more restricted group of species within the genus (see below). A ventral mouth, with its anterior border forming a wide arch, sometimes being almost straight in ventral view, is clearly present in *C. iheringi* (*cf.* Schubart & Gomes, 1959: fig. 1), *C. insidiosa* (*cf.* Steindachner, 1915: pl. 12, fig. 7), *C. nasus* (*cf.* Eigenmann, 1922: pl. 4, fig. 1; Ortega-Lara, 2012: figs. 1-2, 4, 19), and *C. picklei* (*cf.* Schultz, 1944: p. 2, fig. D). In both *C. clathrata* (Figs. 1-3, 5A) and *C. spilopleura* (Figs. 12-14, 15A), the mouth also has a ventral position, but not at the extent of the species above mentioned, nor does it have an almost straight edge. The mouth of *C. boquillae,* on the other hand, has the widespread heptapterid configuration, being subterminal and bearing a contour markedly arched (*cf.* Eigenmann, 1922: pl. 1, fig. 3; Ruiz-C. & Román-Valencia, 2006: fig. 1). Likewise, the snouts of *C. iheringi* (*cf.* Schubart & Gomes, 1959: fig. 1), *C. insidiosa* (*cf.* Steindachner, 1915: pl. 12, fig. 7), *C. nasus* (*cf.* Eigenmann, 1922: pl. 4, fig. 1; Ortega-Lara, 2012: figs. 1-2, 4, 19), and *C. picklei* (*cf.* Schultz, 1944:

pl. 2, fig. D) are distinctly conical, almost triangular, when viewed dorsally. The snout of *C. clathrata* (Figs. 1, 4, 5B) and *C. spilopleura* (Figs. 12, 14, 15B), although also conical, is much more attenuated, bearing ellipsoid contour in dorsal view. *Cetopsorhamdia boquillae,* in turn, exhibits a snout with an anterior contour characteristically rounded in dorsal view, which is the typical plesiomorphic morphology among heptapterids (*cf.* Bockmann, 1998). These last two characters should, therefore, be excluded from the list of *Cetopsorhamdia* synapomorphies.

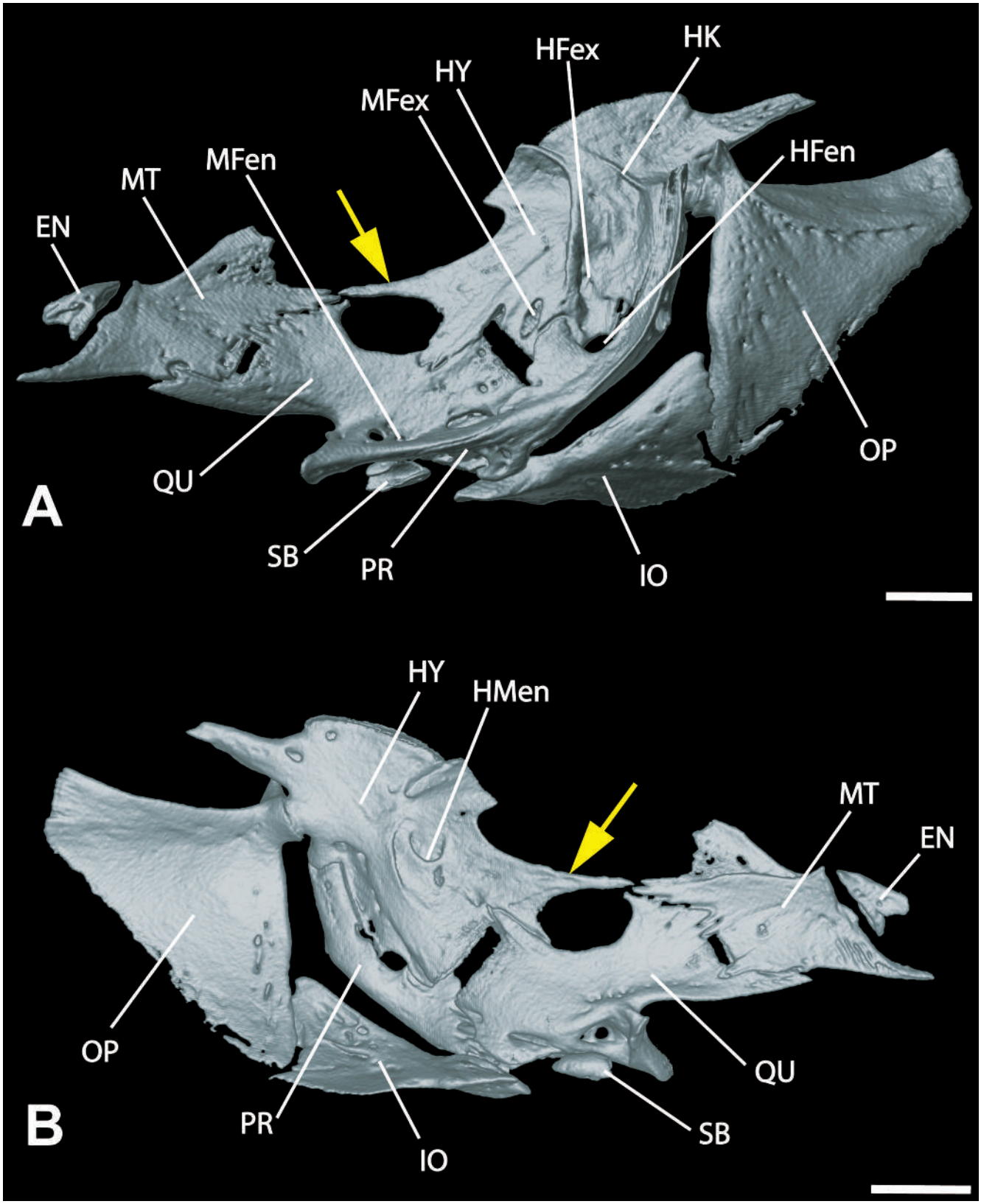

Figure 21. Left suspensorium and opercular series of *Cetopsorhamdia clathrata,* MCP 36064, 50.8 mm SL, holotype (CT reconstructions). (A) lateral view; (B) medial view. Cartilage not represented. Arrow points to the anterior process of the hyomandibula. Scale bars = 1 mm.

On the other hand, our study allowed us to hypothesize other two putative synapomorphies for the genus *Cetopsorhamdia*. One of them, the presence of a vertical, dark band at caudal peduncle, on the region of insertion of caudal-fin rays, had already been mentioned by Eigenmann (1916) in the original description of the genus. Eigenmann (1916) described it as "a dark band at base of caudal", considering it characteristic of *C. nasus*. This condition was explicitly mentioned and illustrated for *C. iheringi, C. insidiosa,* and *C. picklei* in their original descriptions (*cf.* Steindachner, 1915; Schultz, 1944; Schubart & Gomes, 1959). Although this mark cannot be verified in the types of *C. boquillae* because they are strongly faded, the examination of a photograph of a live specimen provided by Armando Ortega leaves no doubt about its presence in the species. Ruiz-C. & Román-Valencia (2006) also reported this caudal mark for *C. boquillae*. *Cetopsorhamdia clathrata* (Figs. 1-3) and *C. spilopleura* (Figs. 12-14) exhibit a state different from the remaining species of *Cetopsorhamdia,* in which the mark is smaller, being mostly restricted to the central portion of the caudal peduncle. In *C. boquillae, C. iheringi, C. insidiosa, C. nasus,* and *C. picklei* the caudal mark is larger, W-shaped, distinctly extending towards the dorsal and ventral borders of the caudal peduncle.

In the course of this investigation we identified another character in the hyomandibular bone that also seems to corroborate the monophyly of *Cetopsorhamdia*. All species of the genus, including *C. clathrata* (Fig. 21A) and *C. spilopleura* (Fig. 22A), have an oblique keel (HK) at the posterodorsal region of the lateral surface of the hyomandibula. In spite of Ortega-Lara (2012) had not described such a structure in the hyomandibula of *C. nasus,* it is possible to identify it, albeit faintly, in his photograph of a c&s specimen (*cf.* Ortega-Lara, 2012: fig. 10).

Putatively informative features to resolve *Cetopsorhamdia*'s internal relationships

Cetopsorhamdia clathrata and *C. spilopleura* share with *C. iheringi, C. insidiosa, C. nasus,* and *C. picklei* two putatively apomorphic characteristics that are absent in *C. boquillae*. One is the presence of a conspicuous pointed process on the anterior border of hyomandibula (Figs. 21-22, see arrows), as illustrated and described for *C. nasus* by Ortega-Lara (2012: fig. 10). On the other hand, *C. boquillae* has the generalized heptapterid hyomandibula, lacking a pointed process at its anterior margin.

In addition, in all *Cetopsorhamdia* species other than *C. boquillae* the ventral lobe of the caudal fin is longer than the dorsal lobe (*cf.* Eigenmann, 1916, 1922: pl. 4, fig. 1; Steindachner, 1915: pl. 12, fig. 7; Schultz, 1944: pl. 2, fig. d; Schubart & Gomes, 1959: fig. 1; Ortega-Lara, 2012: fig. 19). Such a condition, presumably derived, is exhibited by *C. clathrata* (Figs. 1-3) and *C. spilopleura* (Figs. 12-14), although the condition is more discrete in the latter species. Eigenmann (1922) imprecisely characterized the condition of ventral caudal-fin lobe of *C. boquillae* as "probably somewhat the longer" (likely due to the poor state of conservation of its type series). Indeed, the tips of the caudal-fin rays of the holotype and paratypes of *C. boquillae* are heavily damaged so that it is not possible to ascertain its state. However, the examination of a photograph of a live specimen of *C. boquillae* by Armando Ortega allowed us to determine the state of its caudal fin as having a dorsal lobe with the same length of the ventral lobe, or slightly longer. The caudal-fin lobes of approximately the same length or the dorsal lobe slightly longer than the ventral one is plesiomorphic for catfishes (Bockmann & Miquelarena, 2008). A long ventral caudal-fin lobe also occurs homoplastically in the genus *Phenacorhamdia* (*cf.* Britski, 1993; Bockmann, 1998; DoNascimiento & Milani, 2008).

Despite the striking morphological differences distinguishing *Cetopsorhamdia clathrata* from *C. spilopleura,* they share at least seven presumable apomorphies observed in the hyomandibula, in the dorsal and pectoral fins, and in the body coloration, which are suggestive of a sister group relationship between them.

As above commented, *Cetopsorhamdia clathrata* (Fig. 21, see arrow) and *C. spilopleura* (Fig. 22, see arrow) share with most of species of *Cetopsorhamdia* the presence of a conspicuous pointed process on the anterior border of hyomandibula. These two new species exhibit a further elongation in this process that reaches the metapterygoid so that these bones, together with quadrate, forming a large, rounded fenestra in the suspensorium (Figs. 21-22).

In *Cetopsorhamdia clathrata* and *C. spilopleura* the degree of ossification of the first (unbranched) dorsal- and pectoral-fin rays is quite distinct from the remaining *Cetopsorhamdia* species. In these species the first rays of the dorsal and pectoral fins are weakly ossified and stiffened only at their basal portions at most. In *C. clathrata* (Fig. 9) the range of variation of the length of the rigid part of the first dorsal-fin ray is 4.0-6.9% SL (x = 5.7, SD = 0.7) and of the first pectoral-fin ray is 3.4-6.2% SL (x = 4.6, SD = 0.7) (Table 1), while in *C. spilopleura* (Fig. 19) is 5.3-6.4% SL (x = 5.8, SD = 0.4) and 4.1-5.1% SL (x = 4.4, SD = 0.3) (Table 2). In opposition, the basal portion of first, undivided dorsal- and pectoral-fin rays of *C. boquillae, C. iheringi* (Fig. 23A), *C. insidiosa* (Fig. 23B), *C. nasus,* and *C. picklei* is densely ossified in comparison to its distal segment, forming a somewhat rigid strut of about ⅓ and ½ size of the total length of those elements, respectively. This condition exhibited by most species of *Cetopsorhamdia* is closer to that present in several successive basal lineages of the family Heptapteridae in which more than half of the proximal portion of the first ray of the dorsal and the pectoral fins is heavily ossified and stiffened, sometimes forming a spine (*cf.* Bockmann, 1998). Among these last-mentioned species of *Cetopsorhamdia,* the proportions of the rigid part of the first dorsal-fin ray in SL are 8.2-12.9% SL whereas the proportions of the rigid part of the first pectoral-fin ray are 10.4-13.5% SL. No material of *C. nasus* was available to be measured, but examination of the photographs and radiographs of its holotype and data provided by Ortega-Lara (2012) indicates that the first rays of the dorsal and pectoral fins are

unquestionably rigid, at least for their ⅓ and ½ proximal parts, respectively, resembling the conditions exhibited by *C. boquillae, C. iheringi, C. insidiosa,* and *C. picklei*.

At last, most putative synapomorphies clustering together *C. clathrata* and *C. spilopleura* into a clade are observed in their color patterns, namely: (1) a dark stripe across the base of maxillary barbel to the region just posterior to the eye (Figs. 1-4, 12-14); (2) a roughly rectangular unpigmented region just ventral to the eye (Figs. 1-4, 12-14); (3) a dark, vertical bar at the pos-

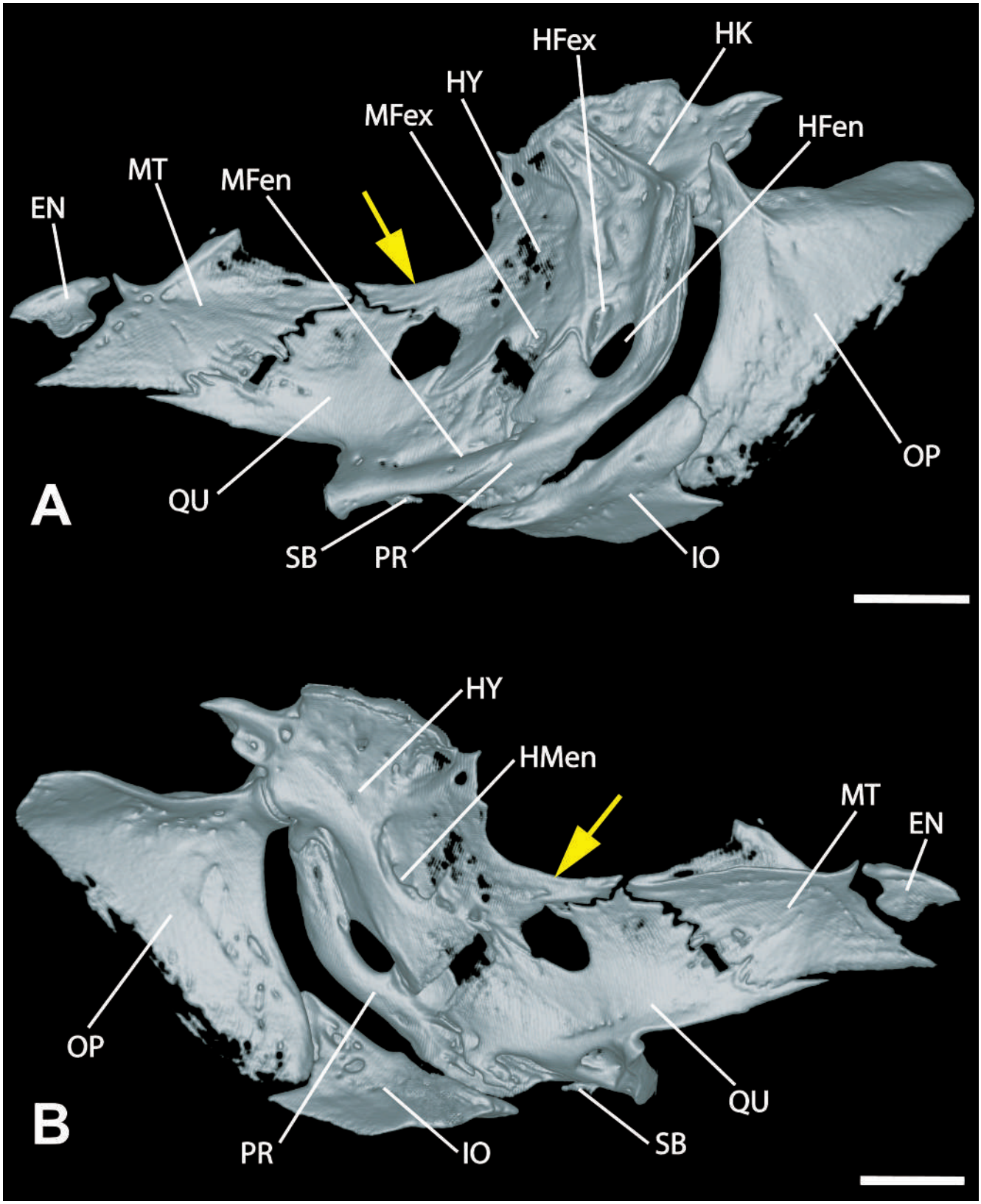

Figure 22. Left suspensorium and opercular series of *Cetopsorhamdia spilopleura,* MZUSP 121503, 47.9 mm SL, holotype (CT reconstructions). (A) lateral view; (B) medial view. Cartilage not represented. Arrow points to the anterior process of the hyomandibula. Scale bars = 1 mm.

terior portion of opercle and branchiostegal membrane (Figs. 1-4, 12-14); (4) a dark, vertical bar at the anterior portion of the trunk, dorsal to the pectoral fin (Figs. 1-4, 12-14); and (5) each lobe of caudal fin with one ovoid, unpigmented area, of milky-looking in life, immediately posterior to the dark mark (Figs. 1-3, 12-14). None of the other species of *Cetopsorhamdia* has any of these characteristics, alternatively possessing a mostly uniform dark coloration in the referred regions, without bands or unpigmented areas.

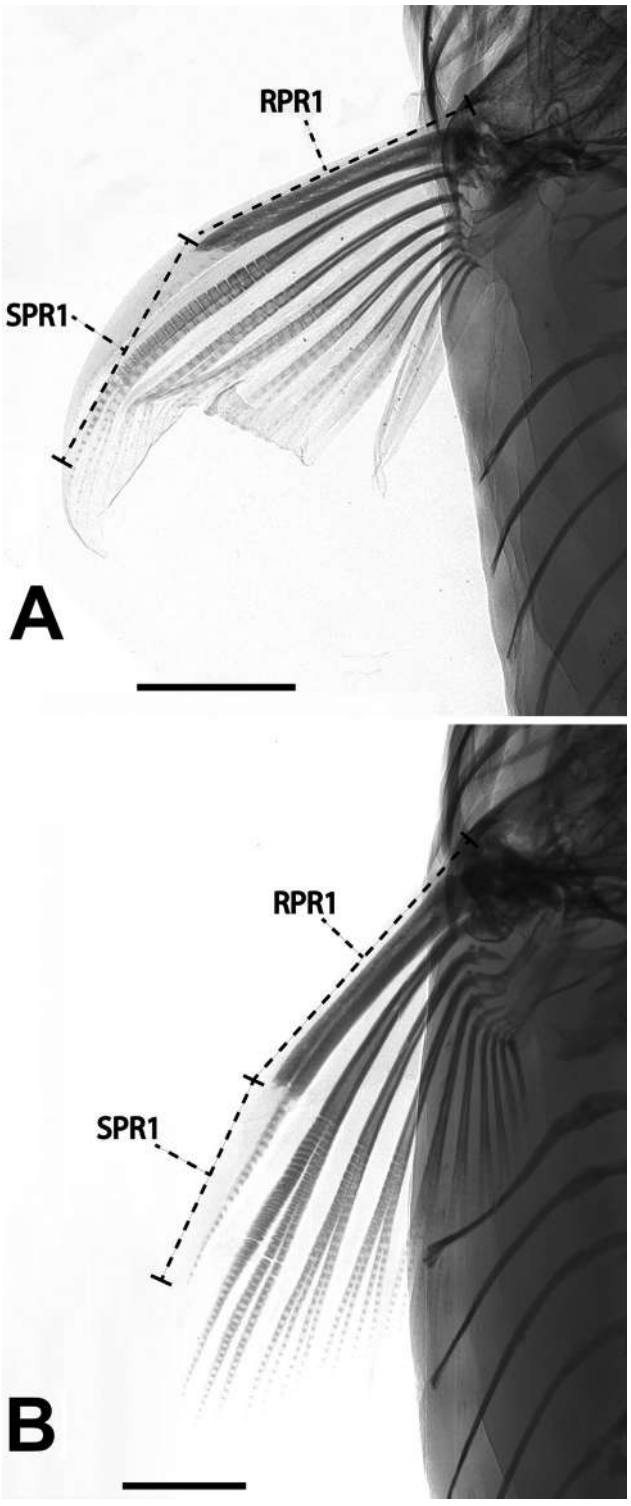

Figure 23. Left pectoral fin of: (A) *Cetopsorhamdia iheringi,* LIRP 2805, 53.9 mm SL (radiograph); (B) *Cetopsorhamdia insidiosa,* NMW 46095:1 (syntype of *Imparfinis insidiosus*), 76.8 mm SL (radiograph). Dorsal view. Scale bars = 3 mm.

Four putative autapomorphies have been identified for *Cetopsorhamdia clathrata:* (1) unpigmented area in the posterodorsal part of the head, dorsally at the end of the opercular cleft (Figs. 1-4); (2) trunk flanks with 10-12 quadrangular marks, separated by unpigmented vertical lines or bars (Figs. 1-4); (3) midlateral region of the trunk, along the lateral line, devoid of pigmentation, forming a white stripe (Figs. 1-3); and (4) trunk with scattered unpigmented, rounded spots, mostly concentrated on its dorsal half (Figs. 1, 3-4).

For *Cetopsorhamdia spilopleura,* in turn, three putative autapomorphies have been recognized: (1) anterodorsal region of the quadrate, outlining part of the suspensorium fenestra, expanded and turned backwards, broadly articulating with the ventral part of the anterior process of the hyomandibula (Fig. 22); (2) trunk flanks with 18-22 irregular, vertical brown bars, sometimes resembling inverted "v", "y" or "x" (Figs. 12-14); and (3) trunk with laterodorsal unpigmented stripe, demarking a broad midlateral dark band along the lateral line (Figs. 12-14).

Distribuition and fish endemism at Chapada dos Parecis

Both species described in this paper inhabit headwater creeks of the Chapada dos Parecis, an elevated geomorphological formation with altitudes between 400 and 700 m, drained by tributaries of the Madeira and Tapajós rivers. This region constitutes what Dagosta & de Pinna (2019) called an extreme shield, an area with an extremely high level of endemism where coexisting closely related lineages are rare, the diversity is low, and few taxa broadly distributed in the remaining Amazon basin occur. Further on the two new *Cetopsorhamdia* species herein described, the following taxa are endemic to the headwaters of the rivers draining the Chapada dos Parecis: *Bryconops piracolina, Hasemania nambiquara* Bertaco & Malabarba, 2007, *Hemigrammus silimoni* Britski & Lima, 2008, *Hemigrammus skolioplatus* Bertaco & Carvalho, 2005b, *Hyphessobrycon hexastichos* Bertaco & Carvalho, 2005a, *Hyphessobrycon lucenorum, Hyphessobrycon petricolus* Ohara, Lima & Barros, 2017, *Hyphessobrycon melanostichos* Carvalho & Bertaco, 2006, *Hyphessobrycon notidanos* Carvalho & Bertaco, 2006, *Moenkhausia cosmops* Lima, Britski & Machado, 2007, and *Moenkhausia parecis* (Characidae), *Corydoras hephaestus* (Callichthyidae), *Ancistrus verecundus,* and the monotypic genus *Araichthys* Zawadzki, Bifi & Mariotto, 2016, with *A. loro* Zawadzki, Bifi & Mariotto, 2016 (Loricariidae) (*cf.* Bertaco & Carvalho, 2005a b; Fisch-Muller *et al.,* 2005; Carvalho & Bertaco, 2006; Bertaco & Malabarba, 2007; Lima *et al.,* 2007; Britski & Lima, 2008; Wingert & Malabarba, 2011; Ohara & Lima, 2015; Ohara & Marinho, 2016; Ohara *et al.,* 2016, 2017; Zawadzki *et al.,* 2016).

Comparative material

Cetopsorhamdia boquillae: FMNH 55212 [ex CM 3923], 71.5 mm SL in ethyl alcohol (ms and xr), holotype, Colombia, Boquilla [Boquía, affluent of Río Cauca, Río Magdalena basin – *cf.* Miles, 1943; Ruiz-C. & Román-Valencia, 2006], coll. C.H. Eigenmann, 18-19 Feb 2012; CAS 63607 [ex IU 15004], 4 ex. in ethyl alcohol (42.4-59.1 mm SL, all ms and xr), 1 ex. c&s (52.9 mm SL), paratypes, Colombia, Río Quondio, in Boquilla [Río Quindío, in Boquía, affluent of Río Cauca, Río Magdalena basin – *cf.* Miles, 1943; Ruiz-C. & Román-Valencia, 2006], coll. C.H. Eigenmann, 18-19 Feb 1912.

Cetopsorhamdia iheringi: Rio São Francisco basin, Rio das Velhas drainage (Brazil): MZUSP 37158, 61 ex. in ethyl alcohol (26.2-67.6 mm SL), 3 ex. c&s (56.8-57.9 mm SL), State of Minas Gerais, Moeda, Pedra Vermelha, unnamed stream affluent of Rio Paraopeba, km 10 on highway BR-040/Moeda, 20°20′00″S, 44°01′59″W, coll. J.C. Oliveira, O.T. Oyakawa, 8 Feb 1987; MCP 16639, 1 ex. in ethyl alcohol (49.7 mm SL, ms and xr), State of Minas Gerais, Abaeté, Rio Marmelada, on road between Pompeu and Frei Orlando, 19°02′59″N, 45°12′00″W, coll. R.E. Reis, J.F.P. da Silva, E.H.L. Pereira, W.G. Saul, 12 Jul 1993; MCP 16640, 1 ex. in ethyl alcohol (42.7 mm SL, ms and xr), State of Minas Gerais, Distrito de Montalvânia, São Sebastião dos Poções, Rio Poções (affluent of Rio Cochá, Rio Carinhanha basin), *ca.* 11 km S of Montalvânia, 14°32′00″S, 44°24′00″W, coll. R.E. Reis, J.F.P. da Silva, E.H.L. Pereira, 16 Jul 1993. Upper Rio Paraná basin, Rio Grande drainage (Brazil): MZUSP 23768, 7 ex. in ethyl alcohol (35.8-61.0 mm SL), State of Minas Gerais, Ribeirão da Prata, on road São João del Rei/Itutinga, 21°07′S, 44°15′W, coll. H.A. Britski, J.C. Garavello, 10 Nov 1969; MZUSP 42294, 1 ex. c&s (57.0 mm SL), same data as MZUSP 23768; AMNH 9090, 1 ex. in ethyl alcohol (28.3 mm SL, xr), State of São Paulo, Franca, Rio Grande basin [possibly at Ribeirão dos Bagres, afluent of Rio Sapucaí, 20°33′23″S, 47°25′10″W], coll. E. Garbe, 1900, LIRP 3512, 17 ex. in ethyl alcohol (15.8-67.8 mm SL, all ms and xr), State of São Paulo, Guará, Córrego São José or Córrego Bocaina (Rio Sapucaí basin), 20°29′20″S, 47°45′47″W, coll. BIOTA Team, 24 Mar 2002; UFRJ 689, 2 ex. c&s (33.9-52.7 mm SL), State of São Paulo, Rio Pardo, near Caconde, 21°33′38″S, 46°38′55″W, coll. C.R.S.F. Bizerril, 13 Nov 1991; LIRP 5671, 1 ex. in ethyl alcohol (39.7 mm SL, ms and xr), State of São Paulo, Pirassununga, Ribeirão Quebra-Cuia or Ribeirão do Sertãozinho (affluent of right margin of Rio Mogi-Guaçu, affluent of Rio Pardo), 21°51′34″S, 47°19′30″W, coll. H.F. Santos, M. Carvalho, M.R. Cavallaro, A. Takako, A. Datovo, 4 Oct 2005; LIRP 5681, 2 ex. in ethyl alcohol (35.5-72.0 mm SL, all ms and xr), State of São Paulo, Leme, Córrego do Sapezal (affluent of right margin of Ribeirão do Meio, affluent of left margin of Rio Mogi-Guaçu, affluent of Rio Pardo), 22°05′48″S, 47°18′39″W, coll. H.F. Santos, M. Carvalho, M.R. Cavallaro, A. Takako, A. Datovo, 4 Oct 2005. Upper Paraná basin, Rio Tietê drainage (Brazil): LIRP 2804, 19 ex. in ethyl alcohol (24.2-76.1 mm SL, 10 ex. xr, 46.4-76.1 mm SL), State of São Paulo, São Pedro, Ribeirão da Ponta do Meio (Rio Piracicaba-Capivari-Jundiaí basin), at Fazenda Santa Maria da Ponta do Meio farm, 22°33′27″S, 47°57′08″W, coll. BIOTA Team, 29 May 2001; MZUSP 47950, 45 ex. in ethyl alcohol (23.5-75.4 mm SL), 3 ex. c&s (46.2-65.4 mm CP), State of São Paulo, Botucatu, Rio da Indiana (affluent of left margin of Rio Capivara, affluent of left margin of Rio Tietê), at Fazenda Indiana farm, in the region of Depressão Periférica, 22°54′14″S, 48°23′25″W, altitude 590 m, coll. M.G. Bueno, 16 Jul 1993. Upper Paraná basin, Rio Aguapeí drainage (Brazil): LIRP 2812, 5 ex. in ethyl alcohol (44.9-54.3 mm SL, all ms and xr), State of São Paulo, Lins, Córrego da Figueira, 21°51′06″S, 49°50′20″W, coll. BIOTA Team, 30 Mar 2001. Upper Paraná basin, Rio do Peixe drainage (Brazil): LIRP 2806, 5 ex. in ethyl alcohol (62.5-91.9 mm SL, all ms and xr), State of São Paulo, Rancharia, Córrego Tupi, 22°04′55″S, 50°54′33″W, altitude 385 m, coll. BIOTA team, 21 May 2000. Upper Paraná basin, Rio Paranapanema drainage (Brazil): LIRP 2807, 5 ex. in ethyl alcohol (43.2-73.4 mm SL, all ms and xr), State of São Paulo, Euclides da Cunha, Rio do Piau, at Fazenda Santa Maria farm, 22°33′04″S, 52°44′36″W, coll. BIOTA team, 5 Aug 2000; LIRP 2805, 46 ex. in ethyl alcohol (28.9-71.6 mm SL, 12 xr (45.1-68.1 mm SL)), State of Paraná, Andirá, Córrego Águas das Antas, at Fazenda das Antas farm, 23°02′56″S, 50°11′51″W, coll. BIOTA team, 4 Nov 2000; NUP 3357, 4 ex. in ethyl alcohol (53.5-73.5 mm SL, all ms and xr), State of Paraná, Maringá, Córrego Miosótis, affluent of Ribeirão Maringá (Rio Pirapó basin), 23°21′59.3″S, 51°57′35.6″W, coll. A.M. Cunico, v.2004; CZUEL 1142, 2 ex. in ethyl alcohol (86.2-87.6 mm SL, all ms and xr), State of Paraná, Londrina, Ribeirão Três Bocas (Rio Tibagi basin), 23°26′S, 51°10′W, coll. ECPUEL, 16.xii.1992.

Cetopsorhamdia insidiosa: Rio Branco-Negro basin: NMW 46094:1, 56.9 mm SL in ethyl alcohol, syntype of *Imparfinis insidiosus,* Rio Surumu, einem Nebenflusse des Rio Miang, der selbst ein sekundärer Nebenfluß des Rio branco, Serra do Mello [Brazil, State of Roraima, Pacaraima, Rio Surumu, affluent of left bank of the Rio Tacutu], coll. J.D. Haseman, 1913; NMW 46094:2, 59.7 mm SL in ethyl alcohol, syntype of *Imparfinis insidiosus,* same data as NMW 46094:1; NMW 46094:3, 63.1 mm SL in ethyl alcohol (ms), syntype of *Imparfinis insidiosus,* same data as NMW 46094:1; NMW 46094:4, 60.0 mm SL in ethyl alcohol (ms), syntype of *Imparfinis insidiosus,* same data as NMW 46094:1; NMW 46095:1, 76.8 mm SL in ethyl alcohol (ms and xr), syntype of *Imparfinis insidiosus,* Rio branco bei Bem Querer [Brazil, State of Roraima, Caracaraí, Rio Branco, near Cachoeira do Bem Querer, 01°51′40.7″S, 61°04′03.5″W], coll. J.D. Haseman, 1913; NMW 46095:2, 25.3 mm SL in ethyl alcohol (ms), syntype of *Imparfinis insidiosus,* same data as NMW 46095:1; NMW 46095:3, 59.5 mm SL in ethyl alcohol (ms), syntype of *Imparfinis insidiosus,* same data as NMW 46095:1; ANSP 179707, 1 ex. in ethyl alcohol (31.1 mm SL, ms and xr), Guyana, Rupununi (Region 9), Moco-Moco River (affluent of Rio Takutu, affluent of Rio Branco), at Moco-Moco Hydro Power, below dam, 18.8 km SE of Lethem, 03°17′48″N, 59°38′41″W, coll. M.H. Sabaj Pérez, J.W. Armbruster, M.R. Thomas, D.C.

Werneke, C.L. Allison, C.J. Chin, D. Arjoon, 5 Nov 2002; INPA 1618, 2 ex. in ethyl alcohol (45.7-63.6 mm SL), Brazil, State of Roraima, Amajari, Ecological Station of Maracá, Furo Santa Rosa (affluent of left margin of Rio Uriracoera, affluent of right margin of Rio Branco), at Cachoeira Fumaça waterfall, 03°22′46.5″N, 61°51′52.2″W, coll. V. Py-Daniel *et al.,* 30.iii.1997; INPA 1654, 2 ex. in ethyl alcohol (60.8-74.5 mm SL, all ms and xr), 1 ex. c&s (64.2 mm SL), Brazil, State of Roraima, Amajari, Ecological Station of Maracá, Furo Santa Rosa (affluent of left margin of Rio Uriracoera, affluent of right margin of Rio Branco), at Cachoeira do Papai Noel waterfall, 03°22′46.5″N, 61°51′52.2″W, coll. V. Py-Daniel *et al.,* 30 Mar 1997; INPA 11833, 1 ex. in ethyl alcohol (67.2 mm SL), Brazil, State of Roraima, Mucajaí, Missão Alto Mucajaí, left margin of Rio Mucajaí (Rio Branco basin), 02°45′01″N, 62°13′44″W, coll. Oncocercose Team IV, 2 May 1994; INPA 22839, 5 ex. in ethyl alcohol (61.1-70.1 mm SL, all ms and xr), 1 ex. c&s (69.2 mm SL), Brazil, State of Roraima, Mucajaí, Rio Mucajaí (Rio Branco basin), at Cachoeira do Paredão 2 waterfall, about 03°22′N, 61°52′W, coll. E. Ferreira, M. Jégu, 19.ii.1987; INPA 11841, 1 ex. in ethyl alcohol (32.1 mm SL), Brazil, State of Amazonas, Rio Tootobi, affluent of Rio Demini (Rio Negro basin), 01°45′57″N, 63°37′02″W, coll. V. Py-Daniel (Oncocercose Team), 9 Sep 1995.

Cetopsorhamdia nasus: Río Magdalena basin: FMNH 58126 [ex CM 7124], 54.4 mm SL (xr) in ethyl alcohol, holotype, Honda, Colombia [likely Bernal Creek (= Quebrada de Bernal, left margin affluent of Río Magdalena, Honda, Departament of Tolima, 05°11′53.74″N, 74°44′17.99″W) – *cf.* Eigenmann, 1922: 16], coll. C.H. Eigenmann, 28 Jan 1912.

Cetopsorhamdia picklei: Lago Maracaibo basin: USNM 121217, 88.3 mm SL (ms and xr) in ethyl alcohol, holotype, Río Motatán, 4 km above Motatán, coll. L.P. Schultz, 25 Mar 1942; USNM 121218, 28 ex. in ethyl alcohol (44.4-116.8 mm SL, 11 ex. xr), 2 ex. c&s (55.5-67.7 mm SL), paratypes, same data as holotype.

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AUTHORS' CONTRIBUTIONS

F.A.B., R.E.R.: Conceptualization, Methodology, Software, Data curation, Formal analysis, Writing – original draft, Visualization, Investigation. Writing – review & editing. Both authors actively participated in the discussion of the results, and reviewed and approved the final version of the paper. Authors declare no conflict of interest related to this paper.

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SUPPLEMENTARY INFORMATION

CT-Scan information for *Cetopsorhamdia* species.
Abbreviations: CNC = computer numerical control; FDD = focus-detector distance; and FOD = focus-object distance.

	***C. clathrata* sp. nov.**	***C. spilopleura* sp. nov.**
	MCP 36064	**MZUSP 121503**
Standard length (mm)	50.8	47.9
Geometry		
Magnification	11.338953	10.644004
Voxel size (µm)	17.688313	18.789923
FOD (mm)	71.354500	76.013252
FDD (mm)	809.0853327	809.0853327
Aquisition		
Number of images	2000	1000
Image width	990	990
Image height (pixels)	1000	1000
Fast scan	0	0
Detector		
Type (rt)	dxr-250	dxr-250
Timing (ms)	333.091000	1000.071000
Averaging	5	4
Skip frames	1	1
X-Ray		
Voltage (kV)	60	60
Current (µA)	200	200
Tube mode	0	0
Filter	Unknown	Unknown
CNC		
XS (mm)	-0.078375	-0.034312
YS (mm)	-28.435750	1.249875
ZS (mm)	71.354500	76.013250
Volume		
Dimensions	990 × 990 × 1000	990 × 990 × 1000
Voxel size (µm)	17.64 × 17.64 × 17.64	18.79 × 18.79 × 18.79
Format	32 bit float	32 bit float
Full size on disk	3738.78 MB	3738.78 MB

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