

Redefinition of *Heptapterus* (Heptapteridae) and description of *Heptapterus carmelitanorum*, a new species from the upper Paraná River basin in Brazil

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Abstract

A new diagnosis and a new classification of *Heptapterus* are provided and a new species, *H. carmelitanorum*, is described. *Heptapterus* is diagnosed by the following character combination: adipose fin confluent with the caudal fin; non-bifurcate caudal fin; anal-fin insertion posterior to vertical through adipose-fin insertion; 10–23 anal-fin rays; anal fin not confluent with caudal fin; and extremely elongate body, with a head length of 16.1–24.9%SL. Species included in *Heptapterus* are *H. borodini*, *H. carmelitanorum*, *H. carnatus*, *H. exilis*, *H. hollandi*, *H. mandimbusu*, *H. mbya*, *H. mustelinus*, *H. ornateps*, and *H. qenqo*. Some of the character states diagnosing *H. carmelitanorum* among its congeners are the anal-fin insertion less than one eye diameter posterior to a vertical through the adipose-fin insertion (vs. more than one eye diameter in all congeners); the isognathous mouth (vs. slightly to moderately retrognathous, except *H. borodini*); and the keel formed by ventral procurrent caudal-fin rays shallow, far from reaching anal-fin base (vs. keel formed by ventral procurrent caudal-fin rays deep, continuing almost to the anal-fin base, except in *H. borodini* and *H. hollandi*).

Key Words

‘*Chasmocranus*’ *brachynema*, Grande River basin, *Heptapterus mustelinus*, *Imparfinis borodini*, *Imparfinis hollandi*, Minas Gerais, *Pariolius*, Sapucaí River basin, Siluriformes

Introduction

Siluriformes is one of the most species-rich actinopterygian orders, with about 4,100 valid species (Fricke et al. 2022). Half of these species occur in the Neotropics (~2,050) although diversity projections indicate that

there are an additional 1,120 species to be described in this region (Ota et al. 2015). This hidden diversity is expected to be discovered within siluriform families that already are species rich, but that have been subject to little taxonomic effort. For example, the Neotropics endemic Heptapteridae has 231 valid species, is especially

common in low-order streams, and has received comparatively little recent attention from taxonomists (Fricke et al. 2022). Notably, only 8.2% of these (19 species) were described in the past ten years, compared to 22.2% of Loricariidae and 29.2% of Trichomycteridae (Fricke et al. 2022). This is despite both families also being endemic to the Neotropics and frequently found in the same environments as heptapterids.

Advancements in the alpha taxonomy of Heptapteridae have been hampered by shortfalls in the classification of those fishes. As presently understood, some heptapterid genera are highly heterogeneous assemblages resulting from unjustified redefinitions and synonymies proposed during the 20th century. Part of that heterogeneity results from the inference that previously proposed generic characters were insufficient to warrant distinction between genera (e.g., Haseman 1911; Miranda-Ribeiro 1911; Gosline 1941; Inger 1956; Mees 1967; Mees 1974; Mees and Cala 1989). However, it can also be explained by the fact that several of earlier species descriptions contained errors regarding important diagnostic characters at specific and generic levels. For instance, *Chasmocranus surinamensis* (Bleeker 1862) was described in *Heptapterus* Bleeker, 1858, because the author thought it had the adipose fin continuous with the caudal fin, but it does not (Inger 1956). Eigenmann and Norris (1900) diagnosed *Imparfinis* Eigenmann & Norris, 1900, by having the eye without free margin and vomerine teeth present, but the type species *I. piperatus* Eigenmann & Norris, 1900, has a free orbital margin and no vomerine teeth (Mees 1974); and Borodin (1927) described *Imparfinis longicauda* Borodin, 1927 (= '*I. borodini* Mees & Cala, 1989) in *Imparfinis* because that species has no free orbital margin and he understood that the adipose fin was not confluent with the caudal. Through that series of misguided taxonomic actions, *Imparfinis* came to include species with lateral eyes with free rim, short body, long barbels, and bifurcate caudal fin, not confluent with the adipose, but also '*I. borodini*, a species with dorsal eyes without free rim, elongate body, short barbels, and non-bifurcate caudal fin, confluent with the adipose. Likewise, '*I. hollandi* Haseman, 1911, which shares with '*I. borodini* all those character states in addition to other non-diagnostic characters, was placed in *Pariolius* Cope, 1872, by Gosline (1941), and subsequently in *Heptapterus* by Mees (1974), who synonymized the latter two genera. In contrast, Bockmann and Guazzelli (2003), in the most recent complete classification of Heptapteridae, listed '*I. hollandi* and '*I. borodini* in their original genus *Imparfinis*, even though both species fit an early definition of *Heptapterus* by Bleeker (1864), except for a slightly different position of the anal fin, relative to the adipose. When it seemed that the confusion could not be further complicated, Baumgartner et al. (2012) placed '*I. hollandi* in *Pariolius*, following Gosline (1941), although *Pariolius* (currently valid) includes only one very small, relatively short-bodied species from western Amazon (Bockmann and Slobodian 2017).

What, then, can phylogeny say about the matter, if pre-cladistic classificatory schemes seem to have failed? A phylogenetic study (Silva et al. 2021) has recovered both '*I. borodini* and '*I. hollandi* as closely related to *H. mustelinus* (Valenciennes, 1835), the type species of *Heptapterus*. Apparently, the sole reason why they are not currently assigned to *Heptapterus* is that they are thought to belong to an undescribed genus, differing from *Heptapterus* by a few characters ('new genus D' of Bockmann and Slobodian 2017). Recently, an undescribed heptapterid species belonging to that lineage was collected in a small stream of the Grande River basin, in the Upper Paraná ecoregion (Azevedo-Santos et al. 2019). Meanwhile, the re-examination of specimens deposited in fish collections, as well as the sampling of previously unknown populations, has been revealing other new species belonging to that lineage – and their description cannot wait for the description of the new genus. Until then, those species must be described in the genus whose definition best matches the observed combinations of characters. As we will argue, in the case of the new species described herein the most appropriate genus is *Heptapterus*.

Heptapterus has also been the subject of considerable taxonomic confusion. The type species, *H. mustelinus*, is most similar phenotypically to *H. carnatus* Faustino-Fuster, Bockmann & Malabarba, 2019, *H. exilis* Faustino-Fuster, Bockmann & Malabarba, 2019, *H. mandimbusu* Aguilera, Benitez, Terán, Alonso & Mirande, 2017, *H. mbya* Azpelicueta, Aguilera & Mirande, 2011, *H. ornateiceps* Ahl, 1936, and *H. qenqo* Aguilera, Mirande & Azpelicueta, 2011. All those species, except *H. ornateiceps*, were described from the southern extreme of the geographic range of Heptapteridae (Lower Paraná, Salí and Uruguay River basins, in Argentina and southern Brazil) (Bleeker 1864; Ahl 1936; Aguilera et al. 2011, 2017; Azpelicueta et al. 2011; Faustino-Fuster et al. 2019). In addition, the type locality of *H. ornateiceps*, "Rio de Janeiro", is inaccurate (Bockmann and Guazzelli 2003). Beyond the aforementioned species and based on the definition of *Heptapterus* by Bockmann and Slobodian (2017), the most recent complete classification of *Heptapterus* by Faustino-Fuster et al. (2019) includes *H. sympterygium* Buckup, 1988, described from coastal drainages in Rio Grande do Sul. However, prior to the publication of those studies, the genus also included *H. bleekeri* Boeseman, 1953 (= *Chasmocranus bleekeri*), *H. fissipinnis* Miranda Ribeiro, 1911 (= *Acentronichthys fissipinnis*), '*H. multiradiatus* Ihering, 1907, '*H. stewarti* Haseman, 1911, and *H. tapanahoniensis* Mees, 1967 (= *Chasmocranus tapanahoniensis*) (Bockmann and Guazzelli 2003, altered by Bockmann and de Pinna 2004; DoNascimento and Milani 2008). All of those diverge from *H. mustelinus* by one or more easily observable characters, and either can be assigned to other valid genera or regarded simply as *incertae sedis* within Heptapterini.

All that considered, a new diagnosis of *Heptapterus* was necessary, based on that provided by Bleeker (1864), but with a few alterations – to reflect available

phylogenetic evidence and make the recognition of the genus more straightforward. Thus, we propose the new diagnosis for *Heptapterus*, present a list of the species which should be regarded as belonging to *Heptapterus*, and the description of a new species from the Grande River basin in southeastern Brazil.

Material and methods

Morphological data

Measurements and counts were taken as in Faustino-Fuster et al. (2019), with some alterations, as follows. Body depth was measured both at the dorsal- and at the adipose-fin origins. Body width was measured at dorsal-fin origin and at cleithrum (cleithral width). Both bony and fleshy interorbital distances were measured. Dorsal-, pectoral-, and pelvic-fin lengths were replaced by the lengths of the first three rays of each fin. Also, the length of the last dorsal-fin ray was added. Other additions include caudal-fin depth; distance between snout tip and terminus of dorsal-fin base; distance between snout tip and dorsal-fin distal end, adpressed; length of stiffened part of first dorsal-fin ray; distance between snout tip and terminus of pectoral-fin base; distance between snout tip and pectoral-fin distal end, adpressed; length of stiffened part of first pectoral-fin ray; distance between snout tip and terminus of pelvic-fin base; distance between snout tip and pelvic-fin distal end, adpressed; distance between pelvic fins; distance between snout tip and terminus of anal-fin base; first branched anal-fin ray length; distance between snout tip and anal-fin distal end, adpressed; distance between snout tip and adipose-fin base end; snout-anus distance; snout-urogenital papilla distance; anus-urogenital papilla distance; dorsal lobe of caudal fin length; ventral lobe of caudal fin length; distance between snout tip and posterior nare; anterior internarial width; and posterior internarial width. The following measurements were excluded: dorsal-, pelvic-, and anal-fin insertion to hypural plate; mandibular isthmus to lower and upper lips; postorbital distance; snout to anterior nostril distance; head depth at interorbital; and head width at posterior nostril.

According to the relative position of the premaxilla and of the dentary, the mouth is classified in one of the following categories: prognathous, when the dentary projects anteriorly to the premaxilla; isognathous, when the premaxilla and the dentary reach the same vertical anteriorly; and retrognathous, when the premaxilla projects anteriorly to the dentary. Cephalic laterosensory canal terminology follows Bockmann and Miquelarena (2008). We propose a new terminology for the melanophoric coloration elements which is based on the examination of the new species and comparative Heptapterini, mainly *Imparfinis minutus* (Lütken, 1874) and *Rhamdioglanis frenatus* Ihering, 1907, which have the most developed marks within the subfamily (Fig. 1). Dorsal bars (DBs) are discrete transversal marks present along the dorsum, from the top of the neurocranium to the end of the caudal peduncle. The usual positions of those marks, in relation to specific body structures, are as follows: DB8 is located on the caudal peduncle, approximately at the base of the anteriormost unbranched caudal-fin rays; DB7, at the terminus of the adipose-fin base or slightly anterior to it; DB6, approximately at adipose-fin insertion; DB5, midway between dorsal and adipose fins; DB4, at dorsal-fin base terminus; DB3, immediately anterior to dorsal-fin insertion; DB2, slightly posterior to supraoccipital; DB1, on supraoccipital and posterior portion of frontal. An interorbital bar is a transverse mark between the eyes. A pre-orbital stripe runs from the base of the maxillary barbel or immediately behind to the anteroventral margin of the eye. A humeral spot is located immediately posterior to the pectoral girdle and either ventral to or crossing the lateral line. A midlateral stripe runs along the lateral line, and may extend from the humeral spot or behind, to the caudal-fin base. A laterodorsal stripe may unite the lateral extremities of DBs 2–5. A caudal spot is located at the base of the upper caudal-fin lobe. Comparisons were undertaken directly through examination of specimens, including types, and original descriptions of valid species of *Heptapterus*. The term ‘allomery’ is used in the same sense as in Deprá et al. (2021). For counts, we considered all free vertebrae; the compound caudal centrum was accounted as a single element and those in Weberian complex were excluded.

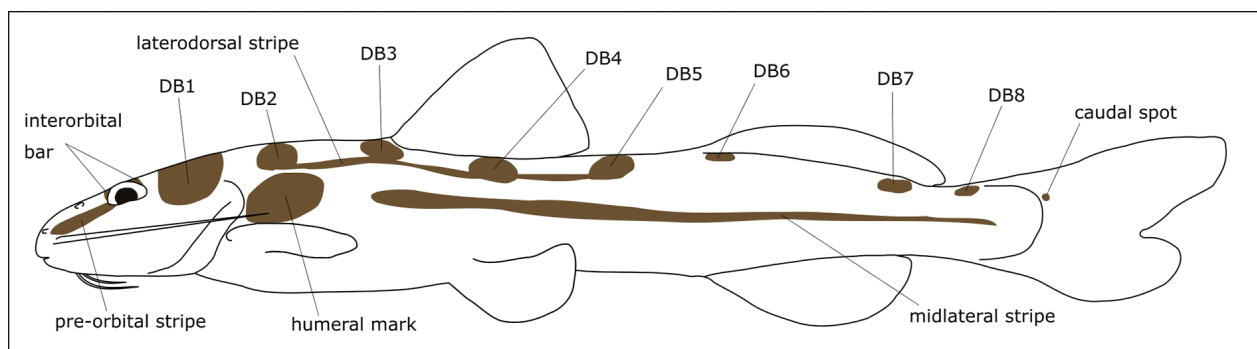


Figure 1. Schematic representation of melanophoric coloration elements that may be present in Heptapterini species, based on the new species described herein and comparative members of the same tribe (mainly *Imparfinis minutus* and *Rhamdioglanis frenatus*, in which most of the elements are present).

The map with the species distribution was modified from Azevedo-Santos et al. (2019) using the Software QGIS (Sherman et al. 2012). Biological collections where type specimens were deposited are LBP (Laboratório de Biologia e Genética de Peixes, UNESP, Botucatu, Brazil) and MNRJ (Museu Nacional, UFRJ, Rio de Janeiro, Brazil). Definitions of all other institutional abbreviations mentioned in this study may be found in Sabaj (2020) – with the exception of CICCAA (for this see Aguiar et al. 2022).

Results

Taxonomic accounts

Genus *Heptapterus* Bleeker, 1858

Type species. *Pimelodus mustelinus* Valenciennes, 1835.

Diagnosis. *Heptapterus* differs from all other Heptapterini except *Acentronichthys* Eigenmann & Eigenmann, 1889, *Nemuroglanis* Eigenmann & Eigenmann, 1889, *Chasmocranus bleekeri*, '*Chasmocranus*' *brachynema* Gomes & Schubart, 1958, '*Heptapterus*' *multiradiatus*, '*H.*' *stewarti*, and '*H.*' *sympterygium* by the presence of an adipose fin extensively fused with the caudal fin (Fig. 2). *Heptapterus* is distinguished from *Acentronichthys* by having a non-bifurcate caudal fin (i.e., caudal fin not divided in two lobes; vs. bifurcate, with distinct dorsal and ventral lobes), and from *Nemuroglanis* by having dark bars and stripes on back of trunk (vs. absence of dark bars

and stripes on back of trunk) and 5–6 pairs of pleural ribs (vs. 8–9 ribs). It is also distinguished from '*C.*' *brachynema* by having an elongate body, with a head length of 16.1–24.9% (vs. 25.5–27.3%); the posterior extension of mouth rim much shorter, with rictus barely reaching vertical line through posterior nostril (vs. posterior extension of mouth rim much longer, with rictus reaching vertical line between posterior nostril and eye); and the premaxillary tooth plate with no posterolateral extension, or with a small one (vs. with a very long posterolateral extension). It is further distinguished from *C. bleekeri* by having the pelvic-fin insertion posterior to vertical through insertion of dorsal fin (vs. anterior) and anal-fin insertion posterior to vertical through adipose-fin origin (vs. anterior). Additionally, *Heptapterus* differs from '*Heptapterus*' *multiradiatus* and '*H.*' *stewarti* by having fewer anal-fin rays (10–23 in *Heptapterus* vs. 38–46 and 33–36 in '*H.*' *multiradiatus* and '*H.*' *stewarti*, respectively). It is further distinguished from '*H.*' *sympterygium* by having the anal and caudal fins separated (vs. anal fin confluent with the caudal fin), and supraorbital pore 6 (s6) fused or closer to each other (vs. separate and closer to the eye than to each other).

Species included. *Heptapterus borodini* (Mees & Cala, 1989), *H. carmelitanorum*, *H. carnatus* Faustino-Fuster, Bockmann & Malabarba, 2019, *H. exilis* Faustino-Fuster, Bockmann & Malabarba, 2019, *H. hollandi* (Haseman, 1911), *H. mandimbusu* Aguilera, Benitez, Terán, Alonso & Mirande, 2017, *H. mbya* Azpeliçueta, Aguilera & Mirande, 2011, *H. mustelinus* (Valenciennes, 1835), *H. ornaticeps* Ahl, 1936, and *H. qenqo* Aguilera, Mirande & Azpeliçueta, 2011.

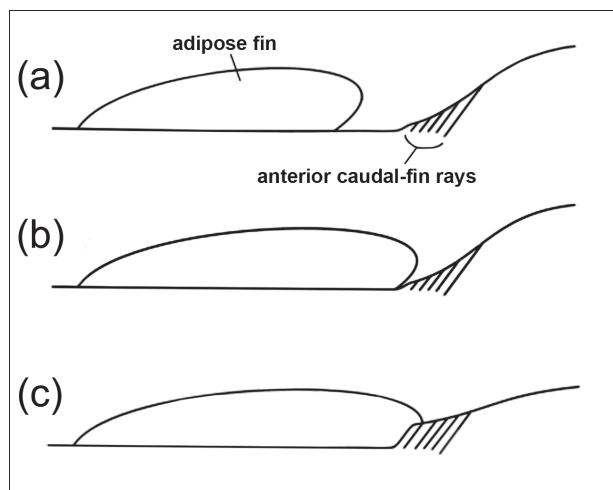


Figure 2. Schematic representation of the different degrees of proximity and connection between the adipose and caudal fins in Heptapterini. **a.** Adipose and caudal fins widely separate, as in *Imparfinis piperatus*, for instance; **b.** Adipose fin reaching the caudal fin, but not connecting to it (i.e., connective tissue in which dorsal procurrent caudal-fin rays are imbedded is not contiguous with connective tissue forming the adipose fin), as in *Chasmocranus longior*, for instance; **c.** Adipose fin connecting with caudal fin (i.e., connective tissue in which dorsal procurrent caudal-fin rays are imbedded is clearly contiguous with connective tissue forming the adipose fin), as in *Heptapterus*.

Heptapterus carmelitanorum sp. nov., Azevedo-Santos, Deprá, Aguilera, Faustino-Fuster & Katz

<https://zoobank.org/995EA984-A1D8-4A4E-8224-7D5D9637AFBF>
Figs 3, 4; Suppl. material 1: Figs S1–S4; Table 1

'*Heptapterus*' sp.: - Azevedo-Santos et al. (2019) (listed in a survey).

Holotype. MNRJ 53174, 144.3 mm SL; Brazil: Minas Gerais State: limit of Carmo do Rio Claro and Ilícinea municipalities: Unknown named stream tributary of Itací stream, tributary of Sapucaí River (stretch flooded by Furnas reservoir), Grande River Drainage, Paraná River basin, ~20°54'57"S, 45°56'21"W, altitude about 830 m asl; A. M. Katz and V. M. Azevedo-Santos, 31 October 2021.

Paratypes. LBP 26570, 1, 95.7 mm SL; same locality as holotype; V. M. Azevedo-Santos and P. N. Coelho, 22 July 2017; LBP 26575, 1, 89.1 mm SL, same locality as holotype; V. M. Azevedo-Santos and P. N. Coelho, 25 May 2018; LBP 23577, 1, 104.4 mm SL, same locality as holotype; V. M. Azevedo-Santos and P. N. Coelho, 10 April 2017.

Diagnosis. *Heptapterus carmelitanorum* differs from all congeners by possessing the anal-fin insertion less than one eye diameter posterior to a vertical through the



Figure 3. *Heptapterus carmelitanorum*, new species, holotype, MNRJ 53174, 144.3 mm SL; **a.** Dorsal view; **b.** Lateral view; **c.** Ventral view.

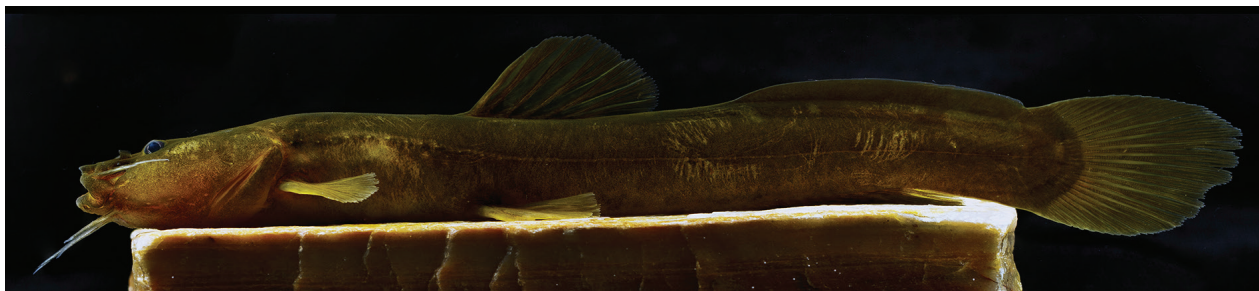


Figure 4. *Heptapterus carmelitanorum*, new species, holotype, coloration in life.

adipose-fin insertion (vs. more than one eye diameter posterior). From all congeners, except *H. borodini*, by an isognathous mouth (vs. slightly to moderately retrognathous). It differs from all other congeners except *H. borodini* and *H. hollandi*, by the keel formed by ventral procurent caudal-fin rays shallow, far from reaching anal-fin base (vs. keel formed by ventral procurent caudal-fin rays deep, continuing almost to the anal-fin base, even though its anterior portion is devoid of fin rays) (Fig. 5). It differs from both *H. borodini* and *H. hollandi* by having an almost elliptical caudal fin (vs. lanceolate in *H. borodini*, obliquely truncate to falcate in *H. hollandi*; Fig. 6), the length of its dorsal lobe 18.3–19.3% SL (vs. 24.4–43.3%

SL in *H. borodini*). Additionally, *H. carmelitanorum* differs from all other congeners, except *H. carnatus*, *H. mbya*, *H. qenqo*, and some specimens of *H. hollandi*, by having inconspicuous dorsal bars (vs. conspicuous). From *H. borodini*, *H. carnatus*, *H. exilis*, *H. hollandi*, *H. mustelinus*, and *H. ornaticeps*, by having 14–15 anal-fin rays (vs. 10–12 in *H. borodini* and *H. hollandi*; 18–21 in *H. carnatus*; 16–19 in *H. exilis*; 18–23 in *H. mustelinus*; and 19 in *H. ornaticeps*). Differs from *H. exilis* by the complete lateral line (in adults), continuous to base of hypural plate (vs. incomplete, not reaching dorsal-fin insertion). *Heptapterus carmelitanorum* further differs from *H. hollandi* by having i,6 dorsal-fin rays (vs. i,7).

Description. General morphology (Figs 3–4, 7; Suppl. material 1: Figs S1–S3). Available specimens (holotype and three paratypes) ranging from 89.1–144.3 mm SL; morphometric data in Table 1. General shape of body presented in photographs of preserved and live specimens. Dorsal profile convex from premaxillary symphysis to end of dorsal-fin base; slightly convex from that point to adipose-fin insertion; slightly convex along adipose-fin base. Caudal-fin base rounded. Ven-

tral profile convex from dentary symphysis to isthmus; straight or slightly convex from that point to anal opening; straight along anal-fin base; concave from its end to caudal-fin base. In dorsal view, mouth rim gently arched, convex; lateral profile of head convex due to well-developed *adductor mandibulae* muscle; lateral profile of body straight to slightly convex along abdomen, tapering gently to about half adipose-fin base, then tapering more abruptly to caudal-fin base.

Table 1. Morphometric data of the type specimens of *Heptapterus carmelitanorum* sp. nov.

	Paratype (LBP 23577)	Paratype (LBP 26575)	Paratype (LBP 26570)	Holotype (MNRJ 53174)	x	SD
Total length	121.5	106.6	114.1	144.3	121.6	16.296
Standard length	104.4	89.1	95.7	120.7	102.5	13.670
	As percentages of SL					
Body depth at dorsal-fin origin	12.5	9.8	9.6	11.5	10.8	0.014
Body depth at adipose-fin origin	12.3	11.0	10.6	11.1	11.2	0.007
Caudal-fin depth	14.1	12.5	14.4	10.6	12.9	0.017
Body width at dorsal-fin origin	12.5	11.4	11.4	11.7	11.7	0.005
Cleithral width	15.8	14.9	15.4	16.9	15.7	0.008
Head length to base of supra-occipital process	17.8	18.9	19.2	18.7	18.7	0.006
Lateral head length (to posteriormost point of opercle)	20.5	20.5	20.6	21.3	20.7	0.004
Maxillary-barbel length	82.2	78.1	92.4	72.4	81.3	0.084
Outer mental-barbel length	44.4	44.3	52.8	45.1	46.6	0.041
Inner mental-barbel length	29.9	29.0	27.9	31.1	29.5	0.014
Predorsal length	37.8	39.6	38.9	39.4	38.9	0.008
Distance between snout tip and terminus of dorsal-fin base	49.8	51.5	50.7	51.2	50.8	0.007
Distance between snout tip and dorsal-fin distal end, adpressed	58.4	60.7	59.8	60.3	59.8	0.010
Dorsal fin to adipose fin	15.7	15.6	16.0	14.8	15.5	0.005
Dorsal-fin base	11.8	11.6	11.1	11.4	11.5	0.003
Length of first dorsal-fin ray (unbranched)	9.5	10.2	10.9	9.9	10.1	0.006
Length of stiffened part of first dorsal-fin ray	3.3	4.5	4.9	4.1	4.2	0.007
Length of second dorsal-fin ray (first branched)	12.4	12.9	14.0	10.5	12.4	0.015
Length of third dorsal-fin ray (second branched)	13.0	13.4	14.1	12.8	13.3	0.006
Length of last dorsal-fin ray	9.0	9.1	10.0	9.4	9.4	0.005
Prepectoral length	20.1	20.0	19.5	20.0	19.9	0.002
Distance between snout tip and terminus of pectoral-fin base	22.8	22.1	23.0	23.0	22.7	0.004
Distance between snout tip and pectoral-fin distal end, adpressed	31.9	32.2	33.4	32.7	32.6	0.007
Length of first pectoral-fin ray (unbranched)	8.7	9.3	9.1	7.9	8.7	0.006
Length of stiffened part of first pectoral-fin ray	3.0	4.0	3.1	3.3	3.4	0.005
Length of second pectoral-fin ray (first branched)	10.2	11.0	10.9	9.8	10.4	0.006
Length of third pectoral-fin ray (second branched)	10.9	11.9	11.1	10.4	11.1	0.006
Pectoral to pelvic-fin distance	20.3	21.9	20.5	20.5	20.8	0.007
Prepelvic length	38.4	39.5	38.9	39.9	39.2	0.007
Distance between snout tip and terminus of pelvic-fin base	39.9	42.1	42.0	41.9	41.5	0.010
Distance between snout tip and pelvic-fin distal end, adpressed	50.9	54.2	54.8	54.3	53.5	0.018
Distance between pelvic fins	6.5	5.8	5.9	6.1	6.1	0.003
Length of first pelvic-fin ray (unbranched)	9.2	9.8	9.9	7.8	9.2	0.010
Length of second pelvic-fin ray (first branched)	10.8	10.1	12.0	12.6	11.4	0.011
Length of third pelvic-fin ray (second branched)	11.6	12.1	13.5	12.2	12.3	0.008
Pelvic to anal-fin distance	27.0	28.6	28.9	28.3	28.2	0.008
Anal-fin base	17.6	16.4	16.1	16.6	16.7	0.007
Preanal length	64.9	69.6	68.7	68.7	68.0	0.021
Distance between snout tip and terminus of anal-fin base	84.1	84.7	84.1	85.0	84.5	0.005
First branched anal-fin ray length	7.1	6.4	7.2	6.5	6.8	0.004
Distance between snout tip and anal-fin distal end, adpressed	90.5	90.8	91.0	91.7	91.0	0.005
Adipose-fin length	28.7	27.5	29.2	28.5	28.5	0.007
Preadipose length	65.3	67.0	66.0	66.6	66.2	0.007
Distance between snout tip and adipose-fin base end	93.3	94.6	96.7	95.4	95.0	0.014
Adipose-fin depth	2.7	2.2	2.5	1.8	2.3	0.004
Caudal-peduncle length	16.5	16.4	16.4	16.3	16.4	0.001
Caudal-peduncle depth at adipose-fin terminus	8.7	8.3	8.6	8.5	8.5	0.002
Snout-anus distance	44.4	46.8	46.0	45.8	45.8	0.010
Snout-urogenital papilla distance	47.9	49.9	48.4	49.7	49.0	0.010
Anus-urogenital papilla distance	3.3	3.0	2.9	3.4	3.2	0.002
Dorsal lobe of caudal fin length	18.9	18.3	19.1	19.3	18.9	0.004
Ventral lobe of caudal fin length	15.2	15.4	16.2	16.6	15.8	0.006

	Paratype (LBP 23577)	Paratype (LBP 26575)	Paratype (LBP 26570)	Holotype (MNRJ 53174)	x	SD
	As percentages of HL (lateral)					
Head depth	46.3	41.5	43.1	43.6	43.6	0.020
Head width	76.6	72.7	74.6	78.6	75.6	0.026
Eye diameter	15.9	15.3	15.2	14.8	15.3	0.005
Fleshy interorbital	15.9	-	16.2	19.1	17.1	0.017
Bony interorbital	9.8	11.5	10.2	10.1	10.4	0.007
Mouth gape	41.1	40.4	39.6	41.6	40.7	0.009
Snout length	33.2	33.9	34.5	33.1	33.7	0.007
Distance between snout tip and posterior nare	22.0	22.4	22.3	23.3	22.5	0.006
Distance between posterior nostril and eye	8.9	7.7	9.1	11.3	9.2	0.015
Anterior internarial width	23.4	25.1	19.3	21.0	22.2	0.026
Posterior internarial width	20.1	21.9	19.8	20.2	20.5	0.009
Intranarial length	22.4	20.2	21.3	24.9	22.2	0.020

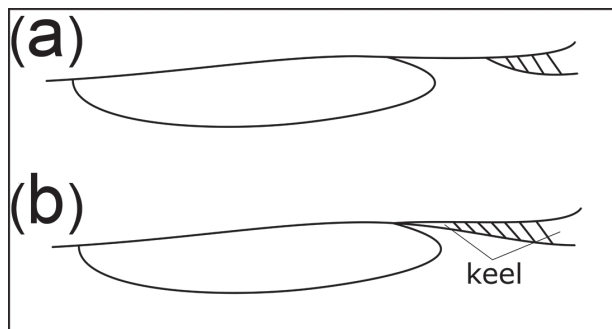


Figure 5. Schematic representation of the different degrees of proximity between the anal and caudal fins in *Heptapterus*. **a.** Keel formed by rigid connective tissue with imbedded ventral procurrent caudal-fin rays not much developed, its anterior end distant from anal-fin base (*Heptapterus borodini*, *H. carmelitanorum* and *H. hollandi*); **b.** Keel well developed, its anterior end reaching or almost reaching anal-fin base (remaining *Heptapterus* species).

Head much depressed, flat dorsally and ventrally, rounded laterally. Mouth isognathous. Mouth rictus fleshy, folding ventrally, with large sub-labial groove beneath it (Fig. 7a). Lips double, i.e., divided by deep labial slit into outer and inner lip (Fig. 7b). Outer dorsal lip thickly and abundantly plicate; outer lower lip thickly, but scarcely plicate; inner dorsal and ventral lips finely and abundantly plicate (Fig. 7b). Tubular anterior nostril not reaching mouth rim. Deep skin fold surrounding entire posterior nostril, but with deep posterior notch (Fig. 7c). Maxillary barbel groove extending from base of barbel almost to the eye; in dorsal view, rim of groove almost parallel with body axis. Dorsal surface of snout with shallow depression posteriorly to posterior nostril, and elongate depression marking anterior cranial fontanel (Fig. 7b). Bulging eyes covered in thick skin with no free rim, almost completely dorsal. Base of inner mental barbel slightly anterior to that of outer mental barbel, distinctly posterior to base of maxillary barbel. Maxillary barbel reaching anterior margin of first pectoral-fin ray. Shallow cleithral skin fold immediately posterior to branchial aperture, posterior terminus medial to base of first pectoral-fin ray (Fig. 7a). Abdominal region depressed, distinctly broader than deep; in cross section, something between elliptic and rectangular. Cross section at

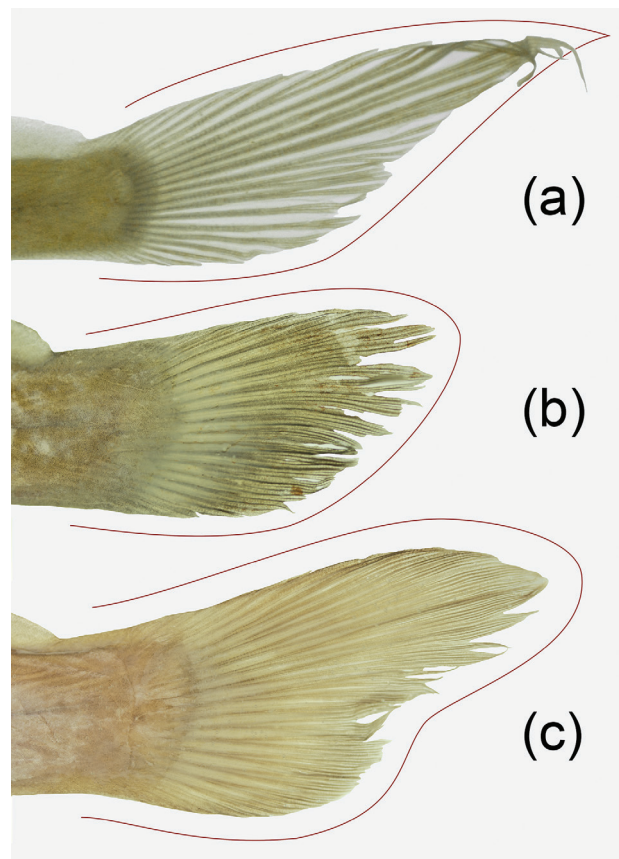


Figure 6. Different caudal-fin shapes in *Heptapterus*. **a.** *H. borodini*, NUP 14882, 74.3 mm; **b.** *H. hollandi*, young; **c.** *H. hollandi*, adult, NUP 5978, 199.1 mm SL.

dorsal-fin base approximately as broad as deep, between round and square. Body compressed from adipose-fin insertion to caudal fin, cross-section distinctly deeper than broad. Vertebrae 43. Ribs 9 (Suppl. material 1: Fig. S4).

Dorsal fin distal margin convex; i,6*(4) rays (first ray rigid only basally); each branched ray with, at least, tertiary branches; thin membrane between rays. Pelvic-fin insertion at same vertical as base of second (first branched) dorsal-fin ray (2 specimens) or between bases of first and second rays (2*). Adipose fin continuous (i.e., connected) with the anteriormost ray of dorsal portion of caudal fin, originating slightly anteriorly to vertical through anal-fin insertion (distance less than one eye diameter); margin

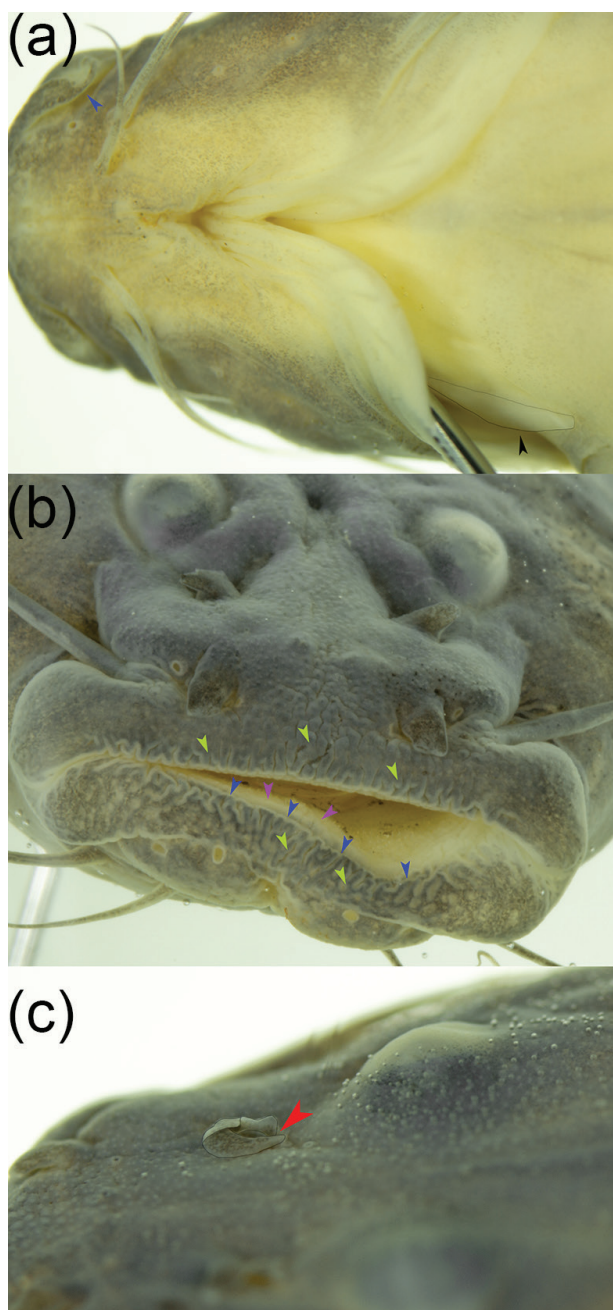


Figure 7. Superficial structures in *Heptapterus carmelitanorum*; **a.** Sub-labial groove (blue arrowhead) and cleithral skinfold (black arrowhead); **b.** Labial slit (blue arrowheads) and plicae on the outer (lemon arrowheads) and inner (pink arrowheads) lips; **c.** Posterior nostril, evidencing shape of posterior notch (red arrowhead).

slightly convex. Caudal fin approximately elliptical, rays of dorsal half little longer than ventral ones; xiii,8,8,xi*(1) xv,7,8,xv(1), xvii,6,7,xiv(1), xvii,6,7,xvi(1) rays (Suppl. material 1: Fig. S5); thin membrane between rays. Pectoral fin approximately elliptical, with anterior rays longer than posterior ones; i,7,i(2), i,8*(2) rays on left side (first ray rigid only basally); on right side, i,7,i*(4); each branched ray with, at least, tertiary branches; thin membrane between rays. Pelvic fin approximately elliptical, with anterior rays longer than posterior ones; i,5 (4) rays

on both sides; each branched ray with, at least, tertiary branches; thin membrane between rays.

Premaxillary toothplate about twice as wide as long, length of lateral margin slightly higher than symphyseal margin; small posterolateral projection present; about six rows of conical teeth (tooth plate virtually identical to the one in Mees 1967, fig. 1c). External gill rakers on first arch 1+6*(3), 1+7(1). Branchiostegal rays 8(2) (Suppl. material 1: Fig. S5).

Laterosensory system. Cephalic laterosensory pores as Bockmann and Miquelarena (2008) described for *Rhamdella cainguae* Bockmann & Miquelarena, 2008, except in following details (Fig. 8): s2+i2 pore much closer to anterior nostril (vs. at about middle of the distance between anterior and posterior nostrils); s4 pore distinctly more medial than s3 pore (vs. slightly more medial); s8 with two pores (s8a and s8p; vs. s8 with one pore); po3 with two pores (po3a and po3p; vs. po3 with one pore); pm1 pore only slightly posterior to transversal line across pm2 pore (vs. much posterior to it); pm1 directed medially, facing antimere (vs. directed ventrally); pm2 and pm3 pores facing anteroventrally (vs. posteroventrally and ventrally, respectively); pm4 and pm5 pores antero-medial to rictus (vs. posteromedial and posterior to it, respectively); pm10 pore slightly closer to po1+pm11 pore than to pm9 pore (vs. much closer to pm9 pore). Eye also more distant from i5, i6, s6, s7, and s8 pores than in *R. cainguae*, seemingly due to anterior displacement of eye in *Heptapterus carmelitanorum*. Lateral line continuous to hypural plate, with 43(1), 46(1), 63(1) pores, or ending on hypural plate, but with large gap between anterior and posterior portions, with 23(1) total pores (smallest specimen, LBP 26575).

Olfactory organ. One specimen (LBP 23577) dissected with two longitudinal series of flat, triangular lamellae on right olfactory canal, each series with 32 lamellae (Fig. 9).

Epidermal papillae. In LBP 23577, external surface of body covered with densely packed, flexible, perpendicularly protruding epidermal papillae (except lips; distal half of barbels, tubular portion of anterior nostril and skin flap of posterior nostril; center of eye; distal margin of branchiostegal membrane; and nearly entire fins). Distance between adjacent papillae ~0.15 mm, equal to their maximum length. Papillae slender, rod-like on most of body (Fig. 10a, b); short, club-like, apparently with widened distal extremity on ventral surface of head (Fig. 10c; widened portion possibly attached mucus). Very small papillae on anterior face of first pectoral- and pelvic-fin ray; on base of caudal-fin rays; on margin of eye; on base of tubular portion of anterior nostril; on base of skin flap of posterior nostril; on ventral half of adipose fin. Scarce, but well-developed papillae on urogenital papilla and anus. All epidermal papillae visible only after removal of body mucus.

Color in alcohol (Fig. 3, Suppl. material 1: Figs S1, S2). Background color greyish-brown, grading to white towards belly and to white beige towards region between anus and anal fin, and ventral side of head; transition

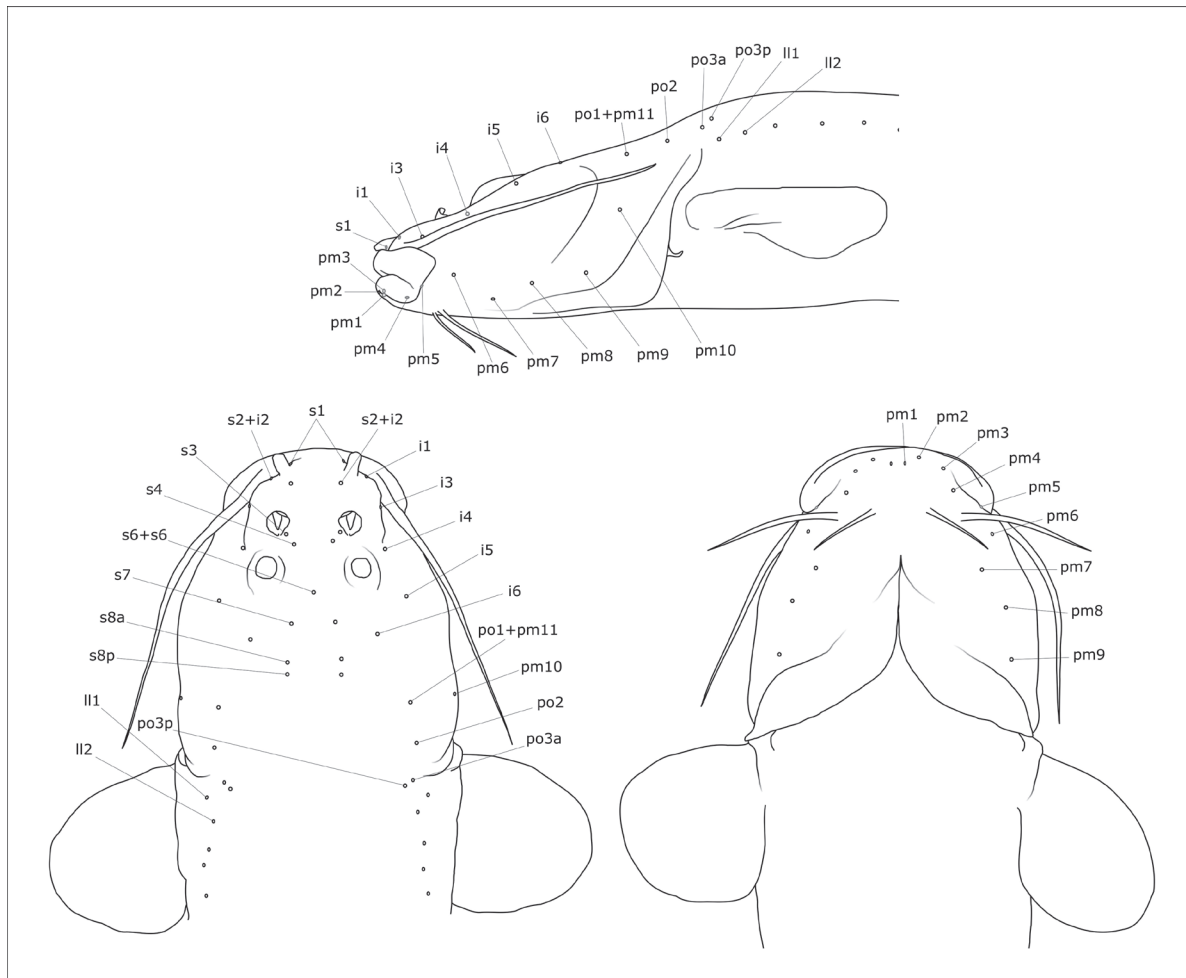


Figure 8. Cephalic laterosensory system of *Heptapterus carmelitanorum*, new species (based on LBP 23577); abbreviations as in Bockmann and Miquelarena (2008).



Figure 9. *Heptapterus carmelitanorum*, LBP 23577, dissected to show the olfactory organ (anterior side to the right). Some of the lamellae in the outer (red arrowhead) and inner (green arrowhead) series are outlined in blue to better evidence their shape.

between brown and light beige more abrupt on head than in remainder of body. Caudal spot very faint, small, at base of dorsalmost branched caudal-fin ray; DB8 and 7 absent; DB6 through 4 inconspicuous, dark-brown (respectively, at adipose-fin insertion; midway between dorsal and adipose fins; and terminus of dorsal-fin base); DB3 present as roundish dark-brown spot immediately anterior to dorsal fin; DB2 very faint, little posterior to supraoccipital, at vertical through posterior end of pectoral-fin base; DB1 dark brown, extending to opercle; interorbital bar indistinct. Pre-orbital stripe very diffuse, dark-brown. Diffuse, dark-brown humeral spot; faint midlateral stripe present in LBP 26570 specimen; laterodorsal stripe absent.

Color in life (Fig. 4, Suppl. material 1: Fig. S3). General pattern of body dark brown, yellowish in the holotype (Fig. 4). Ventral region from isthmus to anal-fin insertion paler than remainder of body and somewhat pinkish, as well as cheek, branchiostegal membrane, cleithrum and lateral line. All fin rays dark brown. Adipose fin brownish yellow or dark yellowish brown. Inter-radial membranes of pectoral, anal and caudal fins yellow. Dorsal-fin interrational membrane hyaline, with scattered melanophores on basal third. Barbels dark brown dorsally and beige ventrally.

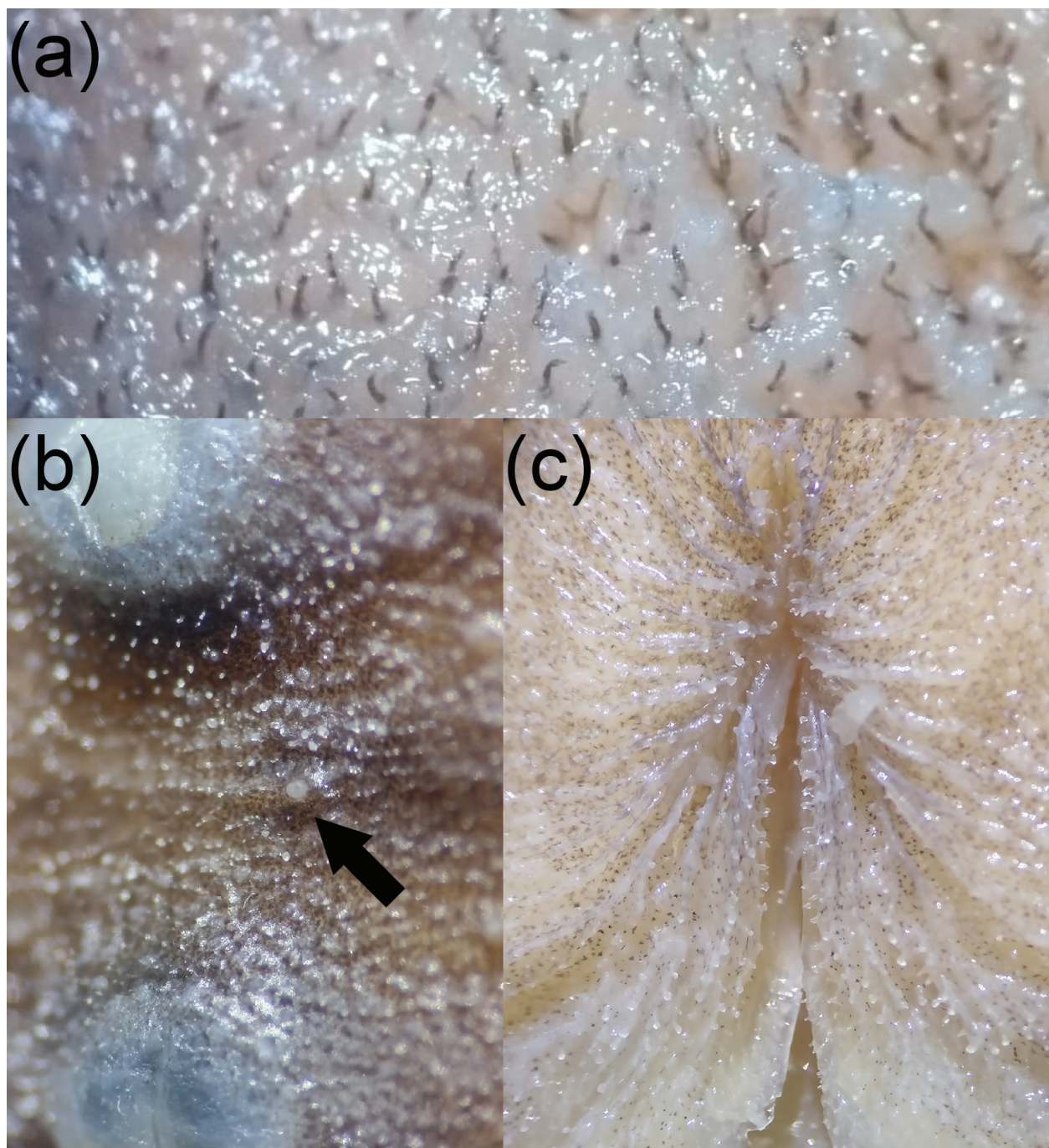


Figure 10. Epidermal papillae in *Heptapterus carmelitanorum*, LBP 23577, paratype. **a, b.** Slender, rod-like papillae are distributed on most of body, such as on the dorsum, between the head and dorsal fin (**a**) and on the head (**b**, arrow shows s6+s6 pore); **c.** Short, club-like papillae are distributed on ventral surface of head.

Ontogeny. Strong positive allometry in cleithral width ($R^2 = 0.997$), head length (0.742), fleshy interorbital distance (0.809), mouth width (0.633), and dorsal caudal-fin lobe length (0.593; compare Fig. 3, Suppl. material 1: Figs S1, S2); moderate positive allometry in ventral caudal-fin lobe length (0.362); moderate negative allometry in bony interorbital distance (0.392), maxillary-barbel length (0.313), first dorsal-fin ray length (0.259), and maximum adipose-fin height (0.317); strong negative allometry in dorsal-adipose distance (0.656), first pectoral-fin ray length (0.993), and first pelvic-fin ray length

(0.918). Positive allometry present in the number of branched rays in the dorsal caudal-fin lobe ($R^2 = 0.5712$) and in the number of lateral-line pores (0.899).

Etymology. The specific name is a noun in apposition derived from *Carmelitanos* (in Portuguese), the local appellation of people born or living in Carmo do Rio Claro (Minas Gerais, Brazil), the city where the species was discovered. The name is in honor of *Carmelitanos*, especially Ana Maria Vilela Soares, José Cândido de Mello Carvalho, Moara Lemos, and Carlos Roberto Bueno Júnior, for their contributions to biological science.

Geographical distribution and ecological notes.

Heptapterus carmelitanorum is recorded only from a single unnamed stream. The watercourse is a tributary of Itací stream – ribeirão Itací, in Portuguese – which is an affluent of Furnas reservoir (in the Sapucaí River arm), Grande River basin, in the upper Paraná River system, in Minas Gerais State, Brazil (Figs 11, 12).

The stream in which specimens of *H. carmelitanorum* were collected has its source on a mountain known as “Chapadão” (in Portuguese), approximately 1,300 meters a.s.l. Its channel crosses successive falls (forming waterfalls), including one over 50 meters high. The type locality lies downstream from the waterfalls. According to the classification proposed by Strahler (1954), the stream may be classified as third order. The water was extremely clear (small characids readily observed) and well oxygenated. The stream depth was shallow (not exceeding 1 meter), and its bed was completely formed by rocks. Light penetration was low during samplings. In

the reach, submerged tree roots and accumulated leaves and fruits (especially Fabaceae) formed some microhabitats for some species, notably *Trichomycterus candidus* (Miranda Ribeiro, 1949) and *Cetopsorhamdia iheringi* Schubart & Gomes, 1959. The specimens of *H. carmelitanorum* were captured in environments that combined rocks (generally juxtaposed) and a more turbulent flow (see Fig. 12). Observation during sampling suggests that the species is demersal.

Species collected with *H. carmelitanorum* include *C. iheringi*, *Hoplias malabaricus* (Bloch, 1794), *Knodus moenkhausii* (Eigenmann & Kennedy, 1903), *Odontotilbe weitzmani* Chuctaya, Bührnheim, & Malabarba, 2018, *Oligosarcus argenteus* Günther, 1864, *Pareiorhina* sp., *Psalidodon* sp., *T. candidus*, *T. septemradiatus* Katz, Barbosa & Costa, 2013 (Azevedo-Santos et al. 2019). New collections in the same reach resulted in the capture of additional species, such as *Apareiodon* sp. (CICCAA06610) and *Rhamdiopsis* sp. (CICCAA06611). In addition to

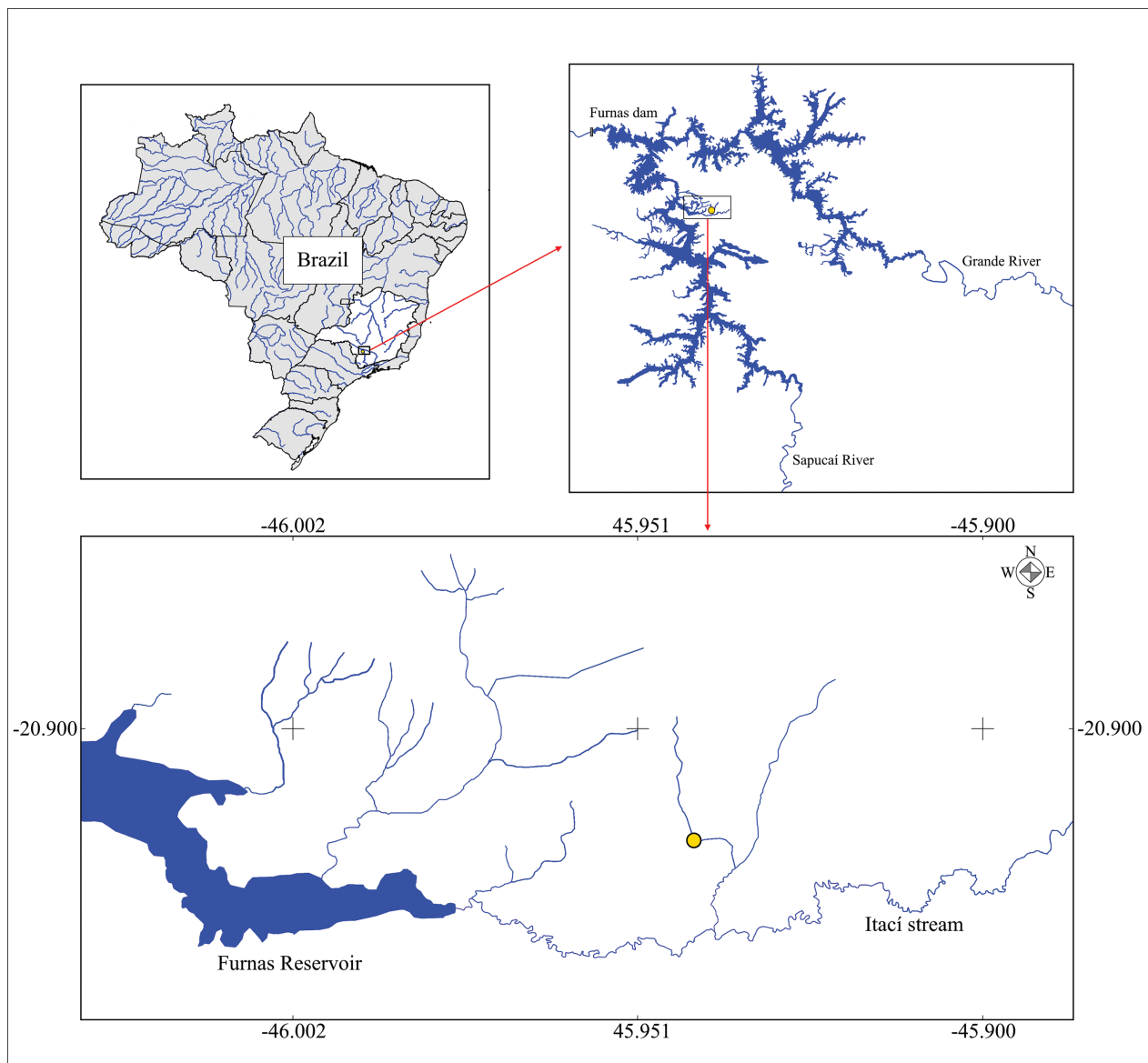


Figure 11. Distribution of *Heptapterus carmelitanorum*.



Figure 12. Partial view (i.e., stretch) of the stream where the type specimens of *Heptapterus carmelitanorum* were sampled.

fishes, aquatic spiders (e.g., *Tetragnatha* sp.) and insects, including specimens of the order Trichoptera in cases formed by small gravels, were captured in the stretch.

Discussion

Definition of *Heptapterus*

We propose a new diagnosis for *Heptapterus*, aiming to facilitate its recognition among members of Heptapterini, based on external characters only. The new definition pursued taxonomic stability by making the fewest possible alterations to the definition of Bleeker (1864), although that means rejecting the definitions proposed by subsequent authors, such as Gosline (1941) and Mees (1967). Our circumscription of *Heptapterus* also reflects that little knowledge is currently available on Heptapterini phylogeny. Because Silva et al. (2021) recovered '*Imparfinis*' (= *Heptapterus*) *borodini* as closely related to *H. mustelinus*, we opted provisionally for including that species, along with the morphologically similar *H. carmelitanorum* and *H. hollandi* in *Heptapterus* [those species are considered by Bockmann and Slobodian (2017) to form "new genus D"].

About the fins of *Heptapterus*, Bleeker (1864:90) said: "pinna dorsali anteriore ventralibus opposita" [dorsal fin

longitudinally aligned with pelvic fin]; "adiposa elongata cum caudali unita, analis subelongata mediae adiposae opposita" [adipose fin elongate, united with caudal fin; anal fin subelongate, longitudinally aligned with the middle of adipose fin]. He was vague about the degree of elongation of the adipose fin in *Heptapterus*; the type species, *H. mustelinus*, and most other congeners have an adipose-fin base length greater than 40% SL (up to 58.5% SL in *H. mbya*), which is a rare condition among Heptapterini, found elsewhere only in *Acentronichthys*. However, *H. mandimbusu*, which is, in general terms, very similar to the type species, may have a length as short as 33.8% SL, which overlaps the values observed in *H. borodini* (31.4–41.0% SL) and *H. hollandi* (29.1–35.1% SL), and is only slightly higher than in *H. carmelitanorum* (27.4–29.1% SL). Thus, we had to adapt Bleeker's diagnosis to recognize that in *Heptapterus* the adipose-fin base length presents a continuum of variation, ranging from moderately to extremely elongate.

Bleeker (1864) was also unclear about the length of the anal fin. Although *H. mustelinus* does have a large number of anal-fin rays (18–23) lying about the middle of the range observed in Heptapterini, other species previously included in *Heptapterus*, viz. *H. mandimbusu*, *H. mbya* and *H. qenqo*, may have lower numbers (respectively, 14–18, 15–17 and 15–17). *Heptapterus borodini*,

H. carmelitanorum and *H. hollandi* have, respectively, 10–12, 14–15, and 10–12 anal-fin rays. The number of anal-fin rays is useful to distinguish *Heptapterus* from the *incertae sedis* ‘*H.*’ *multiradiatus* (38–46 rays), ‘*H.*’ *stewarti* (33–36) and ‘*H.*’ *sympterygium* (22–29). Our adaptations of Bleeker’s (1864) diagnosis render the adipose-fin base length and the number of anal-fin rays inadequate to diagnose between *Heptapterus* and *Chasmocranus* Eigenmann, 1912, a quite similar genus. That is because *C. bleekeri* has an adipose-fin base length of up to about 35% (Mees, 1967), and the number of anal-fin rays in all *Chasmocranus* species overlaps the lower portion of the range observed in *Heptapterus* (which is 10–23). On the other hand, the relative position between the adipose and anal fins differs between the two genera. Some species, such as *H. mustelinus*, do have the anal fin approximately aligned with the center of adipose fin, as described by Bleeker (1864). In other species, the anal-fin insertion may be considerably closer to a vertical through the adipose-fin insertion, such as in *H. mandimbusu*, *H. borodini*, *H. hollandi*, and especially in *H. carmelitanorum* (in which the anal-fin insertion is only slightly posterior to adipose-fin insertion). This, too, makes our definition of *Heptapterus* a little different from that of Bleeker (1864). However, it is worth mentioning that this character state is useful to distinguish *Heptapterus* from all species included in *Chasmocranus* by Bockmann and Slobodian (2017), and by us [viz. ‘*C.*’ *brevior* Eigenmann, 1912, *C. bleekeri* Boeseman, 1953, *C. chimantanus* Inger, 1956, *C. longior* Eigenmann, 1912, *C. surinamensis* (Bleeker, 1862) and *C. tapanahoniensis*], all of which have the anal-fin insertion anterior to a vertical through the adipose-fin insertion. In fact, that character also diagnoses *Heptapterus* from *Pariolius*, which was considered as a junior synonym of the former by Mees (1974).

In other aspects, our diagnosis of *Heptapterus* agrees with that by Bleeker (1864). All species included herein in the genus have the pelvic-fin insertion at the vertical through the base of the first dorsal-fin ray or slightly posterior to it (up to third). By that character, they differ from several members of Heptapterini, such as *C. bleekeri*, *Horiomyzon* Stewart, 1986, *Nannoglanis* Boulenger, 1887, *Pariolius*, and most *Phenacorhamdia* Dahl, 1961 (pelvic-fin insertion anterior to dorsal-fin insertion); and *Cetopsorhamdia* Eigenmann & Fisher, 1916, and most *Imparfinis sensu stricto* (pelvic-fin insertion posterior to vertical through fourth dorsal-fin ray). Still, that character is not helpful to distinguish between *Heptapterus* and the most similar genera, i.e., *Chasmocranus* and *Acentronichthys*.

Used in combination, the adipose fin confluent with the caudal fin and the non-bifurcate caudal fin distinguishes *Heptapterus* from the remaining Heptapterini (except *C. bleekeri*, some *Nemuroglanis*, and some of the species recently removed from *Heptapterus*, viz. ‘*H.*’ *multiradiatus*, ‘*H.*’ *stewarti* and ‘*H.*’ *sympterygium*). Moreover, the extremely elongate body is found otherwise in Heptapterini only in *Acentronichthys*, *Chasmocranus*, some species of *Phenacorhamdia*, large specimens of

Rhamdioglanis Ihering, 1907, and the *incertae sedis* species ‘*I.*’ *longicauda* (Boulenger 1887) and ‘*I.*’ *microps* Eigenmann & Fisher, 1916.

One peculiar species of Heptapterini – the *incertae sedis* ‘*C.*’ *brachynema* – does resemble *Heptapterus* species. Whereupon the adipose fin is confluent with the caudal and the pelvic-fin insertion is positioned between the verticals through the insertion and through the middle of the dorsal-fin base, and the anal-fin insertion located posteriorly to a vertical through the adipose-fin insertion (in which ‘*C.*’ *brachynema* differs from *Chasmocranus*). It is also quite similar to *H. borodini*, *H. carmelitanorum* and *H. hollandi* in having large, bulging, closely set eyes. However, ‘*C.*’ *brachynema* differs from all *Heptapterus* in having a distinctly shorter body (this character also distinguishes it from all *Chasmocranus*, *sensu stricto*); bifurcate caudal fin (although the notch between the two lobes is very shallow and the dorsal one is distinctly longer than the ventral one); and extremely long posterolateral extension of the premaxillary toothplate (even longer than the extension present in *Chasmocranus*, as can be seen in Gomes and Schubart 1958, and Mees 1967, fig. 1; this character is correlated with the peculiar shape of the mouth of ‘*C.*’ *brachynema*).

Heptapterini in the southern Neotropics

The southern Neotropics (including the Paraná-Paraguay River system, the São Francisco River basin and all other river basins that empty in the Atlantic Ocean between the mouths of those major rivers) hold 35 valid Heptapterini species. These are: *Acentronichthys leptos* Eigenmann & Eigenmann, 1889, *A. fissipinnis*, *Cetopsorhamdia iheringi*, ‘*Chasmocranus*’ *brachynema*, ‘*C.*’ *lopezae* Miranda-Ribeiro, 1968, ‘*C.*’ *truncatorostris* Borodin, 1927, *Heptapterus borodini*, *H. carmelitanorum*, *H. carnatus*, *H. exilis*, *H. hollandi*, *H. mandimbusu*, *H. mbya*, *H. mustelinus*, *H. ornateiceps*, *H. qenqo*, ‘*Heptapterus*’ *multiradiatus*, ‘*H.*’ *stewarti*, ‘*H.*’ *sympterygium*, *Imparfinis minutus*, *I. mirini* Haseman, 1911, *I. mishky* Almirón, Casciotta, Bechara, Ruíz Díaz, Bruno, d’Ambrosio, Solimano & Soneira, 2007, *I. piperatus*, *I. schubarti* (Gomes, 1956), ‘*I.*’ *stictonotus* (Fowler, 1940), *Phenacorhamdia roxoi* Silva, 2020, *P. tenebrosa* (Schubart, 1964), *P. unifasciata* Britski, 1993, *P. hoehnei* (Miranda Ribeiro, 1914), *Rhamdioglanis frenatus*, *R. transfasciatus* Miranda Ribeiro, 1908, *Rhamdiopsis krugi* Bockmann & Castro, 2010, *R. microcephala* (Lütken, 1874), *R. moreirai* Haseman, 1911, and *Taunayia bifasciata* (Eigenmann & Norris, 1900). This species richness comprises 39.3% of the tribe. Considering genera, *Acentronichthys*, *Rhamdioglanis*, *Rhamdiopsis* Haseman, 1911, and *Taunayia* Miranda Ribeiro, 1918, are exclusively found in the southern Neotropics, whereas *Heptapterus* is only marginally distributed in the Tocantins River basin.

Some species appear to be quite restricted in some watercourses of southern Neotropics, such as ‘*C.*’ *brachynema* (Mogi-Guaçu River), ‘*C.*’ *lopezae* (record-

ed from type locality in Cubatão and from Ribeira de Iguape River basin, but possibly restricted to the former), *H. carmelitanorum* (restricted to type locality in the Grande River basin), *H. hollandi* (Iguaçu River basin), ‘*H.*’ *multiradiatus* (upper Tietê River basin), ‘*H.*’ *stewarti* (upper stretches of Iguaçu and Tibagi River basins), ‘*H.*’ *sympterygium* (Patos Lagoon basin), *P. unifasciata* (Paranaíba River basin), *R. moreirai* (upper stretches of Iguaçu and Tibagi River basins), *Taunayia bifasciata* (upper stretches of Paraíba do Sul and Tietê River basins). Others are thought to have a wider distribution, such as *H. borodini*, *I. mirini* and *I. schubarti* (Ota et al. 2018; Reis et al. 2020). However, populations assigned to those species, especially in State of Paraná, seem to form species complexes (G. C. Deprá and V.M. Azevedo-Santos, personal observation), which means that, instead of few, widely distributed species, they may represent several relatively restricted ones. The analysis of those populations, which presently is being carried on by G. C. Deprá, V.M. Azevedo-Santos and collaborators, is likely to contribute to an increase in the number of Heptapterini species, as well as our knowledge of the biogeography of the Upper Paraná ecoregion – which already has been demonstrated to comprise different sub-ecoregions, each with a peculiar ichthyofauna (Reis et al. 2020).

Besides investigating the existence of species complexes, we emphasize the importance of sampling poorly known river basins, especially using different methodologies. For example, all the type specimens of *H. carmelitanorum* were collected in a recent survey (Azevedo-Santos et al. 2019; and after new expeditions) carried out in tributary streams of the Grande River system, in southeastern Brazil (Azevedo-Santos et al. 2019). New collections (one in 2020 and three in 2021) at the same locality were performed and in streams with sources in the same mountain (i.e., Chapadão) as the one in which specimens of *H. carmelitanorum* were sampled, but no additional specimens were captured. Publications (Alves et al. 1998; Castro et al. 2004; Andrade and Braga 2005; Ingenito and Buckup 2007; Pompeu et al. 2009; Belei and Sampaio 2012; Casarim et al. 2012; Casatti et al. 2012; Fernandes et al. 2012; Gandini et al. 2012; Fagundes et al. 2015; Santos et al. 2017; Azevedo-Santos et al. 2018; Thereza and Langeani 2019; Ribeiro et al. 2019; Lima et al. 2021), as well as collections (e.g., LBP, DZSJRP) with fishes from the Grande River basin were consulted, but we were not able to find heptapterids (identified as *Imparfinis*, *Chasmocranus* or *Heptapterus*) that represent *H. carmelitanorum*. It is possible, therefore, that a new survey may reveal undescribed heptapterids in single streams or rivers of the upper Paraná River basin.

Conclusion

Here we propose a new diagnosis of the genus *Heptapterus* based on external characters. In addition, we proposed *H. carmelitanorum* sp. nov. from the Grande River basin, upper Paraná River basin, in Minas Gerais,

Brazil. *Heptapterus* comprises ten valid species, viz. *H. borodini*, *H. carmelitanorum*, *H. carnatus*, *H. exilis*, *H. hollandi*, *H. mandimbusu*, *H. mbya*, *H. mustelinus*, *H. ornateps*, and *H. qenqo*. Additional surveys (as in the case of *H. carmelitanorum*) and examination of heptapterid specimens present in biological collections certainly will increase the diversity known to that genus.

Comparative material.

Material listed by Aguilera et al. (2011), Aguilera et al. (2017), Faustino-Fuster et al. (2019) and individuals of heptapterid species listed in Azevedo-Santos et al. (2019; 2020). In addition, the following lots were examined:

Acentronichthys leptos Eigenmann & Eigenmann, 1889: ANSP 174017, 2, 76.1–78.2 mm SL, Macaé River, Rio de Janeiro, Brazil.

Cetopsorhamdia iheringi Schubart & Gomes, 1959: EEBP 368, 76.30 mm SL, Mogi Guaçu River, São Paulo, Brazil.

‘*Chasmocranus*’ *brachynema* Gomes & Schubart, 1958, EEBP 629, 74.2 mm SL, Mogi Guaçu River, São Paulo, Brazil.

Chasmocranus longior Eigenmann, 1912: FMNH 53208, holotype, 92.9 mm SL, Essequibo River, Potaro-Siparuni, Guyana.

‘*Chasmocranus*’ *truncatorostris* Borodin, 1927: AMNH 8640, holotype, 109.9 mm SL, Colonia Hansa, Santa Catarina, Brazil.

Heptapterus borodini (Mees & Cala, 1989): AMNH 8639, holotype (examined by photograph); State of Goiás, Caldas Novas, Corumbá River, São Paulo, Brazil; NUP 5221, 6, 32.8–64.6 mm SL, Gameleira Stream, Goiás, Brazil; NUP 6088, 1, 74.2 mm SL, Piava Stream, Paraná, Brazil; NUP 14882, 3, 44.5–85.9 mm SL, Araponga Stream, Mato Grosso do Sul, Brazil.

Heptapterus hollandi Haseman, 1911: FMNH 54244, holotype, 230.4 mm SL, Iguaçu River, Porto União da Victoria, Paraná, Brazil; NUP 5978, 11, Caxias Reservoir, Capitão Leônidas Marques, Paraná, Brazil.

‘*Heptapterus*’ *multiradiatus* Ihering, 1907: FMNH 56901, 10, 34.3–86.8 mm SL, Tietê River, São Paulo, Brazil. FMNH 93272, 73.1 mm SL, Upper rio Paraná, São Paulo, Brazil.

Imparfinis schubarti (Gomes, 1956): EEBP 391, Paratype, 2, 80.3–90 mm SL, Mogi Guaçu River, São Paulo, Brazil.

Nemuroglanis lanceolatus Eigenmann & Eigenmann, 1889: FMNH 98306, 7, 14.5–35.7 mm SL, Napo River, Sucumbios, Ecuador.

Nemuroglanis mariaii (Schultz, 1944): ANSP 139581, 1, 29.6 mm SL, Venturosa stream, Meta; ANSP 139582, 3, 20.0–23.1 mm SL, El Viento creek, Matazul, Meta, Colombia; ANSP 139583, 1, 35.1 mm SL, unnamed stream tributary to Mozambique lake, Hacienda Humacita, Meta, Colombia.

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Supplementary material 1

Figures S1–S5

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Data type: Figures (docx. file)

Explanation note: **Figure S1.** *Heptapterus carmelitanorum*, new species, paratype, LBP 23577, 104.4 mm SL, (a). Dorsal view, (b). Lateral view, (c). Ventral

view. **Figure S2.** *Heptapterus carmelitanorum*, new species, paratype, LBP 26570, 95.7 mm SL. (a). Dorsal view, (b). Lateral view, (c). Ventral view. **Figure S3.** *Heptapterus carmelitanorum*, new species, paratype, color in life, LBP 23577, 104.4 mm SL. **Figure S4.** X-ray of *Heptapterus carmelitanorum*, holotype, MNRJ 53174, 144.3 mm SL. (a). Lateral view, (b). Ventral view, (c). Dorsal view. **Figure S5.** X-ray of *Heptapterus carmelitanorum*, holotype, MNRJ 53174, 144.3 mm SL. (a). Ventral view of head, (b). Lateral view of caudal fin.

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