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Taxonomical revision of *Cambeva stawiarski* (Miranda Ribeiro, 1968) (Siluriformes, Trichomycteridae) with the description of a new species from the Rio Iguaçu basin, Paraná State, Brazil

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RENAN BORGES DOS REIS

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Orientador: Prof. Dr. Weferson Júnio da Graça
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Prof. Dr. Weferson Júnio da Graça
Universidade Estadual de Maringá/DBI (Presidente)

Dr.ª Carla Simone Pavanelli
Universidade Estadual de Maringá/Nupélia

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Vince te ipsum - Supere a si mesmo.

Revisão taxonômica de *Cambeva stawiarski* (Miranda Ribeiro, 1968) (Siluriformes, Trichomycteridae) com a descrição de uma nova espécie da bacia do Rio Iguaçu, estado do Paraná, Brazil

RESUMO

O objetivo foi redescrever *Cambeva stawiarski*, com base em dados morfológicos internos, morfologia externa, morfometria e dados merísticos, por meio da revisão do material tipo e de material depositado em coleções ictiológicas. Neste processo, fora acrescentado comentários sobre a possível localidade-tipo de *Cambeva stawiarski* e descreveu-se uma nova espécie de *Cambeva*, endêmica da bacia do rio Iguaçu, Brasil. *Cambeva stawiarski* e a nova espécie são diagnosticadas pela combinação de caracteres como número de raios procurrentes caudais dorsais e ventrais; número de vértebras; número de raios na nadadeira peitoral; número de raios branquiostegais; nadadeira caudal com pequeno entalhe na margem distal; comprimento da cabeça; altura do pedúnculo caudal; e padrão de colorido do corpo. As espécies também são comparadas com outras espécies possivelmente relacionadas e os caracteres sinapomórficos desses grupos de espécies são discutidos. Com a confirmação do endemismo de *Cambeva stawiarski* e a descrição de uma nova espécie de *Cambeva* para a bacia do rio Iguaçu, confirmamos importantes padrões biogeográficos sobre o endemismo da bacia hidrográfica e sobre a utilização de dados osteológicos na descrição de espécies de *Cambeva*.

Palavras-chave: Trichomycterinae. *Trichomycterus*. Peixes Neotropicais. Taxonomia de peixes. Baixo Rio Paraná.

Taxonomical revision of *Cambeva stawiarski* (Miranda Ribeiro, 1968) (Siluriformes, Trichomycteridae) with the description of a new species from the Rio Iguaçu basin, Paraná State, Brazil

ABSTRACT

The objective was to redescribe *Cambeva stawiarski*, using internal morphological data, external morphology, morphometry and meristic data, through the revision of the type-material and material deposited in fish collections. In this process, we have also added comments on the possible *Cambeva stawiarski* type-locality and described a new species of *Cambeva*, endemic to the Rio Iguaçu basin, Brazil. *Cambeva stawiarski* and the new species are diagnosed by the number of procurrent caudal-fin rays dorsally and ventrally; number of vertebrae; number of pectoral-fin rays; number of branchiostegal rays; small notch on the distal margin of the caudal-fin; head length; caudal peduncle depth; and the colouration pattern of the body. In addition, the species are compared with other possibly related species and the synapomorphic characters of these groups of species are discussed. With confirmation of the endemism of *Cambeva stawiaski* and the description of a new species of *Cambeva* for the Rio Iguaçu basin, we confirm important biogeographic patterns on the endemism of this hydrographic basin and in the use of osteological data in the description of *Cambeva* species

Keywords: Trichomycterinae. *Trichomycterus*. Neotropical Fishes. Fish Taxonomy. Lower Rio Paraná.

Esta dissertação de mestrado não é considerada uma publicação formal segundo as normas do Código Internacional de Nomenclatura Zoológica, por este motivo o nome para a nova espécie é omitido e uma letra é utilizada provisoriamente para designá-la.

Dissertação elaborada e formatada conforme as normas da publicação científica *Journal of Fish Biology*. Disponível em: <https://onlinelibrary.wiley.com/page/journal/10958649/homepage/forauthors.html#preparing>

SUMMARY

1 INTRODUCTION

Siluriformes is among the most diverse orders of fishes with 39 families, 499 genera and about 4,000 species (Fricke *et al*., 2021a). Trichomycteridae is the second richest family of Siluriformes, with approximately 340 species, being characterized by having a modified opercular system with odontodes in the opercular and interopercular bones (Baskin, 1937; de Pinna, 1992a, 2016). They are popularly known as "candirus", "cambevas" and "guascas".

Trichomycteridae has nine subfamilies, with Trichomycterinae being the richest, with about 240 species and nine genera (Fricke *et al*., 2021a). Ochoa *et al*. (2017a) in a phylogenetic analysis using molecular data, found a monophyletic group (clade D4) compound by species of *Trichomycterus* from coastal drainages of Atlantic and tributaries of the Parana-Paraguay basin, separate from other *Trichomycterus*. Katz *et al*. (2018) in a similar analysis, proposed a new genus for the species of *Trichomycterus* of this clade, *Cambeva* Katz, Barbosa, Mattos & Costa 2018, currently with 32 species (Fricke *et al*., 2021b)

Cambeva species can be found in the South and Southeast regions of Brazil and in the province of Misiones, Argentina. They inhabit extremely diverse habitats, such as streams characterized by being clear, cold, with rocky riverbeds and fast flow (Katz *et al.*, 2018; Wosiacki and de Pinna, 2008a) and many are endemic with restricted distribution (*e. g.* de Pinna, 1992b; Wosiacki and Garavello, 2004; Wosiacki and de Pinna, 2008a, 2008b).

Wosiacki and de Pinna (2008a, 2008b) discussed the hypothesis of monophyletism among *Cambeva crassicaudata*, *C. igobi* and *C. stawiarski*, all from the Rio Iguaçu basin. According to the authors, these species are grouped by having the procurrent caudal-fin rays ossified and rigid, with a slender distal tip and the caudal-fin rays extending along the tips of at least ten neural spines. Terán *et al*. (2017) added *C. ytororo* from the Tabay waterfalls in the Tabay stream, province of Misiones, Argentina, in this group.

The rio Iguaçu basin is characterized by a high endemism and species richness of *Cambeva* (Reis *et al*., 2020). *Pygidium stawiarski* (now *Cambeva stawiarski*) was described from one specimen collected in a small stream tributary to the Rio Paraná basin, locality of Bituruna in the State of Paraná (Miranda Ribeiro, 1968). The original description by Miranda Ribeiro (1968) emphasizes the colouration pattern: "fundamental branco isabelino, mais intensamente para o dorso, pedúnculo, dorsal, anal e caudal, e sobre esse colorido básico, o exemplar apresenta (menos nas regiões gular e ventral) um denso piperado castanho,

pontilhado esse que grupa em máculas distribuídas irregularmente e com maior intensidade sobre a cabeça e dorso", and the description has a black and white drawing (Figure 1a).

Since its description, *Cambeva stawiarski* has been cited in species descriptions (*e. g*. Wosiacki and de Pinna, 2008a, 2008b; Terán *et al*., 2017), where the authors provide data on its osteology and, more recently, by Baumgartner *et al*. (2012), providing a brief description of the species colour pattern. Although, no work has a detailed description of the holotype, informing about its external morphology, photos, osteology and colour pattern.

In a recent fish inventory, Cavalli *et al*. (2018) identified specimens collected in the Rio Piquiri basin as *Trichomycterus* cf. *stawiarski* (=*Cambeva* cf. *stawiarski*). In addition, Morais-Silva *et al*. (2018), in a study using the gene COI, analyzed the phylogeography of *Cambeva* populations in five hydrographic basins in the State of Paraná and confirmed the occurrence of *C. stawiarski* in the Rio Piquiri basin. However, in their results, two clades were formed with a clear separation between populations of *C. stawiarski*, indicating the existence of a species complex in populations of the Piquiri and Iguaçu rivers and the formation of a non-monophyletic group in relation to what has been morphologically identified as *C. stawiarski*.

Information about the type-material should be considered in the identification of species, in order to avoid taxonomic issues (Reis and Pinna, 2019). However, old publications lack sufficient data for the unambiguous delimitation of species (Martins, 1994), mainly with species of Trichomycteridae (*e. g*. Eigenmann, 1917, 1918; Miranda Ribeiro, 1968). For this reason, taxonomic revisions clarify many questions about the taxonomy of species and their geographic distribution; provide accurate data on the conservation status of these species, validation and correct identification of the species studied and the description of possible new species (Martins, 1994; Miranda *et al.*, 2018).

Therefore, the aim of this work is redescribing *Cambeva stawiarski*, using internal morphological data, external morphology, morphometric and meristic data, through the revision of the type-material and material deposited in fish collections. Also, we added comments about the possible type-locality of *Cambeva stawiarski* and described a new species of *Cambeva*, endemic to the Rio Iguaçu basin, Brazil.

2 MATERIAL AND METHODS

2.1 Morphological data

Morphometric data were taken point to point with digital calipers (precision of 0.1 mm) on the left side of specimens following Nascimento *et al*. (2017) and Wosiacki and de Pinna (2008b) for distance between pelvic-fin base and anus. For osteological analysis, 18 specimens were cleared and stained (c&s) according to Taylor and van Dyke (1985), and data from the holotype were obtained from digital X-rays at the Museu Nacional do Rio de Janeiro. For superficial musculature analysis five specimens were double stained for cartilage and bone, following Taylor and van Dyke (1985) protocol with adaptations proposed by Datovo and Bockmann (2010). The nomenclature of the osteological structures, lateral sensory canal system and associated pores follow Bockmann *et al*. (2004). The vertebrae were counted according to Ferrer and Malabarba (2013) excluding the Weberian complex, and the compound caudal centrum (PU1+U1) is counted as one element. The counts of unsegmented rays (represented by lower case Roman numerals) in c&s specimens are given before the number of unbranched and segmented rays. Unbranched rays (represented by upper case Roman numerals) and branched rays (represented by Arabic numerals) were performed on measured specimens. In descriptions, each meristic character is followed by the number of specimens examined in parentheses. Counts for holotype are represented by an asterisk. Counts of the number of branchiostegal rays, procurrent caudal-fin rays, odontodes, ribs, unsegmented rays, basal radial rays, teeth and vertebrae were performed in c&s specimens and in the X-ray image of the holotype. Osteological illustrations were prepared with a camera lucida attached to a stereomicroscope.

2.2 Samples and comparative material

Most of the material used in this dissertation is housed in the Coleção Ictiológica do NUPÉLIA, Maringá (NUP). The vouchers separated by point indicates that it will be dismembered, due to misidentification or wrong locations. We also analyzed lots deposited in the following collections: Coleção de Peixes do Laboratório de Ictiologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto (LIRP); Museu de História Natural Capão da Imbuia, Curitiba (MHNCI); Coleção de Peixes da Universidade Federal do Rio Grande do Sul, Porto Alegre (UFRGS). Remaining institutional abbreviations of comparative material follow Sabaj (2019).

The data obtained were compared with comparative material and the original descriptions of *Cambeva stawiarski* group in Wosiacki and de Pinna (2008a) for *C. crassicaudata* (Wosiacki & de Pinna 2008); Wosiacki and de Pinna (2008b) for *C. igobi* (Wosiacki & de Pinna 2008); Miranda Ribeiro (1968) for *C. stawiarski* (Miranda Ribeiro 1968) and Terán *et al*. (2017) for *C. ytororo* (Terán, Ferrer, Benitez, Alonso, Aguilera & Mirande 2017). We also compared with the originals descriptions of *Cambeva* species, such as Ferrer and Malabarba (2013) for *C. balios* (Ferrer & Malabarba 2013) and *C. brachykechenos* (Ferrer & Malabarba 2013); Costa *et al.* (2021) for *C. barbosae* Costa, Feltrin & Katz 2021; and *C. botuvera* Costa, Feltrin & Katz 2021; de Pinna (1992b) for *C. castroi* (de Pinna 1992); Costa (1992) for *C. concolor* (Costa 1992); Bockmann *et al.* (2004) for *C. diabola* (Bockmann, Casatti & de Pinna 2004); Ferrer and Malabarba (2013) for *C. diatropoporos* (Ferrer & Malabarba 2013); Costa *et al.* (2020) for *C. flavopicta* Costa, Feltrin & Katz 2020; Wosiacki (2005) for *C. guaraquessaba* (Wosiacki 2005); Katz and Costa (2020) for *C. guareiensis* Katz & Costa 2020; Reis *et al.* (2019) for *C. horacioi* Reis, Frota, Fabrin & Graça 2019; Wosiacki and Garavello (2004) for *C. mboycy* (Wosiacki & Garavello 2004) and *C. naipi* (Wosiacki & Garavello 2004); Eigenmann (1917) for *C. paolence* (Eigenmann 1917); Ochoa *et al.* (2017) for *C. pascuali* (Ochoa, Silva, Costa e Silva, Oliveira & Datovo 2017); Datovo *et al.* (2012) for *C. perkos* (Datovo, Carvalho & Ferrer 2012); Wosiacki and Garavello (2004) for *C. papillifera* and *C. plumbea* (Wosiacki & Garavello 2004); Ferrer and Malabarba for *C. poikilos* (Ferrer & Malabarba 2013); Wosiacki and Garavello (2004) for *C. taroba* (Wosiacki & Garavello 2004); Ferrer and Malabarba (2011) for *C. tropeiro* (Ferrer & Malabarba 2011); Wosiacki and Oyakawa (2005) for *C. tupinamba* (Wosiacki & Oyakawa 2005); Costa (1992) for *C. variegata* (Costa 1992) and specific literature for colour variation and redescription of *Cambeva* species such as *C. cubataonis* (Bizerril 1994) in Katz and Barbosa (2014); *C. davisi* in Nascimento *et al.* (2017); *C. iheringi* (Eigenmann 1917) in Silva *et al.* (2010) and Wosiacki (2005); and *C. zonata* (Eigenmann 1918) in Reis and de Pinna (2019).

3 RESULTS

3.1 *Cambeva stawiarski* (Miranda Ribeiro 1968)

Figures 1–12 and Table 1

Pygidium stawiarski Miranda Ribeiro (1968): 1 [original description; MNRJ 9739, holotype; type-locality: “Pequeno córrego pertencente à bacia do Rio Paraná – Localidade de Bituruna – Est. do Paraná”].

Trichomycterus stawiarski.- de Pinna and Wosiacki (2003): 284 [checklist, South America; estimated type-locality’s geographical coordinates].- Bockmann *et al.* (2004): 227 [diagnosis of *Cambeva diabola*]. Ferraris *et al*. (2007): 423–424 [checklist of catfishes].- Wosiacki and de Pinna (2007): 71 [checklist, Brazil].- Wosiacki and de Pinna (2008a): 274 [diagnosis of *Cambeva crassicaudata*].- Wosiacki and de Pinna (2008b): 20 [diagnosis of *Cambeva igobi*].- Datovo and Bockmann (2010): 198 [phylogeny of Trichomycteridae based in miology].- Baumgartner *et al*. (2012): 103 [checklist, Rio Iguaçu; brief species descriptions], figure in p. 109.- Datovo *et al*. (2012): 41 [diagnosis of *Cambeva perkos*].- Frota *et al*. (2016): 5 [checklist, Rio Jordão and Areia].- Terán *et al*. (2017): 9 [diagnosis of *Cambeva ytororo*].- Katz *et al*. (2018): 563 [material examined of *Cambeva* genera].

Cambeva stawiarski.- Reis *et al*. (2019): 12 [diagnosis of *Cambeva horacioi*].

FIGURE 1 *Cambeva stawiarski*, holotype, MNRJ 9739, 67.1 mm L_S, Brazil, Paraná State, municipality of Bituruna, stream tributary to the Rio Iratim, Rio Iguaçu basin, Lower Rio Paraná system. (a) Scientific illustration taken from the original description in Miranda Ribeiro (1968); (b) Photographs by I. C. A. S. Santos.

3.1.1 Diagnosis

Cambeva stawiarski is distinguished from all congeners except *C. crassicaudata*, *C. igobi*, *C. ytororo* and *Cambeva* sp. A by the presence of procurrent caudal-fin rays thickly ossified and rigid with a slender distal tip (*vs*. procurrent caudal-fin rays thin and flexible); and the dorsal procurrent caudal-fin rays extending along the tips of at least eight neural spines (*vs*. procurrent caudal-fin rays extending the tip of less than eight neural spines). *Cambeva stawiarski* is distinguished from *C. crassicaudata* and *C. igobi* by having eight or nine branchiostegal rays (*vs*. 10 or 11 branchiostegal rays). *Cambeva stawiarski* is distinguished from *C. ytororo* by the presence of 21–27 dorsal procurrent caudal fin-rays (*vs*. 31–35 dorsal procurrent caudal fin-rays), by having modally I+6 pectoral-fin rays (*vs*. I+7 pectoral-fin rays), by the presence of a caudal fin truncate with a small notch in distal margin in adults (*vs*. rounded caudal fin in distal margin in adults) and greater nasal barbel length (38.3–60.8 *vs*. 22.5–33.9 nasal barbel length percent of L_H). *Cambeva stawiarski* is further distinguished from *C. crassicaudata* by the presence of a caudal fin truncate with a small notch in distal margin in adults (*vs*. forked caudal fin distal margin in adults), 37 or 38 vertebrae (*vs*. 35 or 36), 33–38 odontodes in the interopercular patch (*vs*. 19–22) and lower caudal peduncle depth (10.1–15.6% *vs*. 22.8–25.4% of L_S). *Cambeva stawiarski* is further distinguished from *C. igobi* by head length (18.4–22.7% *vs*. 23.8–26.8% of L_S) and caudal peduncle depth (11.1–15.6% *vs*. 16.0–19.0% of L_S). *Cambeva stawiarski* is further distinguished from *Cambeva* sp. A by the colour pattern of the dorsal and lateral surface of body in small specimens, composed of dark brown blotches of irregular shapes, forming a homogeneous colour, with few spaces between blotches (*vs*. the dorsal and lateral surface of body in small and some larger specimens, composed of dark brown blotches, with several spaces between blotches in *Cambeva* sp. A), by having modally I+6 pectoral-fin rays (*vs*. I+7), the number of teeth on ceratobranchial 5 (25–27 *vs*. 42–49), number of teeth on plate connected to pharyngobranchial 4 (31–39 *vs*. 46), the insertion of the first dorsal basal radial anteriorly to the 18th neural spine (*vs*. anteriorly to the 19th neural spine) and number of procurrent caudal-fin rays dorsally and ventrally (21–27 and 9–11 respectively *vs*. 30–31 and 13–17). Additionally, *Cambeva stawiarski* is distinguished from the remaining congeners from the Rio Iguaçu basin by the dorsal and caudal fins with scattered dark brown spots over lighter background fading toward distal margins (*vs*. caudal and dorsal fins with a narrow vertical dark brown stripe along the distal margin and caudal fin with a vertical unpigmented band across the proximal region in *C. castroi*); by the colour pattern of the dorsal and lateral surface of the body composed of dark brown rounded blotches, several times coalescent forming irregular shapes in inner skin

layer and a few small black spots in the outer skin layer (*vs*. the colour pattern of body with scattered and juxtaposed spots, some coalesced and forming blotches or body with blotches, irregularly shaped and some individuals with a ringed blotch, with a clear central region in *C. davisi*; several diffuse dark brown spots in *C. mboycy*; dark-brown stripes on the sides of the trunk and caudal peduncle in *C. naipi*; by the colour pattern of body plain gray in *C. papillifera* and *C. plumbea*; the body almost covered by numerous small spots of various sizes and shapes in *C. taroba*). *Cambeva stawiarski* is further distinguished from *C. taroba* by the pectoral-fin with modally I+6 rays and the first pectoral-fin ray not prolonged as a filament (*vs*. pectoral-fin with I+5 rays and the first pectoral-fin ray prolonged as a filament).

3.1.2 Description

External morphology. Morphometric data are provided in Table 1. Maximum size observed 86.6 mm L_S. Body elongate. Trunk roughly cylindrical close to head and gradually becoming laterally compressed towards caudal fin. Dorsal profile of trunk straight to slightly convex along anterior half of body to insertion of dorsal fin. Ventral profile of trunk straight to slightly convex. Dorsal and ventral profiles of caudal peduncle straight to slightly convex.

TABLE 1 Morphometric data for *Cambeva stawiarski*. N = number of specimens; N.A. = Not available; SD = standard deviation.

	Holotype	N	Min	Max	Mean	SD
Standard length (mm)	67.1	28	34.7	86.6	72.5	-
Percents of Standard Length						
Head length	18.7	28	18.4	22.7	20.0	1.11
Predorsal length	67.2	28	59.9	68.4	63.2	1.93
Prepelvic length	59.3	28	51.6	58.6	55.2	2.13
Preanal length	74.8	28	54.9	76.0	69.8	3.87
Pectoral girdle width	13.8	28	14.3	17.4	15.7	0.85
Body length	N.A.	28	79.3	86.9	82.7	2.12
Pectoral-fin length	12.1	28	11.0	15.4	13.0	1.12
Pelvic-fin length	9.1	28	8.1	10.5	9.1	0.57
Distance between pelvic-fin base and anus	11.5	28	8.1	12.3	9.8	1.05
Caudal peduncle length	N.A.	28	19.0	24.1	21.8	1.24
Caudal peduncle depth	N.A.	28	10.1	15.6	13.1	1.16
Body depth	N.A.	28	15.4	21.6	17.3	1.56
Length of dorsal-fin base	13.1	28	7.0	11.2	9.3	1.14
Length of anal-fin base	9.8	28	5.1	8.0	6.6	0.80
Pelvic – anal distance	N.A.	28	13.5	18.4	15.8	1.21
Percents of Head Length						
Head width	N.A.	28	77.8	93.4	84.8	5.01
Nasal barbel length	N.A.	28	38.3	60.8	47.5	5.68
Maxillary barbel length	N.A.	28	30.0	64.2	44.0	6.90

Rictal barbel length	N.A.	28	29.8	50.0	43.0	4.85
Snout length	N.A.	28	37.6	46.0	42.2	2.05
Interorbital	24.6	28	20.0	26.1	22.6	1.66
Mouth width	40.5	28	27.9	45.1	36.1	4.42
Eye diameter	8.7	28	5.4	9.8	7.7	1.14

Head depressed, trapezoidal from dorsal view, wider posteriorly. Dorsal and ventral profiles of head straight to slightly convex in lateral view. Snout straight to slightly convex in dorsal view. Eyes located dorsolaterally on anterior half region of head, at same longitudinal line of nasal barbel, round to antero-posteriorly elliptical, covered by a thin and translucent skin. Orbital rim not free. Each eye located over posterior termination of shallow and small longitudinal crest beginning at posterior nostril and making eyes visible from lateral view.

Anterior nostril of approximately same size as eyes, surrounded by flap of integument posterolaterally continuous with base of nasal barbel. Posterior nostril surrounded anterolaterally by thin flap of integument. Gill openings not constricted united with isthmus anteriorly, forming a free fold reaching pectoral-fin insertion. Mouth subterminal and slightly curved with corners posteriorly oriented. Upper lip thicker distally. Lower lip with fleshy lobes in lateral limits, medial to base of rictal barbels. Lips with numerous small, rounded papillae of approximately same size. Barbels with wide base, tapering gradually towards tips. Nasal barbel emerging from lateral region of anterior nostril, its posterior tip reaching between infraorbital pores i10 and i11 when adpressed to body. Maxillary barbell reaching anterior region of interopercular patch of odontodes.

Pectoral fin with distal margin rounded, I+6* (102), I+7 (7), first ray unbranched and not prolonged as filament. Pelvic fin with I+4 rays, inserted anterior to origin of dorsal fin, with distal margin rounded, reaching or covering anterior margin of urogenital papilla, but never reaching anal fin origin. Inner margins of pelvic fins very close basally and sometimes in contact. Dorsal fin with distal margin straight to slightly convex, ii-II+7 rays. Origin of dorsal fin located at vertical line through last third or tip of pelvic fin. Anal fin elongate with distal margin convex and slightly smaller than dorsal fin, ii-II+5* (60), ii-II+6 (1) rays. Origin of anal fin located vertically in middle or last third of dorsal-fin base. Caudal fin with distal margin truncated with small notch medially (Figure 2a–d), I+11+I* (66), I+9+I (1) rays.

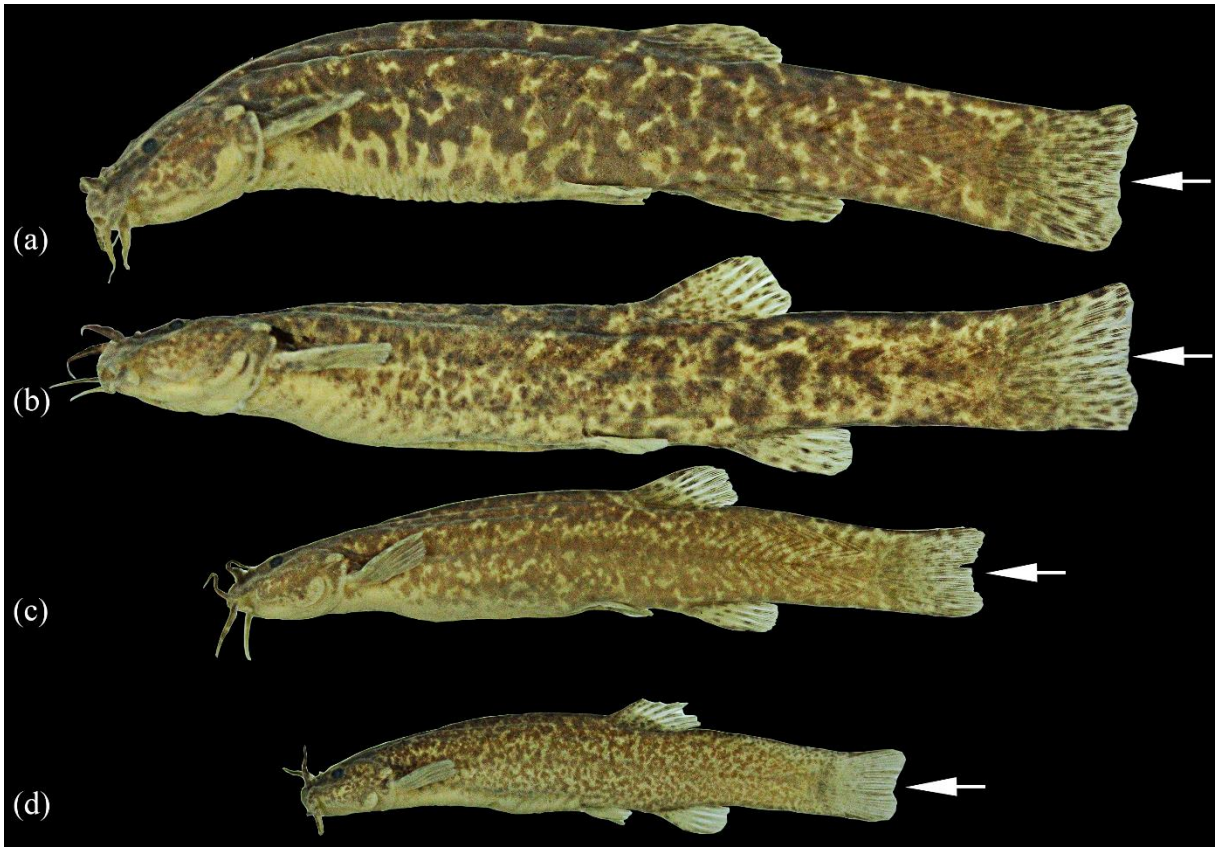

FIGURE 2 Non-type material of *Cambeva stawiarski*, with variation in colouration. NUP 1378, Brazil, Paraná State, municipality of Dois Vizinhos, Rio Jordão, rio Iguaçu basin. (a) 71.0 mm *LS*; (b) 69.5 mm *LS*; (c) 39.5 mm *LS*; (d) 31.1 mm *LS*. Arrow indicates the small notch medially in the caudal fin.

Osteology. Mesethmoid with anterior margin slightly concave and cornua rounded at distal margins, width base similar to their length. Tendon bone supraorbital long and thin, about four times larger than antorbital, with process along proximal margin. Antorbital short and anteriorly expanded with rounded anterior and posterior margins. Anterior cranial fontanel restricted to small, rounded opening situated immediately anterior to epiphyseal bar. Posterior cranial fontanel long extending from posterior portion of frontals to parieto-supraoccipital. Epiphyseal bar longer than wide. Anterior portion of sphenotic laterally directed in dorsal view. Sphenotic, prootic and pterosphenoid fused. Vomer arrow-shaped with long posterior process extending to parasphenoid. Parasphenoid with long and pointed posterior process extending to posteromedial region of basioccipital. Weberian capsule with small lateral openings, much smaller than lateral profile of capsule. Anterior margin fused to basioccipital (Figure 3).

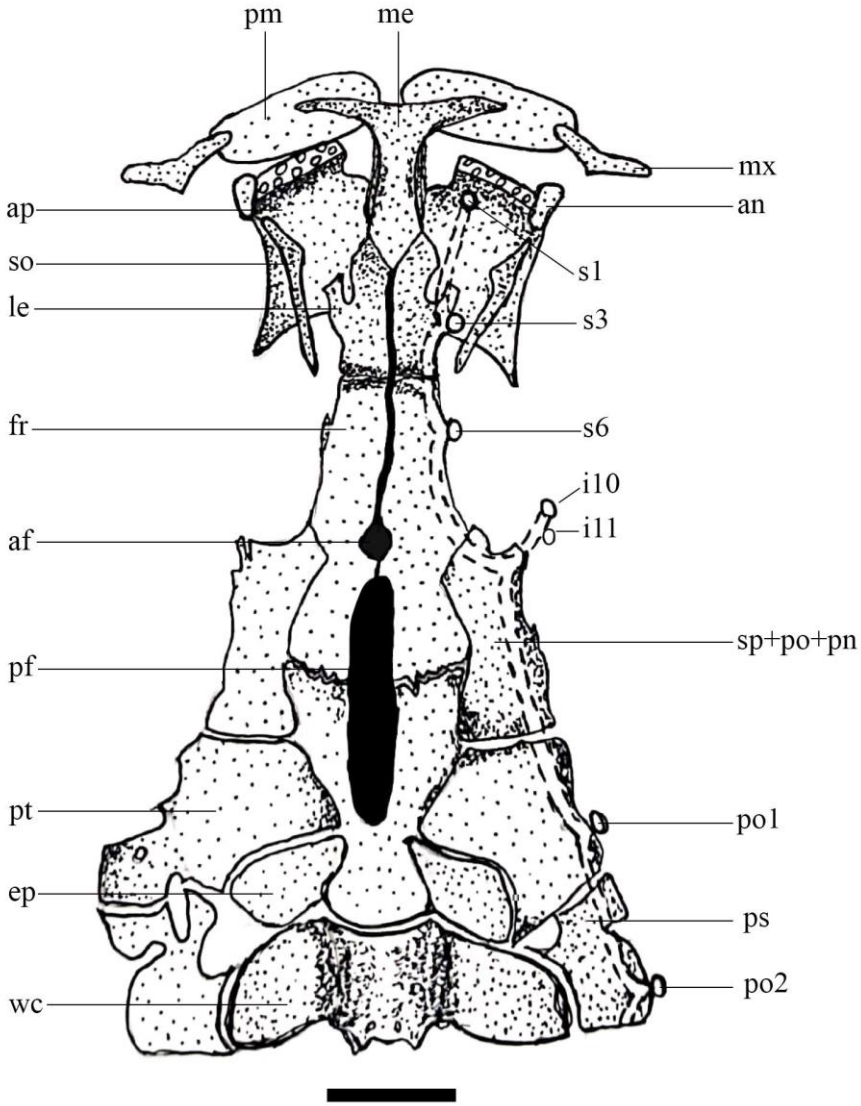

FIGURE 3 Dorsal view of neurocranium of *Cambeva stawiarski*, NUP 1378, 71.4 mm *LS*. Abbreviations: af, anterior fontanel; an, antorbital; ap, autopalatine; ep, epioccipital; fr, frontal; le, lateral ethmoid; i10-11, infraorbital sensory branch 10 and 11; me, mesethmoid; mx, maxilla; pf, posterior fontanel; pm, premaxilla; po1-2, postotic sensory branches 1 and 2; ps, posttemporosupracleithrum; pt, pterotic; s1, supraorbital sensory branch 1; s3, supraorbital sensory branch 3; s6, supraorbital sensory branch 6 (epiphyseal branch); so, tendon-bone supraorbital; sp+po+pn, sphenoticprootic-pterosphenoid complex bone; su, parieto-supraoccipital; wc, Weberian capsule. Scale bar = 2 mm.

Premaxilla elliptical with 61 (n=1) conical teeth similar in size, distributed in four irregular rows. Lower jaw with 53 (n=1) conical teeth distributed in three rows. Teeth range

from base of coronoid process to near dentary symphysis (Figure 4). Maxilla boomerang-shaped and shorter than premaxilla. Autopalatine with distal margin concave, anterior margin slightly convex followed by concave mesial margin with a bony expansion (Figure 5), posterior margin with small process extending slightly over lateral ethmoid and a long postero-lateral process.

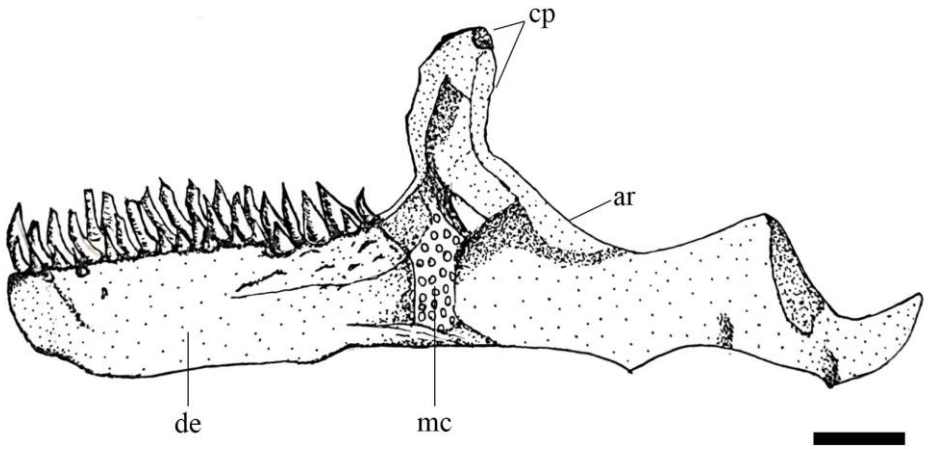

FIGURE 4 Medial view of the left lower jaw of *Cambeva stawiarski*, NUP 1378, 71.4 mm L_S. ar, anguloarticular; cp, coronoid process; de, dentary; mc, Meckel's cartilage. Scale bar = 1 mm. Scale bar = 1 mm.

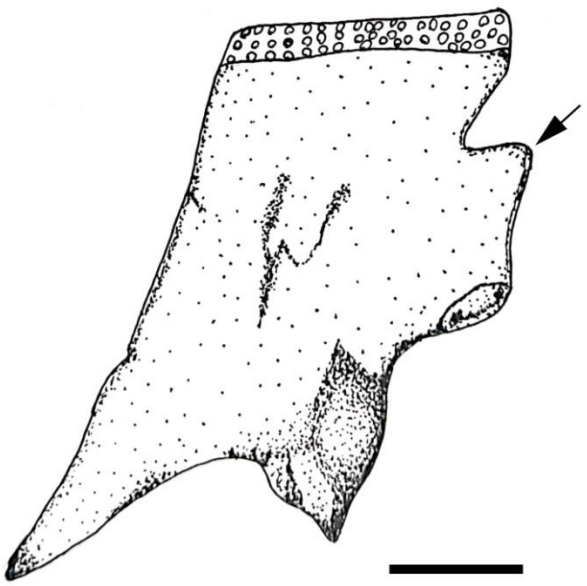

FIGURE 5 Ventral view of the right autopalatine of *Cambeva stawiarski*, NUP 1378, 71.4 mm L_S. Arrow indicates mesial bony expansion. Scale bar = 0.5 mm.

Metapterygoid large and laminar, connected to quadrate through cartilage. Quadrate L-shaped, antero-dorsal arm with deep constriction. Hyomandibula well developed with prominent notch in dorsal margin. Opercular patch of odontodes rounded with 14–17 (n=6) conical odontodes. Interopercular patch of odontodes elongate with 33–38 (n=6) conical odontodes concentrated posteriorly. Odontodes of both opercular and interopercular patches gradually curving medially and increasing in size posteriorly (Figure 6).

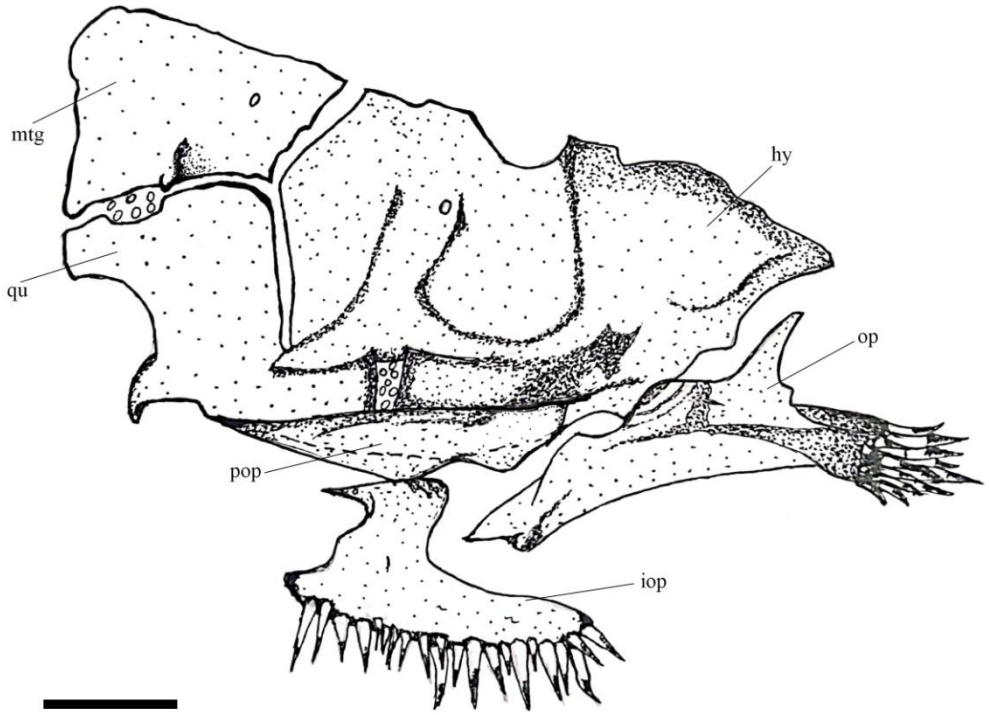

FIGURE 6 Dorsal view of left suspensory of *Cambeva stawiarski*, NUP 1378, 71.4 mm *LS*. hy, hyomandibula; iop, interopercle; mtg, metapterygoid; op, opercle; pop, preopercle. Scale bar = 1 mm.

Ventral hypohyal trapezoid shaped. Anterior ceratohyal elongate and wider at anterior and posterior tips. Posterior ceratohyal short and triangular. Dorsal hypohyal and interhyal absent. Eight (n=7) or nine* (n=3) branchiostegal rays: six in contact with anterior ceratohyal, one with interceratohyal cartilage, one with posterior ceratohyal and some specimens with one

lateral from posterior ceratohyal and not contacting it. Three posterior branchiostegal rays wider distally (Figure 7a, b).

Urohyal with expanded anterior head, two elongate lateral processes with wide bases and decreasing in width distally with rounded tips. Laminar, elongate and narrow posterior process. Posterior process of urohyal shorter than lateral processes (Figure 7c).

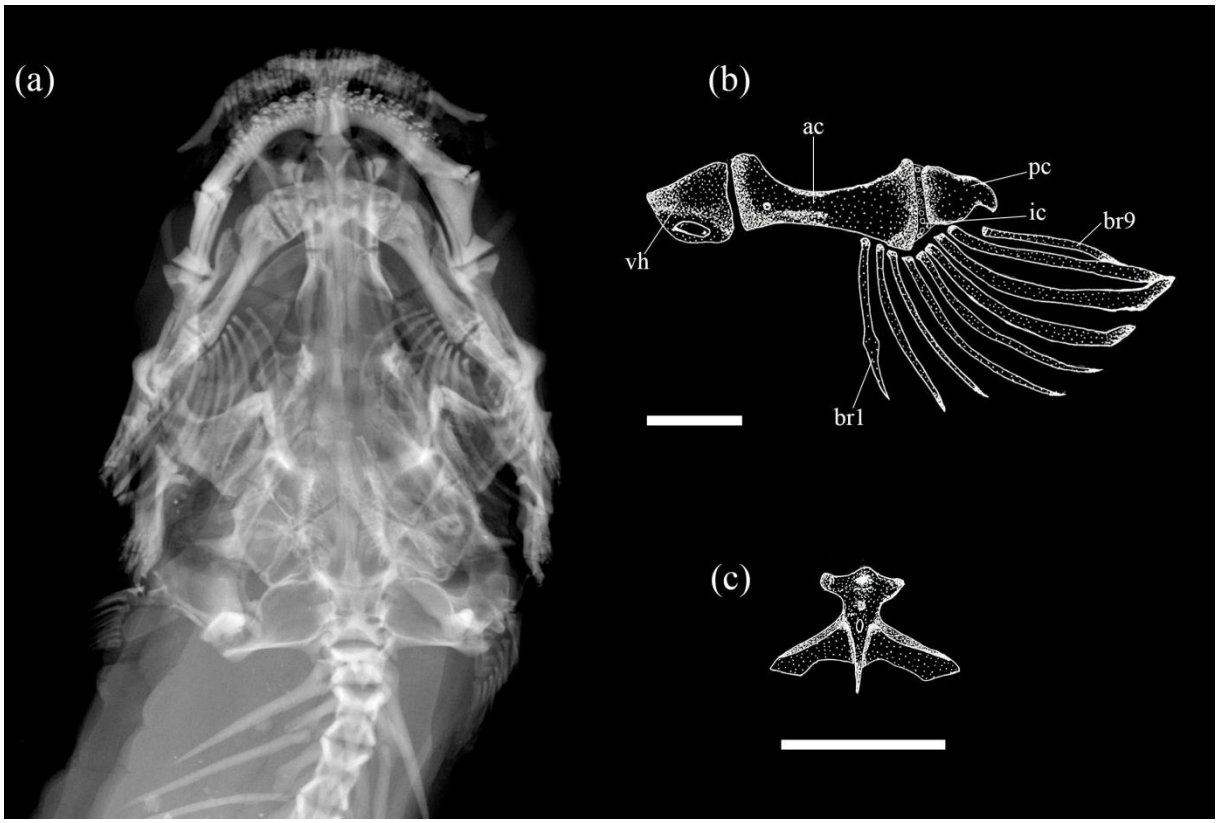

FIGURE 7 (a) X-ray of *Cambeva stawiarski*, holotype, MNRJ 9739. Ventral view of head and pectoral girdle. (b) lateral view of left hyoid arch of *Cambeva stawiarski*, NUP 1378, 71.4 mm L_S. (c) dorsal view of urohyal of *Cambeva stawiarski*, NUP 1378, 71.4 mm L_S. Abbreviations: ac, anterior ceratohyal; br1-9, branchiostegal rays 1 to 9; ic, inter-ceratohyal cartilage; pc, posterior ceratohyal; vh, ventral hypohyal. Scale bar = 1 mm.

Basibranchials 1 absent. Basibranchials 2 and 3 elongated, of approximately equal lengths, connected to each other by cartilage; basibranchial 2 slightly wider than basibranchial 3. Basibranchial 4 hexagonal and entirely cartilaginous. Hypobranchial 1 elongated, with cartilaginous tips, slightly longer than basibranchial 2. Hypobranchials 2 and 3 with

approximately same size and with narrow anterolateral ossified processes with large area of cartilage distally. Five elongate ceratobranchials with cartilaginous tips. Ceratobranchials 1 and 4 with straight margins. Ceratobranchials 2 and 3 with concavity along posterior margin, more prominent in ceratobranchial 3. Ceratobranchial 5 expanded posteromedially with 23–27 (n=3) conical, elongated and pointed teeth. Four epibranchials, first three elongated and narrow with cartilage at tips. Epibranchials 1 and 2 with triangular process along anterior margins; process elongated, pointed and slightly larger in epibranchial 1; epibranchial 3 with distinct curved process on posterior margin. Epibranchial 4 rectangular shaped, produced by broad anterior and posterior crests. Epibranchial 5 small, narrow, curved and completely cartilaginous. Pharyngobranchial 1 and 2 absent. Pharyngobranchial 3 elongated, similar in form but shorter than hypobranchial 1, with cartilage at tips. Pharyngobranchial 4 curved and ossified, connected to plate with 31–39 (n=3) conical, elongated and pointed teeth, arranged in up to three irregular rows, teeth increasing in size posteriorly (Figure 8).

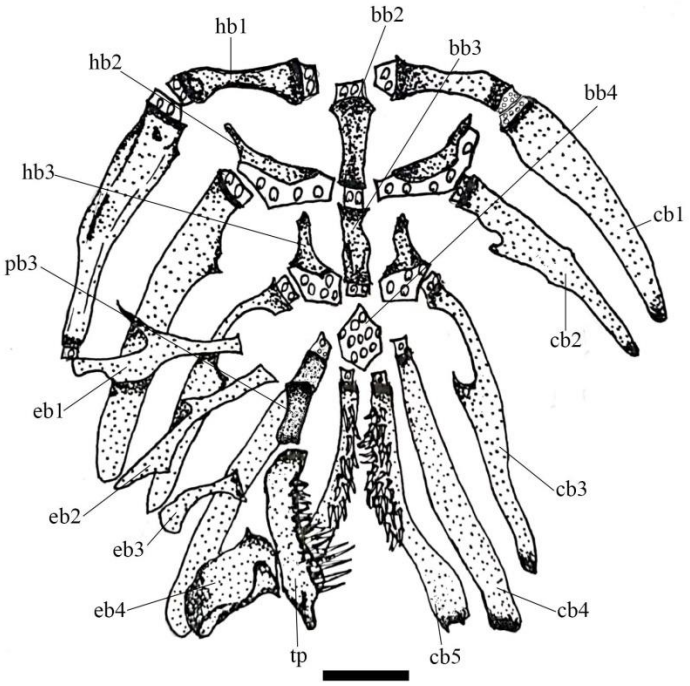

FIGURE 8 Dorsal view of gill arches (right dorsal elements and gill rakers not show) of *Cambeva stawiarski*, NUP 1378, 71.4 mm L_S. Abbreviations: bb2–4, basibranchials 2 to 4; cb1–5, ceratobranchials 1 to 5; eb1–5, epibranchials 1 to 5; hb1–3, hypobranchials 1 to 3; pb3, pharyngobranchial 3; tp; tooth plate. Scale bar = 1 mm.

Dorsal fin with eight basal radials, first inserted anterior to neural spine of the 18th* (n=3) vertebrae. Anal fin with six basal radials, first inserting anterior to haemal spine of the 22nd* to 23rd vertebrae. Procurrent caudal-fin rays 21 to 27 dorsally (9), extending along the tips of 8–11 neural spine (one of nine specimen has the extension of the dorsal procurrent rays anteriorly to eight and two of nine specimens to nine neural spine) and nine to 11 ventrally (9). Upper plate with one unbranched ray and five branched rays; hypural 3 free and hypurals 4 and 5 fused to each other. Lower caudal plate with one unbranched ray and six branched rays. Parhypural and hypurals 1 and 2 co-ossified and fused to compound caudal centrum (Figure 9). Branched caudal fin rays splitting two times. Free vertebrae 37* or 38, 12 or 13* pairs of ribs (Figure 10a, b).

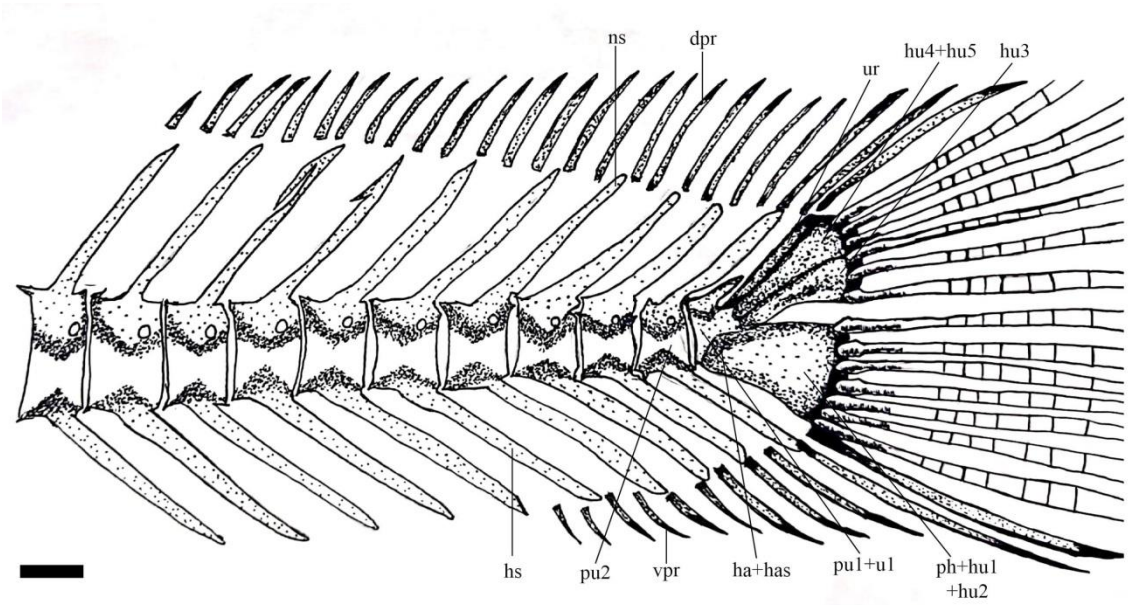

FIGURE 9 Left lateral view of the caudal peduncle of *Cambeva stawiarski*, NUP 611.1, 63.9 mm L_S. Abbreviations: dpr, dorsal procurrent caudal-fin rays; ha+has, complex hypurapophysis composed of hypurapophysis and secondary hypurapophysis; hs, hemal spine; hu3, hypural 3; hu4+hu5, complex plate formed by co-ossification of hypurals 4 and 5; ns, neural spine; ph+hu1+hu2, complex plate formed by co-ossification of hypurals 1 and 2 and parhypural; pu1+u1, complex centrum composed of pleural centrum 1 and ural centrum 1; pu2, pleural centrum; ur, uroneural; vpr, ventral procurrent caudal-fin rays. Scale bar = 1 mm.

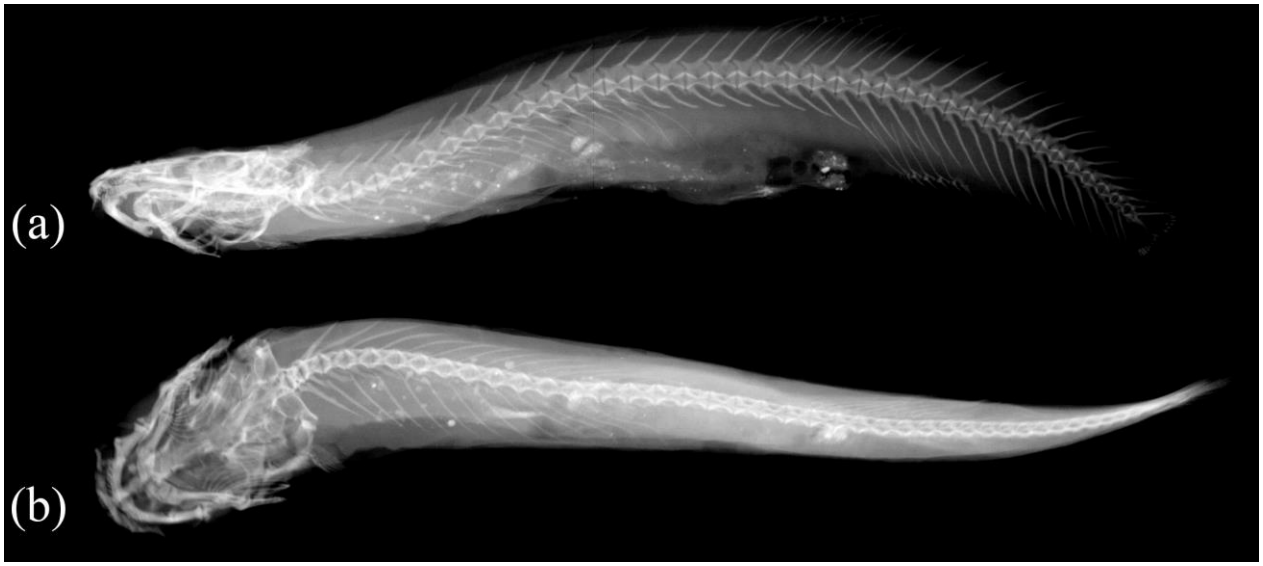

FIGURE 10 X-ray of *Cambeva stawiarski*, holotype, MNRJ 9739. (a) left lateral view of the body. (b) ventral view of the body.

Laterosensory system. Laterosensory canals with simple (non-dendritic) tubes ending in single pores. Supraorbital sensory canal complete, with paired pores s1, s3 and s6. Pore s1 located between anterior nostrils, pore s3 located in same longitudinal row of pore s1 after posterior nostrils and pore s6 in interorbital space; s2, s4, s5, s7 and s8 (parietal) branches and pores absent. Infraorbital sensory canal incomplete; pores i1 and i3 absent, pore i10 located behind eyes and pore i11 located lateral to posterior margin of eye. Postotic pore po1 located lateral to anterior margin of opercular patch of odontodes. Postotic pore po2 located lateral to middle of length of opercular patch of odontodes. Lateral-line canal with two to five (modally three) pores located above insertion of pectoral fin and posterior of gill openings.

Status of *Extensor tentaculi*. *Extensor tentaculi* originating from ventrolateral regions of lateral ethmoid and orbitosphenoid, presence of a ventral bundle originating from anterodorsal region of suspensorium on metapterygoid and hyomandibula. Inserting in posterolateral region of autopalatine (Figure 11).

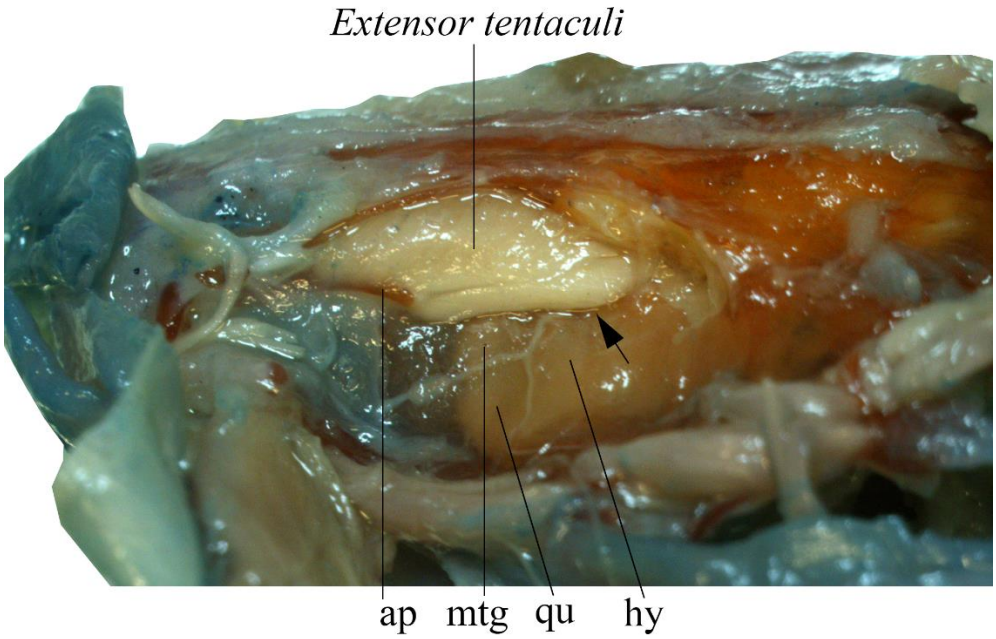

FIGURE 11 Left lateral view of neurocranium region of *Cambeva stawiarski*, NUP 1378, 70.5 mm L_S. Arrow indicates the ventral bundle of the *Extensor tentaculi* originating from the suspensorium. abbreviations: ap, autopalatine; hy, hyomandibula; mtg, metapyerygoid, qu, quadrate.

Colour in alcohol. Background colour of body yellowish in larger specimens (greater than 40.1 mm L_S, Figure 2a,b) with dorsal and lateral surface of body composed of dark brown rounded blotches, several times coalescent forming irregular shapes in inner skin layer and few small black spots smaller or equivalent in size to eye diameter on the outer skin layer. Smaller specimens (between 17.0 to 39.5 mm L_S; Figure 2c,d) background colour of body yellowish with dorsal and lateral surface of body composed of dark brown blotches of irregular shapes, forming a homogeneous color, with few spaces between blotches. Dorsal surface of head in occipital region with concentrated round dark brown blotches variable in size, in some specimens the concentration of pigmentation produces a totally dark appearance; lateral surface of head with dark brown blotches of irregular shapes variable in size; ventral surface of head light yellow with few dark brown spots smaller or equivalent in size to eye diameter. Ventral surface of body light yellow in belly with diffuse dark blotches in pectoral-fin insertion and small dark brown blotches between pelvic-fin insertions, extending to caudal peduncle. Pectoral, anal, dorsal and caudal fins with scattered dark brown spots, smaller or equivalent in size to eye diameter, over lighter background fading towards distal margins.

Pelvic fin unpigmented or some specimens with a few inconspicuous black spots medially. Barbels dorsally with scattered or coalescent dark brown spots, smaller or equivalent in size to eye diameter, and pale yellow ventrally.

3.1.3. Geographic distribution

Cambeva stawiarski is known from the Lower Rio Iguaçu basin (Figure 12), including localities in the Rio Areia, Rio Iratim, Rio Jordão and Rio São Salvador.

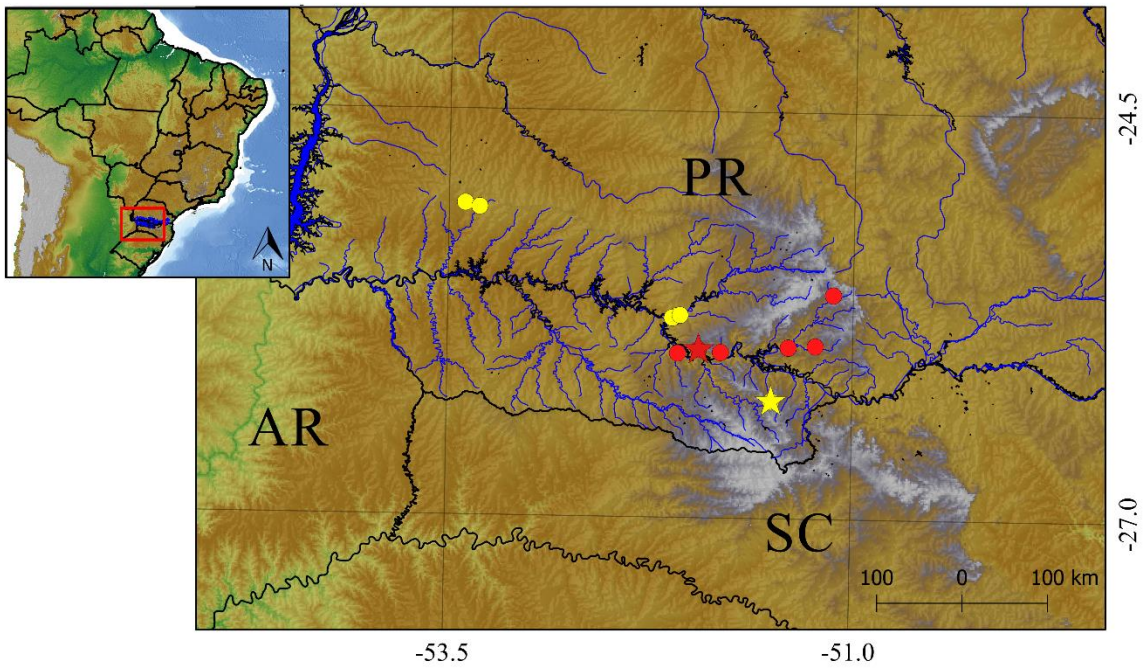

FIGURE 12 Geographic distribution *Cambeva stawiarski* (yellow symbols) and *Cambeva* sp. A (red symbols). Stars represent the type localities. Abbreviations: AR: Argentina; PR: Paraná State; SC: Santa Catarina State.

3.1.4. Ecological notes

The possible type-locality is located at elevation of approximately 1,150 m above sea level and the remaining localities are between 800 to 1,200 m above sea level. Specimens of *Cambeva stawiarski* were collected with *C. castroi*, *C. crassicaudata*, *C. davisi*, *C. igobi*, *C. mboycy*, *C. plumbea* and *C. taroba* in the Rio Jordão basin and presumably occupy the same kind of fast water and rocky-substrate environment.

3.1.5. Conservation status

The species has a restrict range of approximately 5,200 km² considering a polygon uniting all known sites of occurrence. However, the species is abundant in some localities with more than 230 specimens recorded in one collection. Although the hydroelectric power plants installed in the Rio Iguaçu are fragmenting the population of *C. stawiarski*, we are not able to properly recognize it as an impact on the species and we maintain the categorization of ICMio/MMA (2018), categorizing it as Least Concern (LC).

3.1.6. Remarks about the type-locality

Miranda Ribeiro (1968) cited the type-locality of *C. stawiarski* as "Pequeno córrego pertencente à bacía do Rio Paraná – Localidade de Bituruna – Est. do Paraná". Based on these data, Wosiacki and de Pinna (2003) estimated and provided a geographic coordinate of the possible type-locality, 26º10'S, 51º30'W, in a stream in the city of Bituruna, Paraná State. However, Bituruna is a city surrounded by several tributaries of the Rio Iguaçu, such as Rio Iratim, Rio Jacutinga, Rio da Jararaca and Rio Iratizinho. In an attempt to clarify the type-locality of *C. stawiarski*, we contact the Mr. Luiz Cláudio Stawiarski, son of the Prof. Victor Stawiarski, who collected the only specimen used by Miranda Ribeiro (1968) to describe the species.

Mr. Luiz Cláudio Stawiarski gently reported in an email the following memories with his father: "I remember with regards the many hours we spent together searching for butterflies and other insects on the farm Etienne, of his brother-in-law, in the municipality of Bituruna[...]. What I can tell you is that we always fished on the Rio Iratim, which runs through the Etienne farm[...]". Following the recommendation of Mr. Luiz Cláudio Stawiarski we here assume that the possible type-locality of *Cambeva stawiarski* is Brazil, Paraná State, municipality of Bituruna, stream tributary to the Rio Iratim, Rio Iguaçu basin, Lower Rio Paraná system, 26º16'12"S, 51º29'56.72"W.

3.1.7. Material examined

Type-material. Holotype. MNRJ 9739, 67.1 mm L_S, Brazil, Paraná State, municipality of Bituruna, stream tributary to the Rio Iratim, Rio Iguaçu basin, Lower Rio Paraná system,

26º16’12”S, 51º29’56.72”W, V. Stawiarski, 1964. **Non-type material.** 372 specimens (24.3–89.5 mm *LS*), all from Brazil, Paraná State, Rio Iguaçu basin, Lower Rio Paraná system: MHNCI 9402, 3, 74.83–89.27 mm *LS*, municipality of Guarapuava, Rio Pinhãozinho, tributary to the Rio Pinhão, tributary to the Rio Jordão, A. R. R. Jr. Schwarz. MHCNI 12299, 3, 71.0–71.7 mm *LS*, municipality of Candói, Rio Jordão, UHE Santa Clara, A. Barreto. NUP 611.1, 11 (2 c&s, 61.8–63.9 mm *LS*), 61.8–79.6 mm *LS*, municipality of Foz do Jordão, Cachoeira Tia Chica, 25º42’58”S, 52º01’22”W, Nupéla staff, 14 October 1995. NUP 611.2, 1, 70.4 mm *LS*, municipality of Foz do Jordão, Rio Reserva, 25°47'49.27"S, 52°0'31.99”W, Nupéla staff, 14 October 1995. NUP 611.3, 3, 70.2–83.3 mm *LS*, municipality of Foz do Jordão, Rio Reserva, 25º47’49”S, 52º00’32”W, Nupéla staff, 14 October 1995. NUP 1378, 239 (7 c&s, 61.8–89.5 mm *LS*), 24.3–89.5 mm *LS*, municipality of Dois Vizinhos, Rio Jordão, 25°46’16.09”S, 52°6’52.00”W, Nupélia staff, 18 April 1995. NUP 3121, 1, 72.0 mm *LS*, municipality of Foz do Jordão, Córrego Passo do Aterrado, 25º45’13”S, 52º05’09”W, Nupélia staff, 30 June 2003. NUP 3240, 59, 24.8–66.7 mm *LS*, municipality of Foz do Jordão, Córrego Passo do Aterrado, 25º45’13”S, 52º05’09”W, Nupélia staff, 14 October 1995. NUP 3735, 10, 24.5–55.4 mm *LS*, municipality of Foz do Jordão, Nupélia staff, 09 April 2005. NUP 10830, 32, 31.2–86.2 mm *LS*, municipality of Foz do Jordão, reservoir of Rio Jordão, 25°45’35.03”S, 52°5’13.88”W, Nupélia staff, 18 April 1995. NUP 11606, 1, 61.7 mm *LS*, municipality of Foz do Jordão, Rio Jordão, 25°45’17.46”S, 52°3’58.57”W, Nupélia staff, 17 December 2011. NUP 18298, 1, 56.3 mm *LS*, municipality of Inácio Martins, unnamed river, tributary to the Rio da Areia, 25°37’15.11”S, 51°7’21.30”W, W. J. da Graça, 05 October 2015. NUP 19049, 2, 59.0–68.3 mm *LS*, municipality of Cascavel, Arroio Pedregulho, tributary to the Rio Salto, tributary to the Rio São Salvador, 25°6’.19”S, 53°18’41.65”W, R. L. Delariva, 28 April 2015. NUP 19050, 1, 83.4 mm *LS*, municipality of Cascavel, Córrego Bom Retiro, tributary to the Rio São Salvador, 25°4’47.82”S, 53°24’3.51”W, R. L. Delariva, 13 May 2015. NUP 15909, 4, 64.1–84.0 mm *LS,* municipality of Cruz Machado, Rio Jacutinga, 25º56’13”S, 51°13’47”W, W. J. da Graça, 23 January 2014. UFRGS 22662, 4, 31.1–47.6 mm *LS*, municipality of Reserva do Iguaçu, Rio das Torres, 25º48’24.7”, 51º59’26”W, J. Wingert, J. Ferrer, R. Angrizani, A. Fregonezi, 13 October 2013.

3.2 *Cambeva* sp. A

Figures 12–22 and Table 2

Holotype

NUP 2416.1, 79.2 mm L_S, Brazil, Paraná State, municipality of Mangueirinha, Córrego Verde, Lower Rio Iguaçu basin, Lower Rio Paraná system, 25º57'56"S, 51º56'59"W, Nupélia staff, 15 March 1993 (Figure 13).

Paratypes

All from Brazil, Paraná State, Lower Rio Iguaçu basin, Lower Rio Paraná system: NUP 2416.2, 20 (3 c&s, 54.4–89.0 mm L_S), 20.0–97.4 mm L_S, collected with the holotype. NUP 2416.3, 1, 30.4 mm L_S, municipality of Mangueirinha, Rio Butiá, 25º59'19"S, 52º04'40"W, Nupélia staff, 15 March 1993. NUP 2416.4, 9 (2 c&s, 36.3–69.4 mm L_S), 10.3–38.4 mm L_S, municipality of Mangueirinha, Córrego São Pedro, 25º58'52"S, 51º48'50" W, Nupélia staff, 15 March 1993. NUP 15709, 6, 50.3–72.2 mm L_S, municipality of Cruz Machado, unnanamed stream, tributary to the Rio da Areia, 25º56'48"S, 51º23'45"W, W. J. da Graça, 24 January 2014. NUP 15882.1, 3, 68.3–89.6 mm L_S, municipality of Cruz Machado, unnamed stream, tributary to the Rio da Areia, 25º56'48"S, 51º23'45"W, W. J. da Graça, 24 January 2014. NUP 15596, 5, 77.7–86.7 mm L_S, municipality of Cruz Machado, Rio Jacutinga, tributary to the Rio da Areia, 25º56'13"S, 51º13'47"W, W. J. da Graça, 23 January 2014. NUP 18893.1, 5, 30.2–74.8, mm L_S, municipality to the Inácio Martins, unnamed stream, tributary to the Rio da Areia, 25º37'13"S, 51º07'21"W, W. J. da Graça, 05 October 2015.

FIGURE 13 *Cambeva* sp. A, holotype, NUP 2416.1, 79.2 mm L_S, Brazil, Paraná State, municipality of Mangueirinha, Córrego Verde, Rio Iguaçu basin, Lower Rio Paraná system.

3.2.1 Diagnosis

Cambeva sp. A can be distinguished from all congeners except *C. crassicaudata*, *C. igobi*, *C. ytororo* and *C. stawiarski* by the presence of procurrent caudal-fin rays thickly ossified and rigid with a slender distal tip (*vs*. procurrent caudal-fin rays thin and and flexible); and the dorsal procurrent caudal-fin rays extending along the tips of at least eight neural spines (*vs*. procurrent caudal-fin rays extending over the tip of less than eight neural spines). *Cambeva* sp. A is distinguished from *C. crassicaudata* and *C. igobi* by having 30–31 dorsal procurrent caudal fin-rays (*vs*. 24–26 and 26, respectively). Furthermore, *Cambeva* sp. A is distinguished from *C. crassicaudata* by the presence of a caudal fin truncate with a small notch in the distal margin in adults (*vs*. forked caudal fin distal margin in adults), vertebrae number (38–42 *vs*. 35–36), the number of odontodes in the interopercular patch (23–34 *vs*. 19–22) and the lower caudal peduncle depth (10.3–18.7% *vs*. 22.8–25.4% of L_S); *Cambeva* sp. A is distinguished from *C. igobi* by the shorter head length (18.4–22.2% *vs*. 23.8–26.8% of L_S) and vertebrae number (38–42 *vs*. 37). *Cambeva* sp. A is distinguished from *Cambeva stawiarski* by the colour pattern of the dorsal and lateral surface of body in small and some larger specimens,

composed of dark brown blotches, with several spaces between blotches (*vs*. smaller specimens with the dorsal and lateral surface of body composed of dark brown blotches of irregular shapes, forming a homogeneous color, with few spaces between blotches in *C. stawiarski*), modally having I+7 pectoral-fin rays (*vs*. I+6), the number of teeth on ceratobranchial 5 (42–49 *vs*. 25–27), number of teeth on the plate connected to pharyngobranchial 4 (46 *vs*. 31–39), the insertion of the first dorsal basal radials anteriorly to the 19th neural spine (*vs*. anteriorly to the 18th neural spine) and number of procurrent caudal-fin rays dorsally and ventrally (30–31 and 13–17, respectively *vs*. 21–27 and 9–11, respectively). *Cambeva* sp. A is distinguished from *C. ytororo* by the presence of a caudal fin truncate with a small notch in the distal margin in adults (*vs*. rounded caudal fin in distal margin in adults), lower body depth (10.6–18.0% *vs*. 18.0–20.4% of L_S) and longer nasal barbel length (36.5–69.3% *vs*. 22.5–33.9% of L_H). Additionally, *Cambeva* sp. A is distinguished from the remaining congeners from the Rio Iguaçu basin by the presence of a dorsal and caudal fin with scattered dark brown spots over lighter background fading towards distal margins (*vs*. by the narrow vertical dark stripe along the distal margin of the caudal and dorsal fins and a vertical unpigmented band across the proximal region of caudal fin in *C. castroi*); by the colour pattern of the dorsal and lateral surface of body composed of dark brown rounded blotches, several times coalescent forming irregular shapes in inner skin layer and few small black inconspicuous spots or dark brown blotches, with several spaces between blotches (*vs*. caudal and dorsal fins with a narrow vertical dark stripe along the distal margin and caudal fin with a vertical unpigmented band across the proximal region in *C. castroi*); by the colour pattern of the dorsal and lateral surface of the body composed of dark brown rounded blotches, several times coalescent forming irregular shapes in inner skin layer and a few small black spots in the outer skin layer (*vs*. the colour pattern of body with scattered and juxtaposed spots, some coalesced and forming blotches or body with blotches, irregularly shaped and some individuals with a ringed blotch, with a clear central region in *C. davisi*; several diffuse dark brown spots in *C. mboycy*; dark-brown stripes on the sides of the trunk and caudal peduncle in *C. naipi*; by the colour pattern of body plain gray in *C. papillifera* and *C. plumbea*; the body almost covered by numerous small spots of various sizes and shapes in *C. taroba*). *Cambeva* sp. A is further distinguished from *C. taroba*; by the pectoral-fin with modally I+7 rays and the first pectoral-fin ray not prolonged as a filament (*vs*. by the pectoral-fin with I+5 rays and the first pectoral-fin ray prolonged as a filament).

3.2.2 Description

External morphology. Morphometric data are provided in Table 2. Maximum size observed 97.43 mm L_S. Body elongate. Trunk roughly cylindrical close to head and gradually becoming laterally compressed towards caudal fin. Dorsal profile of trunk straight to slightly concave along anterior half of body to insertion of dorsal fin. Ventral profile of trunk straight to slightly convex. Dorsal profile of caudal peduncle straight to slightly convex and ventral profiles of caudal peduncle straight to slightly concave or convex in some specimens.

TABLE 2 Morphometric data for *Cambeva* sp. A. N = number of specimens; SD = standard deviation.

	Holotype	N	Min	Max	Mean	SD
Standard length (mm)	79.2	25	34.0	97.4	70.7	-
Percents of Standard Length						
Head length	20.0	25	18.4	22.2	20.5	1.02
Predorsal length	58.9	25	55.5	69.5	63.7	2.98
Prepelvic length	54.6	25	50.0	59.3	55.0	2.19
Preanal length	67.9	25	52.3	74.7	70.0	4.27
Pectoral girdle width	15.2	25	13.3	17.5	15.7	1.23
Body length	82.4	25	76.2	86.6	82.3	2.88
Pectoral-fin length	14.5	25	10.5	18.5	14.0	1.60
Pelvic-fin length	10.4	25	7.7	11.5	9.5	0.84
Distance between pelvic-fin base and anus	9.8	25	6.2	12.4	9.0	1.38
Caudal peduncle length	24.6	25	17.3	25.6	21.0	1.94
Caudal peduncle depth	16.0	25	10.3	18.7	13.9	2.04
Body depth	14.3	25	10.6	18.0	14.9	1.99
Length of dorsal-fin base	9.8	25	7.0	12.0	9.5	1.33
Length of anal-fin base	5.4	25	5.0	9.0	6.8	1.11
Pelvic–anal distance	14.5	25	9.7	17.6	15.0	1.91
Percents of Head Length						
Head width	84.6	25	77.2	99.6	86.1	5.07
Nasal barbel length	45.0	25	36.5	69.3	49.6	8.67
Maxillary barbel length	47.0	25	27.6	72.5	48.1	10.50
Rictal barbel length	43.6	25	30.4	64.0	44.8	8.75
Snout length	43.5	25	39.0	48.8	43.3	2.27
Interorbital	20.9	25	10.3	24.5	20.2	2.81
Mouth width	34.7	25	27.6	52.9	37.9	5.08
Eye diameter	9.0	25	6.1	11.0	8.3	1.43

Head depressed, trapezoidal from dorsal view, wider posteriorly. Dorsal and ventral profiles of head straight to slightly convex in lateral view. Snout straight to slightly convex in dorsal view. Eyes located dorsolaterally on anterior half region of head, at same longitudinal line of nasal barbel, round to antero-posteriorly elliptical, covered by a thin and translucent skin. Orbital rim not free. Each eye located over posterior termination of shallow and small longitudinal crest beginning at posterior nostril and making eyes visible from lateral view.

Anterior nostril of approximately same size as eyes, surrounded by flap of integument posterolaterally continuous with base of nasal barbel. Posterior nostril surrounded anterolaterally by thin flap of integument. Gill openings not constricted, united with isthmus anteriorly, forming a free fold reaching pectoral-fin insertion. Mouth subterminal and slightly curved with corners posteriorly oriented. Upper lip thicker distally. Lower lip with fleshy

lobes in lateral limits, medial to base of rictal barbels. Lips with numerous small, rounded papillae of approximately same size.

Barbels with wide base, tapering gradually towards tips. Nasal barbel emerging from lateral region of anterior nostril, its posterior tip reaching between infraorbital pores i10 and i11 when adpressed to body. Maxillary barbell reaching anterior region of interopercular patch of odontodes.

Pectoral fin with distal margin rounded, modally I+7* rays (seven of 25 specimens with I+6; and one with I+8), first ray unbranched and not prolonged as filament. Pelvic fin with I+4* rays, inserted anterior to origin of dorsal fin, with distal margin rounded, reaching or covering anterior margin of urogenital papilla, but never reaching anal fin origin. Inner margins of pelvic fins very close basally and sometimes in contact. Dorsal fin with distal margin slightly convex, ii/iiii–II+7* rays (one of 25 specimens with II+8 rays). Origin of dorsal fin located at vertical line near middle of pelvic fin. Anal fin elongate with distal margin convex and slightly smaller than dorsal fin, ii/iii-II+5* rays (one of 25 specimens with II+7). Origin of anal fin located at vertical line in last third of dorsal fin base. Caudal fin with distal margin truncated to slightly concave, with small notch medially in some specimens, I+11+I* rays (one of 25 specimens with I+13+I).

Osteology. Mesethmoid with anterior margin slightly concave and cornua rounded at distal margins, width base at anterior margin similar to their length. Tendon bone supraorbital long and thin, about four times larger than antorbital, with process along proximal margin. Antorbital short and anteriorly expanded with rounded anterior and posterior margins. Anterior cranial fontanel restricted to small, rounded opening situated immediately anterior to epiphyseal bar. Posterior cranial fontanel long extending from posterior portion of frontals to parieto-supraoccipital. Epiphyseal bar longer than wide. Anterior portion of sphenotic laterally directed in dorsal view. Sphenotic, prootic and pterosphenoid fused. Vomer arrow-shaped with long posterior process extending to parasphenoid. Parasphenoid with long and pointed posterior process extending to posteromedial region of basioccipital. Weberian capsule with small lateral openings, much smaller than lateral profile of capsule. Anterior margin fused to basioccipital (Figure 14).

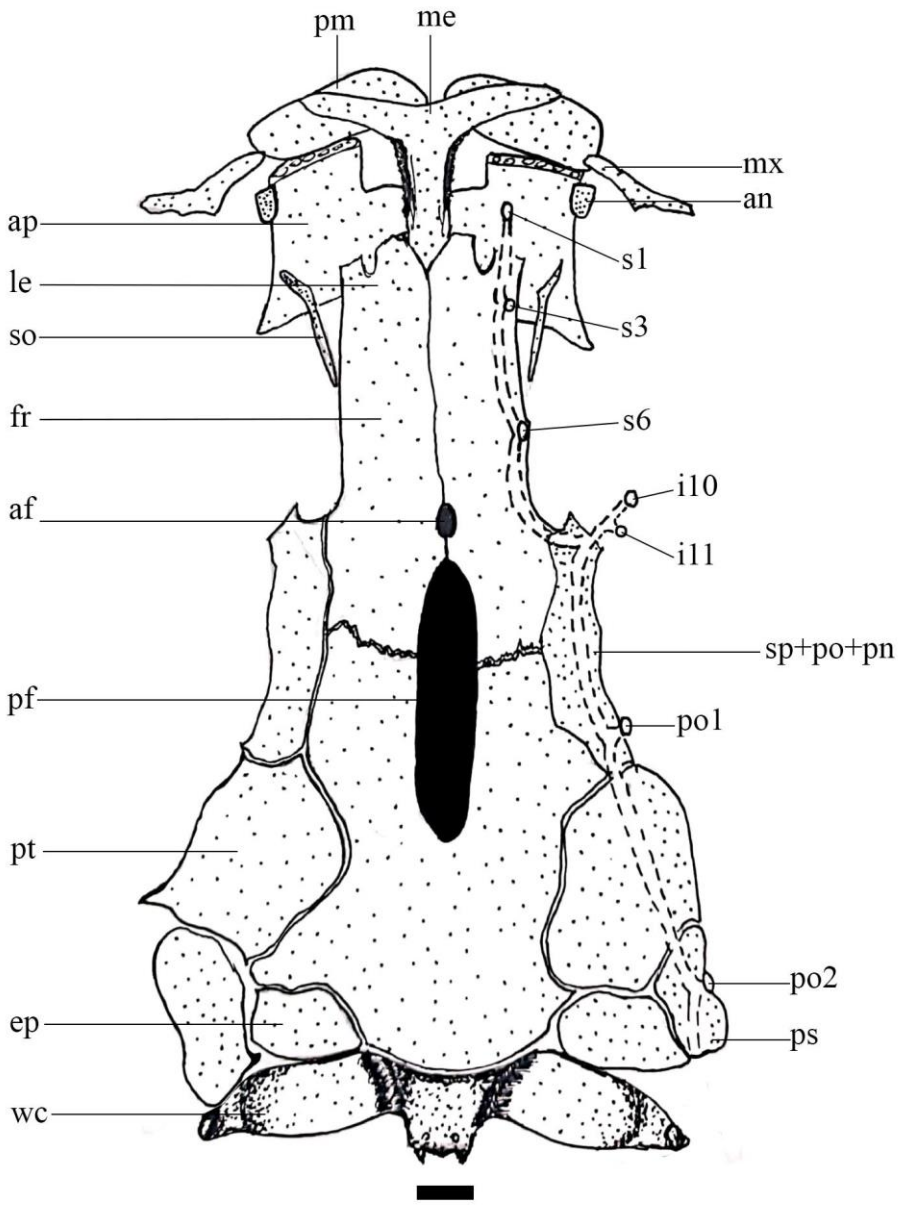

FIGURE 14 Dorsal view of neurocranium of *Cambeva* sp. A, NUP 2416.2, paratype, 89.0 mm L_S. Abbreviations: af, anterior fontanel; af, antorbital; ap, autopalatine; ep, epioccipital; fr, frontal; le, lateral ethmoid; i10–11, infraorbital sensory branch 10 and 11; me, mesethmoid; mx, maxilla; pf, posterior fontanel; pm, premaxilla; po1–2, postotic sensory branches 1 and 2; ps, posttemporosupracleithrum; pt, pterotic; s1, supraorbital sensory branch 1; s3, supraorbital sensory branch 3; s6, supraorbital sensory branch 6 (epiphyseal branch); so, tendon-bone supraorbital; sp+po+pn, sphenoticprootic-pterosphenoid complex bone; su, parieto-supraoccipital; wc, Weberian capsule. Scale bar = 1 mm.

Premaxilla elliptical with 90 (n=1) conical teeth similar in size, distributed in four irregular rows. Lower jaw with 56 (n=1) conical teeth distributed in three rows (Figure 15). Teeth range from base of coronoid process to near dentary symphysis. Maxilla boomerang-shaped and shorter than premaxilla. Autopalatine with distal margin concave, anterior margin slightly convex followed by concave mesial margin with a bony expansion (Figure 16), posterior margin with small process extending slightly over lateral ethmoid and a long postero-lateral process.

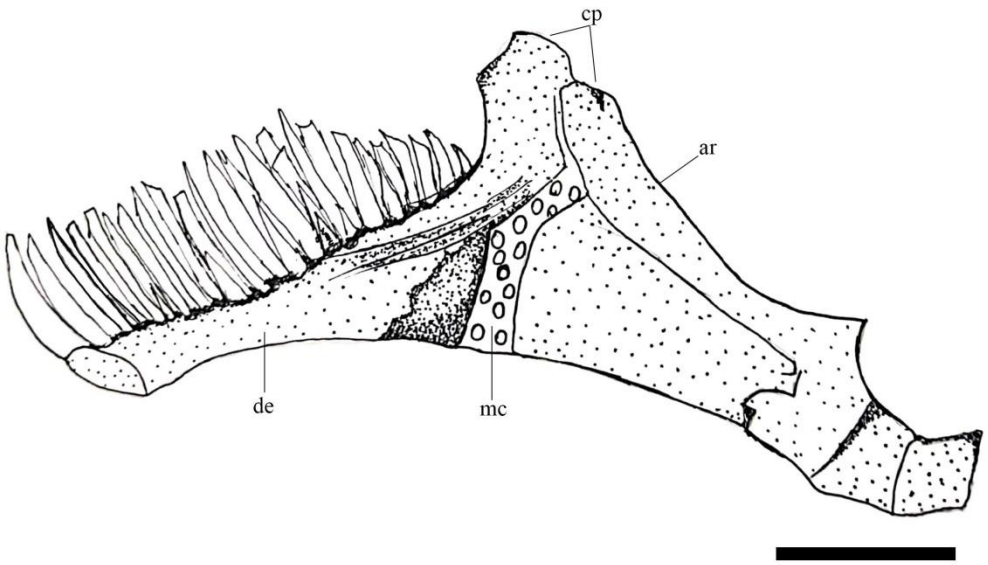

FIGURE 15 Medial view of the left lower jaw of *Cambeva* sp. A, NUP 2416.4, 69.5 mm L_S. ar, anguloarticular; cp, coronoid process; de, dentary; mc, Meckel's cartilage. Scale bar = 1 mm.

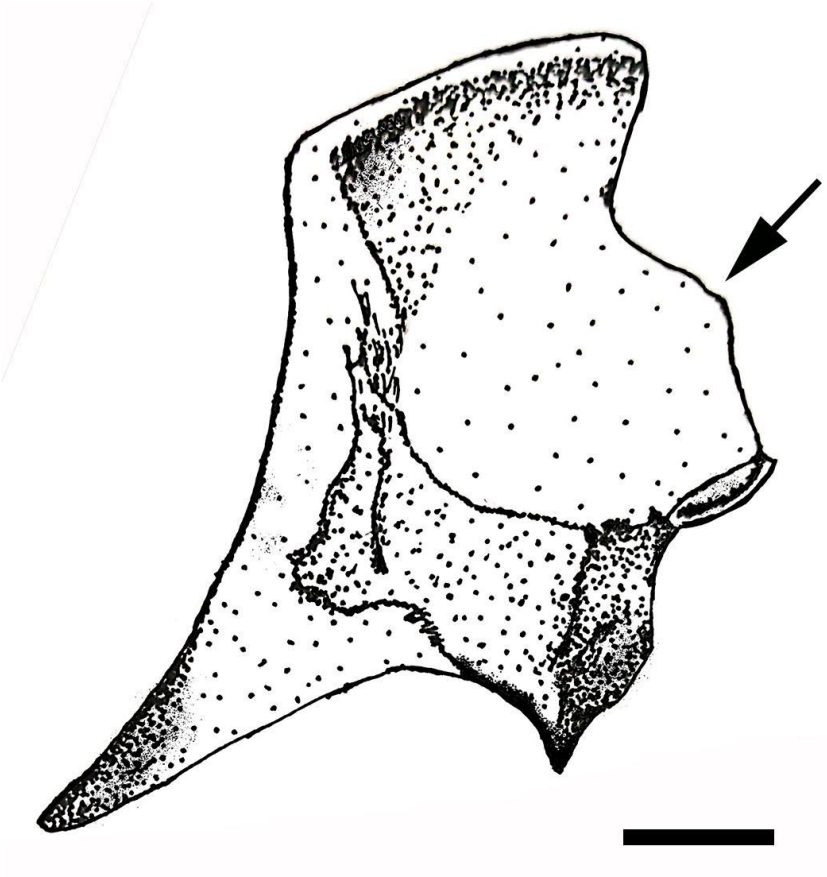

FIGURE 16 Ventral view of the right autopalatine of *Cambeva* sp. A, NUP 2416.2, paratype, 54.4 mm L_S. Arrow indicate mesial bony expansion. Scale bar = 0.5 mm.

Metapterygoid large and laminar, connected to quadrate through cartilage and a pointed process on the ventral region of the metapterygoid (Figure 17). Quadrate L-shaped, antero-dorsal arm with deep constriction. Hyomandibula well developed with prominent notch in dorsal margin. Opercular patch of odontodes rounded with 14–25 (n=4) conical odontodes. Interopercular patch of odontodes elongate with 27–34 (n=4) conical odontodes concentrated posteriorly. Odontodes of both opercular and interopercular patches gradually curving medially and increasing in size posteriorly.

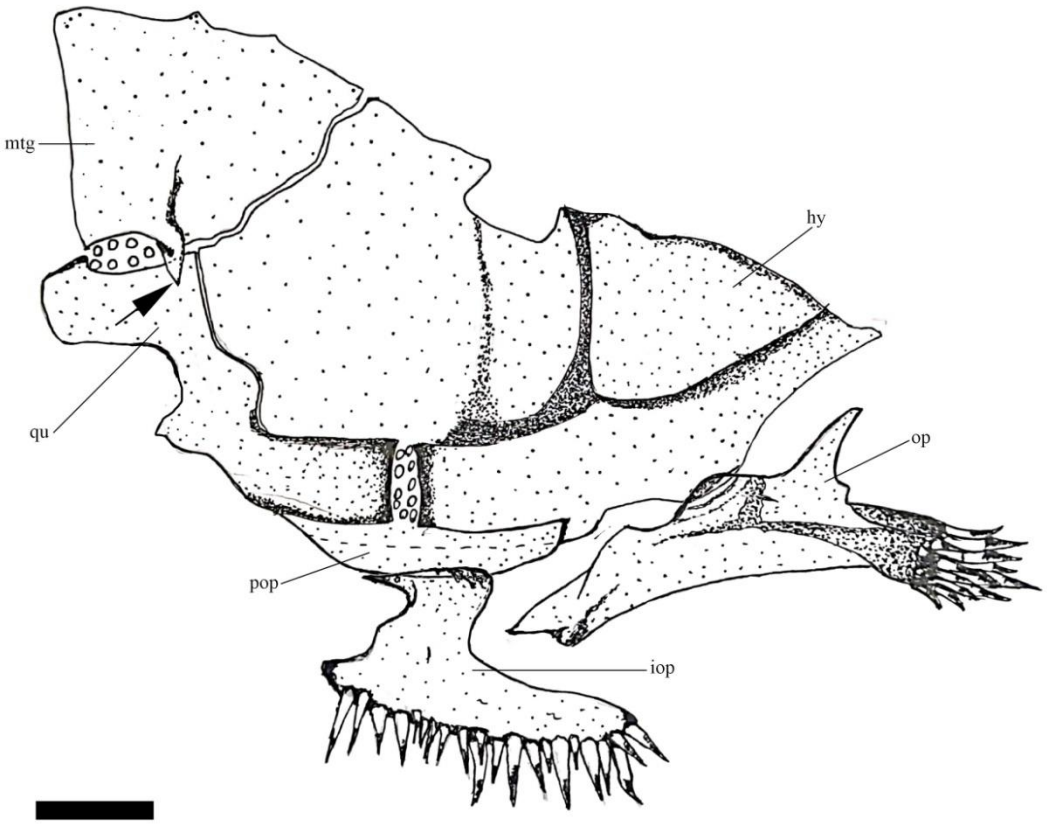

FIGURE 17 Dorsal view of left suspensory of *Cambeva* sp. A, NUP 2416.2, paratype, 54.4 mm L_S. hy, hyomandibula; iop, interopercle; mtg, metapterygoid; op, opercle; pop, preopercle. Arrow indicate the pointed process on the ventral region of the metapterygoid. Scale bar = 1 mm.

Ventral hypohyal trapezoid shaped. Anterior ceratohyal elongate and wider at anterior and posterior tips. Posterior ceratohyal short and triangular. Dorsal hypohyal and interhyal absent. Nine (n=2), ten (n=3) or eleven (n=1) branchiostegal rays (1 of 5 specimens with ten and eleven branchiostegal rays on each side of hyoid arch): six, seven or eight in contact with anterior ceratohyal, one with interceratohyal cartilage, one with posterior ceratohyal and some specimens with one lateral from posterior ceratohyal and not contacting it. Three or four posterior branchiostegal rays wider distally (Figure 18).

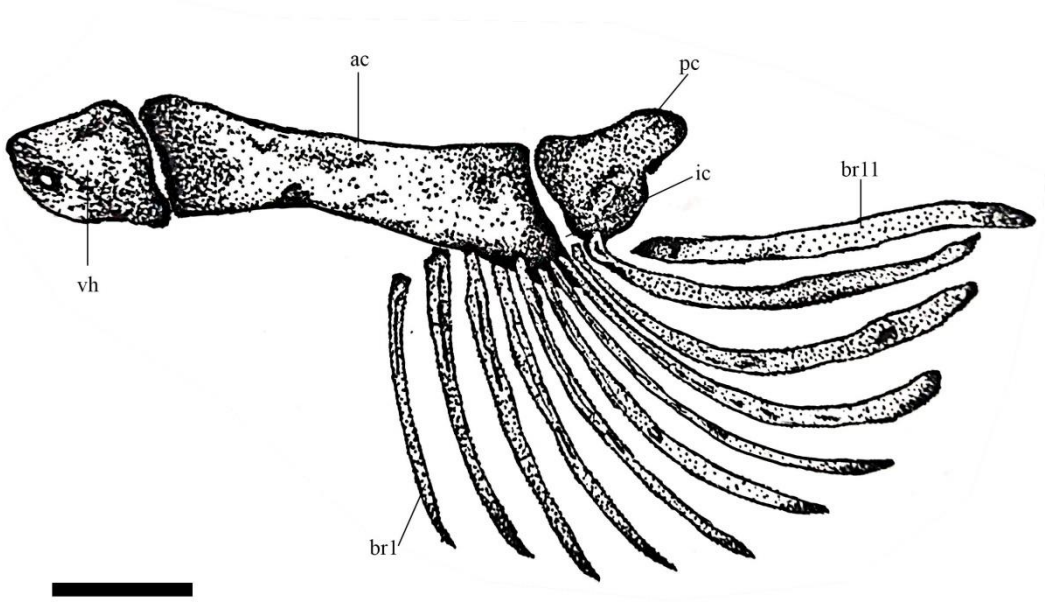

FIGURE 18 Lateral view of left hyoid arch of *Cambeva* sp. A, NUP 2416.2, 54.4 mm L_S Abbreviations: ac, anterior ceratohyal; br1–10, branchiostegal rays 1 to 10; ic, inter-ceratohyal cartilage; pc, posterior ceratohyal; vh, ventral hypohyal. Scale bar = 1 mm.

Urohyal with expanded anterior head, two elongate lateral processes with wide bases and decreasing in width distally with rounded tips. Laminar, elongate and narrow posterior process. Posterior process of urohyal shorter than lateral processes (Figure 19).

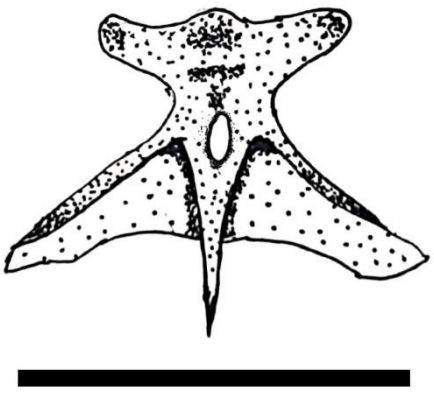

FIGURE 19 Dorsal view of urohyal of *Cambeva* sp. A, NUP 2416.2, 54.4 mm L_S. Scale bar = 1 mm.

Basibranchials 1 absent. Basibranchials 2 and 3 elongated, of approximately equal lengths, connected to each other by cartilage; basibranchial 2 slightly wider than basibranchial 3. Basibranchial 4 hexagonal and entirely cartilaginous. Hypobranchial 1 elongated, with cartilaginous tips, slightly longer than basibranchial 2. Hypobranchials 2 and 3 with approximately same size and with narrow anterolateral ossified processes with large area of cartilage distally. Five elongate ceratobranchials with cartilaginous tips. Ceratobranchials 1 and 4 with straight margins. Ceratobranchials 2 and 3 with concavity along posterior margin, more prominent in ceratobranchial 3 (one of five specimens lacks the concavity in ceratobranchial 3 Figure 20b). Ceratobranchial 5 expanded posteromedially with 42–49 (n=2) conical, elongated and pointed teeth. Four epibranchials, first three elongated and narrow with cartilage at tips. Epibranchials 1 and 2 with triangular process along anterior margins; process elongated pointed and slightly larger in epibranchial 1; epibranchial 3 with distinct curved process on posterior margin. Epibranchial 4 rectangular shaped, produced by broad anterior and posterior crests. Epibranchial 5 small, narrow, curved and completely cartilaginous. Pharyngobranchial 1 and 2 absent. Pharyngobranchial 3 elongated, similar in form but shorter than hypobranchial 1, with cartilage at tips. Pharyngobranchial 4 curved and ossified, connected to plate with 46 (n=1) conical, elongated and pointed teeth, arranged in up to three irregular rows; teeth increasing in size posteriorly (Figure 20a).

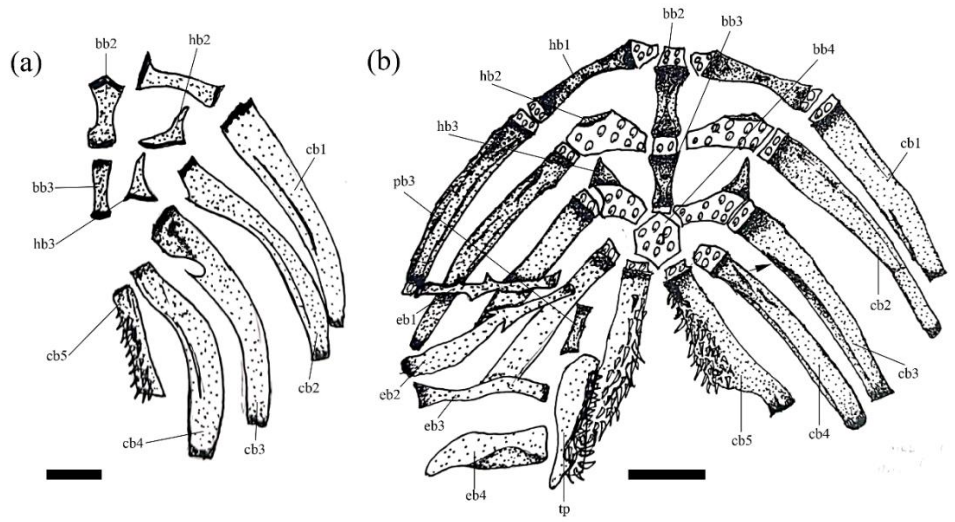

FIGURE 20 Dorsal view of gill arches (right dorsal elements and gill rakers not show) (a) *Cambeva* sp. A, paratype, NUP 2416.2, 89.0 mm L_S. (b) *Cambeva* sp. A, paratype, NUP 2416.2, 54.4 mm L_S. Abbreviations: bb2–4, basibranchials 2 to 4; cb1–5, ceratobranchials 1 to

5; eb1–5, epibranchials 1 to 5; hb1–3, hypobranchials 1 to 3; pb3, pharyngobranchial 3; tp; tooth plate. Arrow indicates lack of the concavity in ceratobranchial 3. Scale bar = 1 mm.

Dorsal fin with eight basal radials, first inserted anterior to neural spine of the 19th (n=3) vertebrae. Anal fin with six (one of three specimens with seven) basal radials, first inserting anterior to haemal spine of the 23rd to 25th vertebrae. Procurrent caudal-fin rays 30 to 31 dorsally (4) extending over the tip of 10–13 neural spines and 13 to 17 procurrent caudal-fin rays ventrally (4) (Figure 21). Upper plate with one unbranched ray and five branched rays; hypural 3 free and hypurals 4 and 5 fused to each other. Lower caudal plate with one unbranched ray and six branched rays. Parhypural and hypurals 1 and 2 co-ossified and fused to compound caudal centrum. Branched caudal fin rays splitting two times. Free vertebrae 38 to 42 (n=2), 12 or 13 (n=3) pairs of ribs.

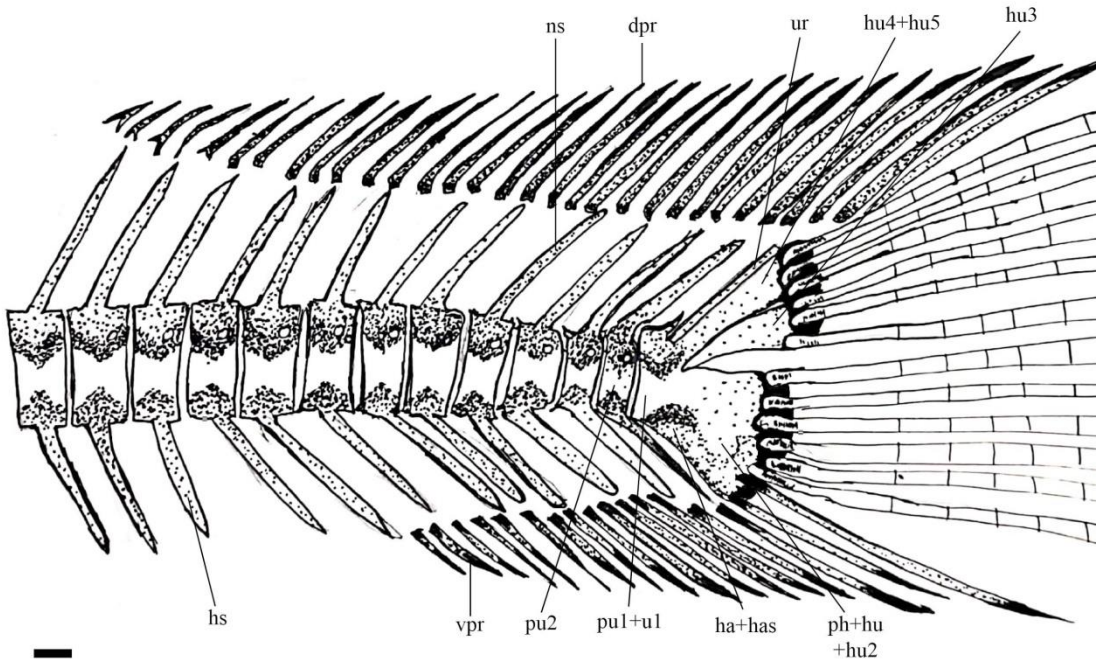

FIGURE 21 Left lateral view of the caudal peduncle of *Cambeva* sp. A, paratype, NUP 2416.2, 89.0 mm L_S. Abbreviations: dpr, dorsal procurrent caudal-fin rays; ha+has, complex hypurapophysis composed of hypurapophysis and secondary hypurapophysis; hs, hemal spine; hu3, hypural 3; hu4+hu5, complex plate formed by co-ossification of hypurals 4 and 5; ns, neural spine; ph+hu1+hu2, complex plate formed by co-ossification of hypurals 1 and 2 and parhypural; pu1+u1, complex centrum composed of pleural centrum 1 and ural centrum

1; pu2, pleural centrum; ur, uroneural; vpr, ventral procurrent caudal-fin rays. Scale bar = 1 mm.

Laterosensory system. Laterosensory canals with simple (non-dendritic) tubes ending in single pores. Supraorbital sensory canal complete, with paired pores s1, s3 and s6. Pore s1 located between anterior nostrils, pore s3 located in same longitudinal row of pore s1 after posterior nostrils and pore s6 in interorbital space; s2, s4, s5, s7 and s8 (parietal) branches and pores absent. Infraorbital sensory canal incomplete; pores i1 and i3 absent, pore i10 located behind eyes and pore i11 located lateral to posterior margin of eye. Postotic pore po1 located lateral to anterior margin of opercular patch of odontodes. Postotic pore po2 located lateral to middle of length of opercular patch of odontodes. Lateral-line canal with two to five pores located above insertion of pectoral fin and posterior of gill openings.

Status of *Extensor tentaculi*. *Extensor tentaculi* originating from ventrolateral regions of lateral ethmoid and orbitosphenoid, presence of a ventral bundle originating from anterodorsal region of suspensorium on metapterygoid and hyomandibula. Inserting in posterolateral region of autopalatine (Figure 22).

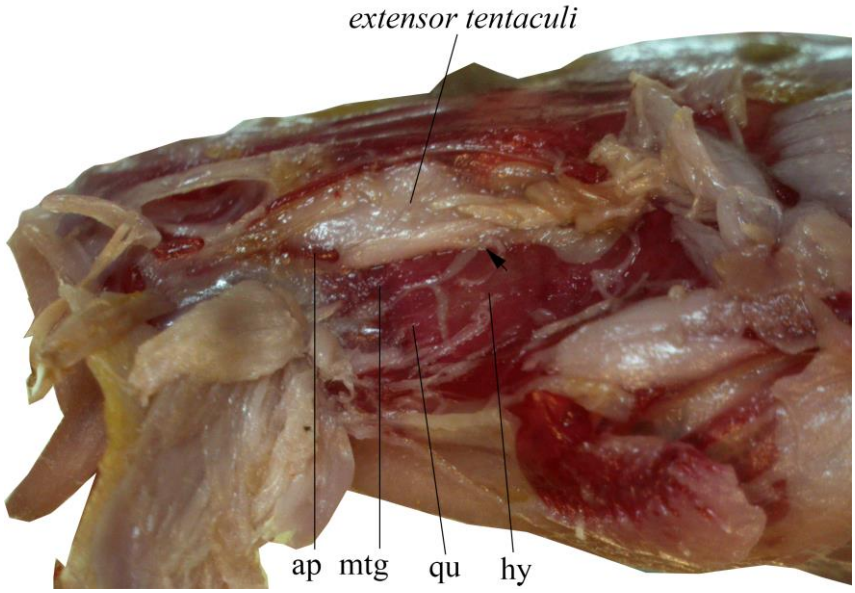

FIGURE 22 Left lateral view of neurocranium region of *Cambeva* sp. A, NUP 15882.1, 68.3 mm L_S. Arrow indicates the ventral bundle of the *Extensor tentaculi* originating from the suspensorium.

Colour in alcohol. Background colour of body yellowish (Figure 13, 23b,c) in larger specimens (greater than 38.4 mm L_S) with dorsal and lateral surface of body composed of dark brown rounded blotches, several times coalescent forming irregular shapes in inner skin layer and few small black inconspicuous spots, smaller or equivalent in size to eye diameter on the outer skin layer. Smaller specimens (between 30.7 to 38.4 mm L_S; Figure 23d; and some larger specimens Figure 23a) with background colour of body yellowish with dorsal and lateral surface of body composed of dark brown blotches, with several spaces between blotches. Dorsal surface of head in occipital region with concentrated round dark brown blotches variable in size, in some specimens the concentration of pigmentation produces a totally appearance dark dorsal surface of head; lateral surface of head with dark brown blotches of irregular shapes variable in size; ventral surface of head light yellow. Ventral surface of body light yellow in belly with diffuses dark blotches in pectoral-fin insertion and small dark brown blotches between pelvic-fin insertions, extending to caudal peduncle. Pectoral, anal, dorsal and caudal fins with scattered dark brown spots, smaller or equivalent in size to eye diameter, over lighter background fading towards distal margins. Pelvic fin unpigmented or some specimens with a few inconspicuous dark spots medially. Barbels dorsally with scattered or coalescent dark brown spots, smaller or equivalent in size to eye diameter, and pale yellow ventrally.

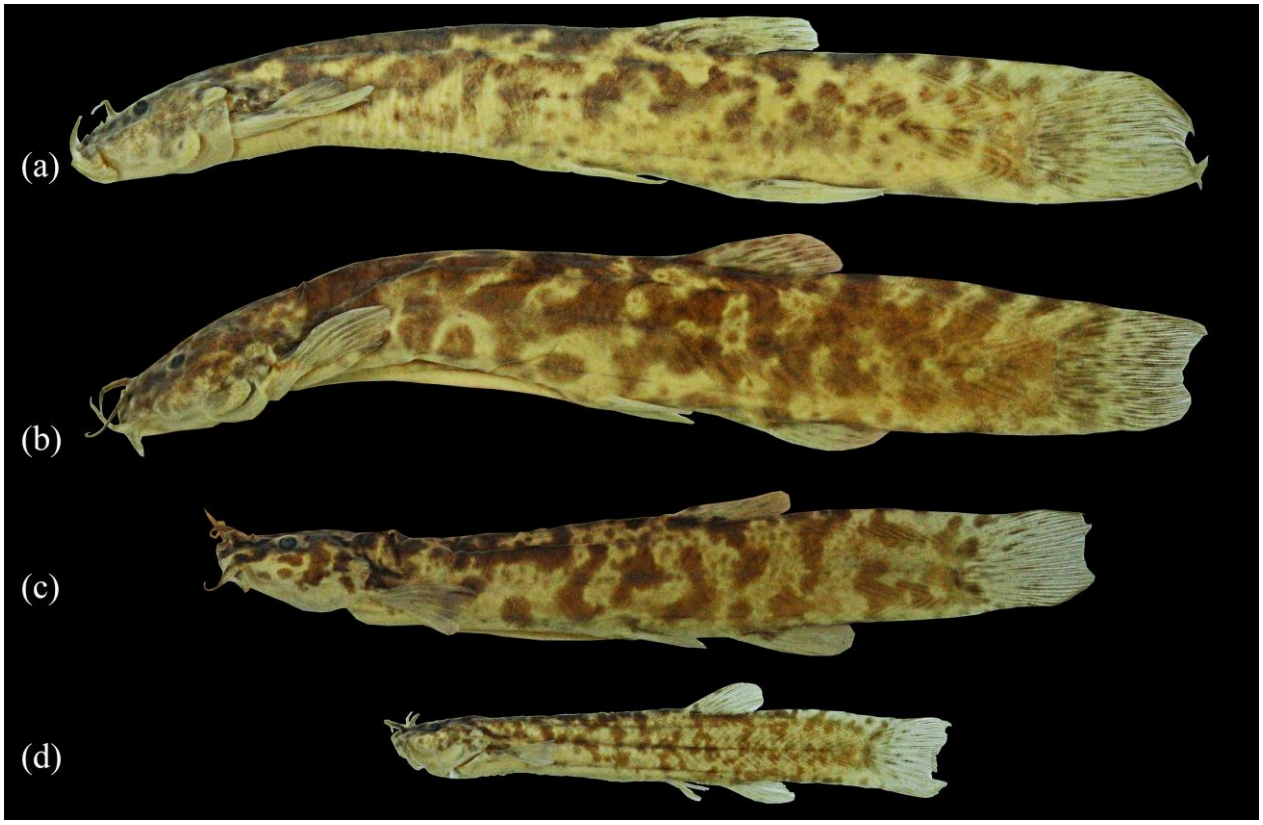

FIGURE 23 Paratypes of *Cambeva* sp. A, with ontogenetic variation in colouration. (a) NUP 2416.2, 87.4 mm L_S; (b) NUP 2416.2, 74.6 mm L_S; (c) NUP 2416.4, 38.3 mm L_S; (d) NUP 2416.4, 31.2 mm L_S.

3.2.3 Geographic distribution

Cambeva sp. A is known from five tributaries from the Lower Rio Iguaçu (Figure 12): Córrego Verde (type-locality), Rio Areia, Rio Butiá, Rio Jordão and Rio São Pedro.

3.2.4 Ecological notes

The type-locality is located at elevation of approximately 950 m above sea level. Other localities are between 650 and 950 m above sea level. Specimens of *Cambeva* sp. A were collected with *Ancistrus agostinhoi* Bifi, Pavanelli & Zawadzki 2009, *Astyanax jordanensis* Vera Alcaraz, Pavanelli & Bertaco 2009, *Cambeva davisi*, *C. papilliferus*, *C. stawiarski* and *Jenynsia diphyes* Lucinda, Ghedoti & da Graça 2006 in the Rio Jordão basin, and presumably occupy the same kind of fast water and rocky-substrate environment.

3.2.5 Conservation status

Cambeva sp. A is endemic to the Rio Iguaçu basin. The species is known from six different localities, and the extent of occurrence (EOO) of the species is approximately 1,400 km², considering a polygon uniting all known sites. Although the hydroelectric power plants installed in the Rio Iguaçu are fragmenting the population of *Cambeva* sp. A, we are not able to properly recognize it as an impact on the species and suggest categorizing it as Least Concern (LC), according to IUCN categories and criteria (IUCN, 2019).

4 DISCUSSION

4.1 Generic allocation

The redescription of *Cambeva stawiarski* and the new species proposed here are allocated in *Cambeva* Katz, Barbosa, Mattos & Costa 2018 for having the interopercle shorter than the opercle (Fig. 6;17), a deep constriction on the basal portion of the antero-dorsal arm of the quadrate in lateral view, its width less than 50% quadrate width at its dorsal limits (Fig. 6; 17), teeth absent in the coronoid process of the dentary (Fig. 4; 15), and by having the maxilla shorter than the premaxilla (Fig. 3; 14), all combinations of derived and primitive morphological characters proposed by Katz *et al.* (2018). The proposal of the genus suffered with much criticism (*e.g*. Reis and de Pinna, 2019; Ochoa *et al*. 2020) due to the lack of synapomorphies, but by the existence of these derived and primitive characters in *Cambeva stawiarski* and *Cambeva* sp. A leads us to allocate these species in *Cambeva*.

4.2 Intrageneric relationship

Bockmann *et al.* (2004) described an osseous contact area between metapyerygoid and quadrate in *Cambeva diabola*. Costa *et al.* (2021) mentioned this character and the existence of a reinforced contact in metapterygoid-quadrate, like a flat small process on the dorsal margin of quadrate, laterally overlapping metapterygoid and situated just posterior to the syncondrial joint between the metapterygoid and the quadrate, present in *C. davisi* group, including at least *C. barbosae*, *C. castroi*, *C. davisi*, *C. diabola*, C. *guareiensis* and *C. zonata*. This process and the reinforced area are present in the ventral region of the metapterygoid (Figure 17), but not in the quadrate from *Cambeva* sp. A, indicating a possible autapomorphy for the species, but it's necessary to analyze more species.

Furthermore, *Cambeva stawiarski* and *Cambeva* sp. A have the synapomorphy proposed by Datovo and Bockmann (2010) for the clade formed by *C. davisi* and *C. stawiarski*, which is the *extensor tentaculi* originating from both the neurocranium and suspensorium. Katz *et al*. (2018) and Reis *et al*. (2019) found this derived condition in *C. castroi*, *C. cubataonis*, *C. davisi*, *C. horacioi*, *C. naipi* and *C. zonata*, being able to indicate an intrageneric relationship between these species, and these characters proposed by Datovo and Bockmann (2010) should be better analyzed in more species of *Cambeva*.

4.3 *Cambeva stawiarski* group monophyly

The *Cambeva stawiarski* group is hypothesized by Wosiacki and de Pinna (2008a,b) based on the presence of (1) the procurrent caudal-fin rays thickly ossified and rigid with a slender distal tip, (2) the dorsal procurrent caudal-fin rays extending along the tips of at least 10 neural spine and (3) 10–11 branchiostegal rays. The holotype of *C. stawiarski* and all specimens in the examined material lacks the third character (specimens of *C. stawiarski* analyzed have 8 or 9 branchiostegal rays), and the procurrent caudal-fin rays could not be seen on radiography, but the majority of specimens analyzed here have the others synapomorphies. Between the species in the group, only *C. ytororo* and some specimens of the new species proposed here have nine branchiostegal rays, but this character is present in several other *Cambeva* species (see Datovo *et al.*, 2012; Ferrer and Malabarba, 2013; Reis *et al.*, 2019; Wosiacki and Garavello, 2004). Thus, the presence of this character in *C. stawiarski* seems to be a plesiomorphy and should not be used to diagnose the group. Therefore, for now, the *Cambeva stawiarski* group encompasses the following species: *Cambeva stawiarski*, *C. crassicacudata*, *C. igobi*, *C. ytororo* and *Cambeva* sp. A, and can be diagnosed by having (1) the procurrent caudal-fin rays thickly ossified and rigid with slender distal tips; and (2) the dorsal procurrent caudal-fin rays extending along the tips of at least eight neural spine.

4.4 Phylogenetic relationships within the *Cambeva stawiarski* group

Internal morphology is useful in identification of new species and to establish the relationship of *Cambeva* species (see Costa *et al.*, 2020, 2021; Datovo and Bockmann, 2010; Katz *et al.*, 2018; Terán *et al.*, 2017; Wosiacki and de Pinna, 2008b). The presence of ten branchiostegal rays in some specimens of the new species proposed here suggests the close relationship among *C. crassicaudata*, *C. igobi* and *Cambeva* sp. A, but the high number of dorsal

procurrent caudal-fin rays (>30) suggests the relationship between *C. ytororo* and the new species. Therefore, without the analysis of molecular data from all species of the group, the hypothesis of the relationship between these species remains provisional, because species that share some osteological similarities have correspondents in different groups, such as species without pelvic fin and girdle (see Costa *et al.*, 2020; Donin *et al.*, 2020).

Wosiacki and de Pinna (2008a) consider the mesial expansion of the autopalatine (Figure 5; 16) an autapomorphy of *C. igobi*, however this condition is also present in *C. stawiarski* and *Cambeva* sp. A. This character cannot be seen in *C. crassicaudata* and *C. ytororo* because their descriptions do not provide these data. Even so, the hypothesis of the relationship of the species through this derived character cannot be discarded. In addition, in a single specimen of *Cambeva* sp. A, the notch in the ceratobranchial 3 was not present (Figure 20b). This character was found by the same authors in the description of *C. igobi*, but due to the existence in only one specimen of *Cambeva* sp. A, we have considered this character as a variation in the species.

4.5 Colour pattern

The colour pattern is commonly used in the diagnosis of Trichomycterinae, but in some species it is highly variable (Ferrer and Malabarba, 2013; Nascimento *et al.*, 2017; Reis *et al.*, 2019; Silva *et al.*, 2010; Wosiacki and Garavello, 2004). The original description of *Cambeva stawiarski* is based in only one specimen and Miranda Ribeiro (1968) cannot see the variation in the colour pattern of the species. In small individuals of *Cambeva stawiarski* and *Cambeva* sp. A there is a variation in the colour pattern according to the ontogeny of the species (see description of the colour pattern above), showing that small specimens should be considered in the species colouration pattern descriptions. Although the two species have similarities in the colour pattern of adult specimens, the small specimens are clearly distinct (Figure 2c,d; 23c,d) indicating the validity of the new species proposed here.

4.6 Cambeva sp. A discovery

The similarity in the external morphology of some *Cambeva* species can hide the real diversity of the group, the real geographic distribution and the conservation status of some species, since some species descriptions do not provide complete osteological data (Costa *et al.*, 2020, 2021). It happened to *Cambeva* sp. A, which has been identified many times as *C.*

stawiarski, because the description of this species did not contain any information about the osteology. These taxonomic problems affect all fields that need accurate identification, even when interpreting molecular data. An example is the identification of the clades of *C. stawiarski* in Morais-Silva *et al.* (2018), which we analyzed the vouchers used and none of them corresponded to *C. stawiarski*. The vouchers used corresponding to the clades formed by the specimens of the Rio Piquiri, Rio Ivaí and Rio Iguaçu basins seem to be a new species, however, due to the lack of data about specimens not used in molecular analysis and the variation in external morphology, we prefer not to describe it here.

All these problems caused by identification problems emphasize the importance of taxonomic reviews for all scientific fields. With technological developments, such as the triplet stereo method used by Reis and Pinna (2019) to analyze the type-material of *Trichomycterus alternatus* (Eigenmann 1917) and *Cambeva zonata*, and the implementation of standard X-ray methods, old holotypes of original descriptions with minimal osteological information can be analyzed without injuries to the type-material.

4.7 *Cambeva* diversity in the Rio Iguaçu basin

With the restriction of the geographic distribution of *Cambeva stawiarski* and the new species proposed here, the Rio Iguaçu basin from now on has 66 endemic species. Eleven of the 22 species of *Cambeva* (50.0%) reported from the Paraná State are endemic from the Rio Iguaçu basin (modified percentages from Reis *et al.*, 2020), indicating the high endemic species richness of this basin compared to others. Reis *et al.* (2020) explained the high richness and endemism of the species of this basin by the possible evolution of species to occupy niches that would be occupied by *taxa* from other genera in other basins and are absent in the Rio Iguaçu basin. Furthermore, the basin is isolated from the Rio Paraná by the Iguaçu waterfalls and the compartmentalization promoted by the biogeographic barrier that arose because of tectonic reactivation along the basin, introducing significant modifications on the habitat structure, can explain the endemism of the basin (Garavello and Sampaio, 2010; Maack, 2002; Mello *et al.*, 2015; Petri and Fulfaro, 1983). Therefore, the redescription of *C. stawiarski* and the description of the new species confirm important biogeographic patterns about the endemism of the Rio Iguaçu and about the usage of osteology data in the description of Trichomycterinae species.

5 COMPARATIVE MATERIAL

5.1 *Cambeva crassicaudata*

All specimens of Rio Iguaçu basin, Paraná State, Brazil: MHNCI 12297, 4, 47.0–164.3 mm L_S, municipality of Candói/Pinhão, Rio Jordão, UHE Santa Clara. NUP 3123, 1, 52.3 mm L_S, municipality of Foz do Jordão, Córrego Passo do Aterrado. NUP 3783, 3, 78.6–134.5 mm L_S, municipality of Candói, Rio Jordão. NUP 4006, 3, 107.5-114.3 mm L_S, municipality of Candói, Rio Jordão. NUP 4826, 1, 109.7 mm L_S, municipality of Candói, Rio Jordão. NUP 9998, 1, 95.1 mm L_S, municipality of Guarapuava, Rio Pinhãozinho. NUP 10827, 4, 50.7–102.4 mm L_S, municipality of Foz do Jordão, Jordão reservoir.

5.2 *Cambeva davisi*

Rio Ribeira de Iguape basin: NUP 17409, 8 (2 c&s), 31.7–63.1 mm L_S, municipality of Ponta Grossa, Paraná, Brazil, Rio da Mata, tributary to the Rio Açungui. NUP 17423, 4, 39.7–48.0 mm L_S, municipality of Campo Largo, Paraná, Brazil, Rio Santa Cruz, tributary to the Rio Açungui. **Rio Iguaçu basin:** NUP 4008, 11, 22.14–82.12 mm L_S, munipality of Santa Clara, Paraná, Brazil, Rio da Lage, tributary to the Rio Jordão. NUP 15914, 67, 21.3–78.2 mm L_S, municipality of Cruz Machado, Paraná, Brazil, Rio Jacutinga, tributary to the Rio Santana. NUP 16097, 29, 28.89–79.86 mm L_S, municipality of Laranjeiras do Sul, Paraná, Brazil, Rio Tapera. NUP 17364, 34, 38.7–74.3 mm L_S, municipality of Pinhão, Paraná, Brazil, unnamed river, tributary to the Rio Lajeado Feio. **Rio Ivaí basin:** NUP 15810, 3, 52.7–75.3 mm L_S, municipality of Prudentópolis, Paraná, Brazil, Rio São João, tributary to the Rio Ivaí. NUP 15817, 33, 23.8–68.3 mm L_S, municipality of Prudentópolis, Paraná, Brazil, Rio Barra Grande, tributary to the Rio Ivaí. NUP 15858, 3, 42.2–51.3 mm L_S, municipality of Cândido de Abreu, Paraná, Brazil, unnamed river, tributary to the Rio Maromba. **Rio Itararé basin:** NUP 19251, 10, 30.0–103.1 mm L_S, municipality of Jaguariaíva, Paraná, Brazil, unnamed river, tributary to the Rio das Mortes. **Rio Tibagi basin:** NUP 17390, 14, 31.6–110.1 mm L_S, municipality of Teixeira Soares, Paraná, Brazil, arroio Cachoeira, tributary to the Rio Guarauninha**. Rio Piquiri basin:** NUP 15760, 3, 48.3–52.1 mm L_S, municipality of Janiópolis, Paraná, Brazil, Rio Barreiro, tributary to the Rio Piquiri. NUP 15782, 33, 27.8–103.6 mm L_S, municipality of Goioxim, Paraná, Brazil, Rio Bonito, tributary to the Rio Piquiri.

5.3 *Cambeva diabola*

Rio Tibagi basin: NUP 17403, 4, 31.9 67.20 mm L_S, municipality of Teixeira Soares, arroio Lajeado, tributary to the arroio Chapada. NUP 17447, 2, 109.3–114.8 mm L_S, municipality of Palmeira, Rio São Benedito, tributary to the Rio Caniú. NUP 17457, 2, 53.8–92.9 mm L_S, municipality of Carambeí, Rio Jotuba, tributary to the Rio Pitangui. NUP 17471, 2, 57.8–83.2 mm L_S, municipality of Carambeí, unnamed river, tributary to the Rio Maracanã. NUP 18830, 2, 46.10–59.6 mm L_S, municipality of Palmeira, Rio São Benedito, tributary to the Rio Caniú. NUP 18832, 1, 62.5 mm L_S, municipality of Carambeí, Rio Jotuba, tributary to the Rio Pitangui. Rio das Cinzas basin: NUP 14772, 3, 34.9–78.2 mm L_S, municipality of Jacarezinho, ribeirão Ubá, tributary to the Rio das Cinzas. NUP 20510, 10, 39.9–54.8 mm L_S, municipality of Ibaiti, unnamed river, tributary to the Rio das Pedras**. Rio Itararé basin**: NUP 20439, 9, 40.5–62.9 mm L_S, municipality of Sengés, Rio Pelame, tributary to the Rio Itararé. **Rio Pirapó basin**: NUP 4802, 2, 55.0–60.0 mm L_S, municipality of Pulinópolis, Rio Atlântico, tributary to the Rio Pirapó. NUP 5579, 2, 46.0–72.7 mm L_S, municipality, corrégo Remo, tributary to the Rio Pirapó. **Rio Ivaí basin**: NUP 5482, 3, 19.4–35.3 mm L_S, municipality of Prudentópolis, Rio Barra Grande, tributary to the Rio Ivaí.

5.4 *Cambeva igobi*

All specimens of Rio Iguaçu basin, Paraná State, Brazil: MHNCI 12298, 1, 170.0 mm L_S, municipality of Candói/Pinhão, Rio Jordão, UHE Santa Clara. NUP 611, 4, 107.6–150.2 mm L_S, municipality of Foz do Jordão, Córrego Passo do Aterrado. NUP 3704, 4, 59.4–129.9 mm L_S, municipality of Candói, Rio Capivara. NUP 3824, 2, 21.2–68.0 mm L_S, municipality of Candói, Rio Jordão. NUP 4007, 2, paratypes, 62.0–66.3 mm L_S, municipality of Candói, Rio do Sobradinho, tributary to the Rio Jordão. NUP 4009, 4, 20.8–32.3 mm L_S, municipality of Pinhão, Rio Capivara. NUP 4743, 3, 119.4–144.1 mm L_S, municipality of Reserva do Iguaçu, Rio das Torres. NUP 4827, 1, 66.2 mm L_S, municipality of Candói, Rio Sobradinho. NUP 9866, 1, 125.9 mm L_S, municipality of Guarapuava, Rio Pinhãozinho. NUP 16101, 74.4 mm L_S, municipality of Pinhão, unknown name stream. NUP 18280, 6, 69.0–99.6 mm L_S, municipality of Guarapuava, unnamed river stream. NUP 18873, 2, 71.23–82.93 mm L_S, municipality of Guarapuava, unnamed river stream.

5.5 *Cambeva iheringi*

All specimens of Rio Itararé basin, Paraná State, Brazil: NUP 20440, 1, 57.9 mm L_S, municipality of Sengés, Rio Pelame. NUP 20463, 2, 61.6–77.8 mm L_S, municipality of Jaguariaíva, unnamed river, tributary to the Rio Espigão Alto. NUP 20480, 1, 74.1 mm L_S, Rio das Lanças, tributary to the Rio Jaguariaíva. NUP 21042, 1, 51.0 mm L_S, municipality of Sengés, Rio Pelame. NUP 21059, 1, 69.2 mm L_S, municipality of Jaguariaíva, unnamed river, tributary to the Rio Espigão Alto.

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