

Field inventory reveals high diversity of new species of mountain catfishes, genus *Cambeva* Katz, Barbosa, Mattos & Costa, 2018 (Siluriformes: Trichomycteridae), in south-eastern Serra Geral, southern Brazil

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*Cambeva panthera* n. sp., UFRJ 6984, holotype, 66.5 mm SL., dorsal view.

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# Field inventory reveals high diversity of new species of mountain catfishes, genus *Cambeva* Katz, Barbosa, Mattos & Costa, 2018 (Siluriformes: Trichomycteridae), in south-eastern Serra Geral, southern Brazil

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## ABSTRACT

During a field inventory in the southeastern nucleus of the Serra Geral, southern Brazil, ten undescribed species of *Cambeva* Katz, Barbosa, Mattos & Costa, 2018 were found in a small area of about 2800 km<sup>2</sup>. These species are herein formally described: *Cambeva diffusa* n. sp., *Cambeva duplimaculata* n. sp., *Cambeva grisea* n. sp., *Cambeva imaruhy* n. sp., *Cambeva longipalata* n. sp., *Cambeva notabilis* n. sp., *Cambeva orbitofrontalis* n. sp., *Cambeva panthera* n. sp., *Cambeva pericoh* n. sp., and *Cambeva urubici* n. sp. They are diagnosed based on external morphology and osteological characters, which indicate that they belong to five intrageneric lineages. Most species occur in small areas, and some are rare. Five of these species here described are endemic to the upper Rio Uruguai basin, in a western open plateau belonging to the Araucaria Forest biogeographical province, and other five to the Rio Araranguá and Rio Tubarão basins, in the eastern forested plateau belonging to the Brazilian Atlantic Forest biogeographical province. The reported data suggest that some lineages are adapted to live in specific altitudinal zones, including the occurrence of three new species closely related to *C. tropeira* (Ferrer & Malabarba, 2011) found between 905 and 1325 m asl, contrasting with *C. brachykechenos* (Ferrer & Malabarba, 2013) and *Cambeva grisea* n. sp. found between 155 and 300 m asl. Finally, we compare the studied area to another mountain area, the Maciço de Itatiaia nucleus of the Serra da Mantiqueira in south-eastern Brazil, where a high number of endemic species have been recorded.

## KEY WORDS

Araucaria Forest,  
Atlantic Forest,  
Mountain biodiversity,  
osteology,  
Rio Araranguá,  
Rio Tubarão,  
Rio Uruguai,  
new species.

## RÉSUMÉ

*Un inventaire de terrain révèle une grande diversité de nouvelles espèces de poissons-chats de montagne, genre *Cambeva* Katz, Barbosa, Mattos & Costa, 2018 (Siluriformes : Trichomycteridae), dans le sud-est de Serra Geral, Brésil méridional.*

Au cours d'un inventaire de terrain dans le noyau sud-est de la Serra Geral, Brésil méridional, dix espèces non décrites de *Cambeva* Katz, Barbosa, Mattos & Costa, 2018 ont été trouvées dans une petite zone d'environ 2800 km<sup>2</sup>. Ces espèces sont formellement décrites ici : *Cambeva diffusa* n. sp., *Cambeva duplimaculata* n. sp., *Cambeva grisea* n. sp., *Cambeva imaruhy* n. sp., *Cambeva longipalata* n. sp., *Cambeva notabilis* n. sp., *Cambeva orbitofrontalis* n. sp., *Cambeva panthera* n. sp., *Cambeva pericob* n. sp., et *Cambeva urubici* n. sp. Elles ont été diagnostiquées sur la base de la morphologie externe et des caractères ostéologiques, qui indiquent qu'elles appartiennent à cinq lignées intragénériques. La plupart des espèces se trouvent dans de petites zones, et certaines sont rares. Cinq parmi les espèces décrites ici sont endémiques du bassin supérieur du Rio Uruguai, dans un plateau ouvert situé à l'ouest et appartenant à la province biogéographique de la forêt d'Araucaria, et cinq autres sont endémiques des bassins du Rio Araranguá et du Rio Tubarão, dans le plateau forestier oriental appartenant à la province biogéographique de la Forêt atlantique brésilienne. Les données rapportées suggèrent que certaines lignées sont adaptées pour vivre dans des zones altitudinales spécifiques, y compris la présence de trois nouvelles espèces étroitement liées à *C. tropeira* (Ferrer & Malabarba, 2011) trouvées entre 905 et 1325 m au dessus du niveau de la mer, contrastant avec *C. brachykechenos* (Ferrer & Malabarba, 2013) et *Cambeva grisea* n. sp. trouvée entre 155 et 300 m au dessus du niveau de la mer. Enfin, nous comparons la zone étudiée à une autre zone de montagne, le noyau Maciço de Itatiaia de la Serra da Mantiqueira au sud-est du Brésil, où un nombre élevé d'espèces endémiques a été enregistré.

## MOTS CLÉS

Forêt d'Araucaria,  
forêt atlantique,  
biodiversité montagnarde,  
ostéologie,  
Rio Araranguá,  
Rio Tubarão,  
Rio Uruguai,  
espèces nouvelles.

## INTRODUCTION

Mountains shelter a high biological diversity, with remarkable rate of endemic species with restricted geographical distribution (Antonelli *et al.* 2018; Rahbek *et al.* 2019). In tropical and subtropical areas of the globe, mountain biotas are often responsible for the recognition of biodiversity hotspots (Myers *et al.* 2000), but the fauna of some mountain ranges of South America are still incompletely known (Costa *et al.* 2021a). This is the case of the Serra Geral, a subtropical mountain range in southern Brazil, hiding a diversified biota mostly revealed in recent years. There is a high rate of endemic plants, and recent studies have also shown the presence of a rich aquatic fauna, with several records of endemism for different groups (Boldrini *et al.* 2009). The number of known valid fish species endemic to the Serra Geral has quickly increased in recent years (*e.g.* Reis & Schaefer 1992; Rosa & Costa 1993; Ghedotti & Weitzman 1995; Bertaco & Malabarba 2001), but field inventories have been more concentrated in the southern portion of the mountain range (Malabarba *et al.* 2009). These studies have reported high levels of endemism in short sections of river headwaters (*e.g.* Pereira & Reis 1992, 2002; Reis & Schaefer 1992; Ghedotti & Weitzman 1995; Bertaco & Malabarba 2001; Ottoni & Cheffe 2009; Mattos *et al.* 2014).

Catfishes of the Trichomycterinae Bleeker, 1858, a trichomycterid subfamily with a broad geographical range in South America, form the most diversified component of the Neotropical mountain ichthyofauna, with numerous taxa found in several habitats along the Andes and most other high altitude South American headwaters (Katz *et al.* 2018; Costa *et al.* 2020a, 2021b; Vilardo *et al.* 2020). Trichomycterines are represented in southern Brazil mountains by the genus *Cambeva*

Katz, Barbosa, Mattos & Costa, 2018, but taxonomical studies approaching the genus diversity in the southernmost parts of Brazil are restricted to a few recent papers (Ferrer & Malabarba 2011, 2013; Costa *et al.* 2020b, 2021a). The only detailed taxonomic study encompassing a broad geographical area of rivers draining the Serra Geral was the revision of *Cambeva* from the Lagoa dos Patos system (Ferrer & Malabarba 2011, 2013). This study recognised a total of five species allopatrically distributed in the system. Three species, *C. brachykechenos* (Ferrer & Malabarba, 2013), *C. diatropoporos* (Ferrer & Malabarba, 2013), and *C. tropeira* (Ferrer & Malabarba, 2011), were restricted to small areas, whereas two, *C. balios* (Ferrer & Malabarba, 2013) and *C. poikilos* (Ferrer & Malabarba, 2013), have a wider geographical range. More interestingly, *C. tropeira* was only found in the headwaters of the Rio das Antas, in altitudes about 1000 m asl (Ferrer & Malabarba 2011), whereas *C. balios* and *C. diatropoporos*, also occurring in the Rio das Antas drainage, were found between about 680 and 940 m asl and between about 640 and 825 m asl, respectively (Ferrer & Malabarba 2013), suggesting the existence of some level of altitudinal zonation. On the other hand, *C. brachykechenos* was the only species always found in lower altitudes, between about 110 and 265 m asl (Ferrer & Malabarba 2013).

The present study reports a field inventory made by one of us (CRMF) since 2015, directed to sample trichomycterine habitats, in the south-eastern nucleus of the Serra Geral (hereafter SESG), where this mountain range reaches the highest altitudes, with peaks reaching about 1800 m asl. With temperate climate, annually snowing in higher zones, this area comprises the uppermost section of the Rio Uruguai basin,



Rio da Prata system, with tributaries running to west, as well as two smaller isolated river basins, the Rio Araranguá and Rio Tubarão basins, running to east and shortly reaching the Atlantic Ocean. Western and eastern portions of SESG greatly differ in both physical and biological factors. The western portion (hereafter western open plateau) comprises a plateau drained by the upper Rio Uruguai tributaries, characterised by the presence of grasslands intercalated by forests with a high occurrence of the gymnosperm *Araucaria angustifolia* (Berthol.) Kuntze, constituting part of a biogeographical province known as the Araucaria plateau or Araucaria Forest (Ab'Sáber 1977; Morrone 2006). The eastern portion (hereafter eastern forested slope) comprises a steep slope and valleys drained by the Rio Araranguá and Rio Tubarão basins, occupied by the southern end of the biogeographical province of the Brazilian Atlantic Forest (Morrone 2006).

This study represents the first taxonomic study focusing on *Cambeva* from SESG, which is based on specimens sampled during field studies conducted between 2015 and 2021. First collections provided evidence on the existence of new species, but although intensive sampling efforts, only one or few specimens of each species were found. More recently, new neighbouring areas were sampled, but instead of enlarging the distribution of previously collected species, other new species were then found, revealing the presence of a rich diversity of rare species geographically restricted to small areas. Herein we provide descriptions of ten new species collected in streams draining the south-eastern Serra Geral, in an area of only about 2800 km<sup>2</sup>.

## MATERIAL AND METHODS

Morphometric and meristic data were taken following Costa (1992), with modifications proposed by Costa *et al.* (2020c); measurements are presented as percent of standard length (SL), except for those related to head morphology, which are expressed as percent of head length. Fin-ray counts include all elements; vertebra counts include all vertebrae except those participating in the Weberian apparatus; the compound caudal centrum was counted as a single element. Specimens were cleared and stained for bone and cartilage following Taylor & Van Dyke (1985). In addition to morphological characters commonly used in taxonomical studies on trichomycterines, descriptions include osteology, which have been consistently used to establish relationships hypotheses and to diagnose trichomycterines (*e.g.* Costa 2021; Costa *et al.* 2021b). Osteological characters here included in diagnoses and descriptions are those belonging to structures with informative variability for diagnosing species of *Cambeva* (*e.g.* Costa *et al.* 2020b, 2021a), including the mesethmoidal and cheek regions, as well as parurohyal morphology. Terminology for bones followed Costa (2021). Osteological illustrations were made using a stereomicroscope Zeiss Stemi SV 6 with camera lucida. Cephalic laterosensory system terminology follows Arratia & Huaquin (1995), with modifications proposed by Bockmann *et al.* (2004). Comparative material is

listed in Costa *et al.* (2020a), besides including specimens of species described more recently (Costa *et al.* 2021a, b), with the addition of *Cambeva tropeira* UFRJ 6935, 2 (C&S). Along text, geographical names follow Portuguese terms used in the region, thus avoiding common errors or generalizations when tentatively translating them to English, besides making easier their identification in the field.

## ABBREVIATIONS

asl	above sea level;
C&S	cleared and stained specimens for bone and cartilage;
ex	exemplars;
SL	standard length.

## Institutions

CICCAA	ichthyological collection of the Centre of Agrarian and Environmental Sciences, Federal University of Maranhão, Campus Chapadinha;
UFRJ	ichthyological collection of the Institute of Biology of the Federal University of Rio de Janeiro, Rio de Janeiro city.

## RESULTS

### COMPARATIVE MORPHOLOGY

This study, based on external morphology (Figs 1-10) and osteological structures (Figs 11-13), supports the recognition of ten species of *Cambeva* in SESG, all new and apparently endemic. Five of them are endemic to the western open plateau, Rio Uruguai basin, and the other five, to the eastern forested slopes, Rio Araranguá and Rio Tubarão basins. The comparative morphology suggests that the five species endemic to the western open plateau belong to only two main lineages, herein tentatively classified as species complexes (*i.e.*, the *C. balios* and *C. tropeira* complexes) in order to facilitate individual species diagnoses. On the other hand, the five species endemic to the eastern forested slopes belong to four different species complexes as here delimited (*i.e.*, the *C. barbosa*, *C. botuvera*, *C. brachykechenos*, and *C. tropeira* complexes).

Four new species, three from the western open plateau, and one from the eastern forested slopes, in the upper Rio Tubarão basin, belong to the *C. tropeira* complex, which also includes *C. tropeira* that is endemic to the upper Rio das Antas drainage, in the Lagoa dos Patos system. Species of this complex are readily distinguishable from other congeners by the unique combination of a colour pattern consisting of black rounded spots on the flank, at least in some life stage, and the presence of an anterior segment of the infraorbital latero-sensory canal, which is an uncommon condition among species of the clade comprising *Cambeva* and *Scleronema* Eigenmann, 1917 (see Ferrer & Malabarba 2011: fig. 2 and Costa *et al.* 2020b: fig. 1B), not occurring in any other species of the SESG. The three new species of the western open plateau share with *C. tropeira* the presence of a deep abrupt constriction in the opercle, just anterior to the base of the opercular patch of odontodes (Figs 12G, H, J), suggesting that they form a monophyletic group.

The *C. balios* complex comprises two new species of the western open plateau and *C. balios* from the Lagoa do Patos system. This complex is similar to the *C. tropeira* complex by the presence of black rounded spots on the flank in all their members, but differing from all other congeners by the unique morphology of the interopercle, including a deeply concave anterior margin, ventrally bordered by an anteriorly directed prominent process, as well as by the relatively short odontodes that are distinctively shorter than the opercular odontodes (Figs 12A, B), instead of the interopercular odontodes being nearly equal in length to opercular odontodes as in other congeners. In contrast to species of the *C. tropeira* complex, the anterior section of the infraorbital canal is always absent in species of the *C. balios* complex. In addition, species of the *C. balios* complex are large, apparently comprising the larger species of *Cambeva* in southern Brazil, reaching at least about 100 mm SL. The two new species share the presence of a slightly folded extremity of the dorsal process of the opercle and a narrow postero-dorsal projection of the preopercle (Figs 12A, B), conditions that are absent in *C. balios* and other congeners, thus suggesting that the two new species are more closely related among themselves than to *C. balios*.

The *C. barbosa* complex comprises a new species from the Rio Tubarão basin, and *C. barbosa* Costa, Feltrin & Katz, 2021 and *C. cubataonis* (Bizerril, 1994) from smaller coastal basins north to the Rio Tubarão basin. Although having high variation in colouration (Costa *et al.* 2021a), these three species share the presence of grey spots on the dorsal portion of the flank that are darker along its longitudinal midline. The most distinctive character shared by all these three species is the presence of a compact opercle, with a prominent articular facet for the preopercle (Fig. 12C), thus differing from other congeners that have a slenderer opercle, with a shorter or rudimentary articular facet for the preopercle. Species of the *C. botuvera* complex, including two new species, one from the Rio Araranguá basin and another from the Rio Tubarão basin, and *C. botuvera* from the Rio Itajaí-Mirim basin, are similar to species of the *C. barbosa* complex in the presence of round dark grey spots on the flank at least in some life stage, but their opercular bone is slender (Figs 12D-F), thus differing from the derived compact shape occurring in the *C. barbosa* complex. Species of the *C. botuvera* complex also differ from species of the *C. barbosa* complex in the presence of a flap on the intersection of the mesethmoid cornua, making this part of the bone relatively wider (Figs 1D-E), and the presence of a minute projection on the metapterygoid anteroventral margin, close to the articular cartilage block (Figs 12D-E), conditions that are derived and widespread among taxa of a southern generic clade (Costa *et al.* 2021a), but absent in species of the *C. barbosa* complex.

The *C. brachykechenos* complex, including a new species of the Rio Araranguá basin and *C. brachykechenos* from the Lagoa dos Patos system, is diagnosed, uniquely among trichomycterines of the clade comprising *Cambeva* and *Scleronema*, by the absence of the anterior cranial fontanel and a short posterior fontanel, mostly restricted to the parieto-supraoccipital (Ferrer & Malabarba 2013: fig. 2D), thus contrasting with

other species of this clade, in which the anterior fontanel is present, and the posterior fontanel is long, extending between the frontals to reach a transverse line close to lateral sphenotic process (*e.g.* Ferrer & Malabarba 2013: figs 2A-C). Species of the *C. brachykechenos* complex also share the presence of small light grey vermiculate marks over a brown ground colour, at least on the dorsum (Fig. 6; see also Ferrer & Malabarba 2013: fig. 15), a condition not occurring in other congeners. In addition, species of the *C. brachykechenos* complex have six pectoral-fin rays, a rare condition among congeners, which commonly have seven or eight pectoral-fin rays, distinguishing species of this complex from all other species occurring in the SESG.

## TAXONOMICAL ACCOUNTS

Order SILURIFORMES Cuvier, 1817

Family TRICHOMYCTERIDAE Bleeker, 1858

Genus *Cambeva* Katz, Barbosa, Mattos & Costa, 2018

*Cambeva balios* complex

*Cambeva diffusa* n. sp.

(Figs 1, 11A, 12A, 13A; Table 1)

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**MATERIAL EXAMINED.** — **Holotype.** Brazil • 1 ex., 112.3 mm SL; Santa Catarina state: Urubici Municipality: Rio Urubici, Rio Canoas drainage, Rio Uruguaí basin; 28°01'37"S, 49°35'20"W; about 935 m asl; C. R. M. Feltrin; 8.II.2021; UFRJ 6968.

**Paratypes.** Brazil • 4 ex., 19.0-49.2 mm SL; collected with holotype; UFRJ 6980 • 3 ex. (C&S), 26.0-103.4 mm SL; collected with holotype; UFRJ 6981 • 4 ex., 22.4-72.4 mm SL; same locality and collector as holotype; 14.III.2021; UFRJ 6978 • 6 ex., 21.7-55.9 mm SL; upper Rio Canoas, road between Urubici and Rio dos Bugres; 27°59'24"S, 49°32'39"W; about 905 m asl; C. R. M. Feltrin; 14.III.2021; UFRJ 6977 • 5 ex., 30.3-67.9 mm SL; same data as UFRJ 6977; CICC AA 04111 • 1 ex., 43.9 mm SL; same locality and collector as UFRJ 6977; 8.II.2021; UFRJ 6982 • 7 ex., 29.4-65.1 mm SL; stream tributary to Rio Urubici; 28°00'52"S, 49°35'31"W; about 920 m asl; C. R. M. Feltrin; 14.III.2021; UFRJ 6979.

**DIAGNOSIS.** — *Cambeva diffusa* n. sp. is distinguished from all other species of the *C. balios* complex by the presence of a lighter general colouration, highly differing by the presence of a great concentration of small dark brownish grey dots in a superficial skin layer, contrasting with rounded diffuse pale grey spots, almost inconspicuous, in a deeper layer (Fig. 1; vs never a similar colouration, Fig. 2; see also Ferrer & Malabarba 2013: fig. 1). *Cambeva diffusa* n. sp. is similar to *C. pericob* n. sp. and distinguished from *C. balios* in having a slightly posteriorly folded extremity of the dorsal process of the opercle (Fig. 12A, vs unfolded), a narrow postero-dorsal projection on the preopercle (Fig. 12A, vs no projection), and eight branchiostegal rays (vs nine). *Cambeva diffusa* n. sp. differs from *C. pericob* n. sp. in having more dorsal procurrent caudal-fin rays (17, vs 13 or 14), fewer ribs (12, vs 15), and opercular and interopercular postero-dorsal odontodes distinctively wider and more curved than other odontodes (Fig. 12A; vs opercular and interopercular postero-dorsal odontodes only slightly wider and more curved than other odontodes, Fig. 12B).

**DISTRIBUTION.** — *Cambeva diffusa* n. sp. occurs in the western open plateau. It is known from three localities in the upper Rio Canoas



FIG. 1. — *Cambeva diffusa* n. sp., UFRJ 6968, holotype, 112.3 mm SL.: **A**, left lateral view; **B**, dorsal view; **C**, ventral view.

drainage, Rio Uruguai basin, in altitudes between about 910 and 940 m asl (Fig. 14).

**ETYMOLOGY.** — From the Latin, the name *diffusa* (diffuse) refers to the colour pattern of the new species, with diffuse grey spots in a deeper skin layer, overlapped by a great concentration of minute brownish grey dots, conferring a unique general colouration that is lighter than in close related congeners.

#### DESCRIPTION

##### *General morphology*

Morphometric data in Table 1. Body moderately slender, subcylindrical anteriorly to compressed posteriorly. Greatest body depth in area just anterior to pelvic-fin base. Dorsal and ventral profiles of head and trunk slightly convex, approximately straight on caudal peduncle. Skin papillae minute. Anus and urogenital papilla in vertical through anterior third of dorsal-fin base. Head trapezoidal in dorsal view, anterior profile of snout convex. Eye small, dorsally positioned in anterior half of head. Posterior nostril located nearer anterior nostril than orbital rim. Tip of maxillary barbel reaching middle of interopercular patch of odontodes; tip of rictal barbel reaching area just anterior to interopercular patch of odontodes; tip of nasal barbel reaching anterior portion of orbit. Mouth subterminal. Jaw teeth slightly pointed to incisiform, slightly curved in premaxilla

and strongly curved in dentary, irregularly arranged, 36-45 in premaxilla, 33-46 in dentary. Branchial membrane attached to isthmus only at its anterior point. Branchiostegal rays 8. Cranial fontanels present, posterior fontanel long, anteriorly extending between frontals to reach transverse line close to lateral sphenotic process. Dorsal and anal fins subtriangular, distal margin slightly convex; total dorsal-fin rays 12 (iii + II + 7), total anal-fin rays 10 (iii + II + 5); anal-fin origin in vertical slightly posterior to middle dorsal-fin base. Dorsal-fin origin in vertical through centrum of 21st vertebra; anal-fin origin in vertical through centrum of 25th vertebra. Pectoral fin subtriangular in dorsal view, posterior margin slightly convex, first pectoral-fin ray not terminating in filament; total pectoral-fin rays 7 (I + 6). Pelvic fin subtruncate, its extremity in vertical through dorsal-fin origin or just anterior to it; pelvic-fin bases medially in contact; total pelvic-fin rays 5 (I + 4). Caudal fin subtruncate, postero-dorsal and postero-ventral extremities rounded; total principal caudal-fin rays 13 (I + 11 + I), total dorsal procurrent rays 17 (xvi + I), total ventral procurrent rays 12-13 (xi-xii + I). Vertebrae 40-42. Ribs 12. Two dorsal hypural plates, corresponding to hypurals 4 + 5 and 3, respectively; single ventral hypural plate corresponding to hypurals 1 and 2 and parhypural.



TABLE 1. — Morphometric data of *Cambeva diffusa* n. sp.

	holotype	paratypes (n = 10)
Standard length (mm)	112.3	38.8-103.4
Percent of standard length		
Body depth	13.6	12.6-15.4
Caudal peduncle depth	10.8	9.7-12.1
Body width	10.8	9.3-12.8
Caudal peduncle width	3.6	2.9-5.1
Pre-dorsal length	61.5	63.0-68.9
Pre-pelvic length	59.6	55.5-61.7
Dorsal-fin base length	11.0	10.5-12.5
Anal-fin base length	8.1	8.3-9.2
Caudal-fin length	12.3	11.5-16.8
Pectoral-fin length	10.6	10.3-12.6
Pelvic-fin length	7.4	7.1-9.0
Head length	17.8	18.1-22.1
Percent of head length		
Head depth	47.6	47.7-54.9
Head width	82.3	77.9-84.8
Snout length	43.5	38.3-45.4
Interorbital length	22.7	19.0-23.3
Preorbital length	15.6	12.9-16.0
Eye diameter	10.0	10.2-13.7

*Latero-sensory system*

Supraorbital sensory canal continuous, connected to infraorbital sensory canal posteriorly. Supraorbital sensory canal with 3 pores: s1, adjacent to medial margin of anterior nostril; s3, adjacent to medial margin of posterior nostril; and s6, on middle part of dorsal surface of head, in transverse line just posterior to orbit; pore s6 nearer midway between orbit and its paired homologous pore. Infraorbital sensory represented by single segment, with two pores: pore i10, adjacent to ventral margin of orbit, and pore i11, posterior to orbit. Postorbital canal with 2 pores: po1, in vertical line above posterior portion of interopercular patch of odontodes, and po2, in vertical line above posterior portion of opercular patch of odontodes. Lateral line of body short, with 2 pores, posterior-most pore in vertical just posterior to pectoral-fin base.

*Mesethmoidal region (Fig. 11A)*

Mesethmoid robust, its anterior margin about straight to gently concave; mesethmoid cornu subtriangular in dorsal view, extremity pointed; narrow lateral flap on intersection between cornu and main bone axis. Minute lateral projection on lateral ethmoid margin close to sesamoid supraorbital. Antorbital thin, short, drop-shaped; sesamoid supraorbital flattened, its length about thrice antorbital length, with lateral pointed expansion on its anterior half. Premaxilla sub-trapezoidal in dorsal view, slightly laterally narrowing, slightly longer than maxilla. Maxilla boomerang-shaped, slender, slightly curved. Autopalatine sub-rectangular in dorsal view, moderate in width, longer than wide, with deep notch on medial margin, lateral margin straight to slightly curved at posterolateral process base; autopalatine posterolateral process subtriangular in dorsal view, its length shorter than osseus portion of autopalatine length excluding posterolateral process.

*Cheek region (Fig. 12A)*

Metapterygoid thin, subtriangular, large, its largest length greater than horizontal length of quadrate excluding dorsal process. Quadrate slender, dorsal process with constricted base, dorsoposterior margin in contact with hyomandibula outgrowth. Hyomandibula long, with well-developed anterior outgrowth; middle portion of dorsal margin of hyomandibula slightly concave. Opercle broad, opercular odontode patch depth about three fourths of dorsal hyomandibula articular facet, with 13-14 odontodes; odontodes pointed, straight to curved, arranged in irregular transverse rows, postero-dorsal odontodes larger and distinctively more curved; dorsal process of opercle short, extremity slightly posteriorly folded; opercular articular facet for hyomandibula with small, subtrapezoidal flap, articular facet for preopercle minute. Interopercle moderate, about two thirds hyomandibula length, anterior margin deeply concave, ventrally terminating in anteriorly directed prominent process; interopercular odontode patch with 18-20 pointed odontodes, arranged in irregular longitudinal rows, postero-dorsal odontodes larger and strongly curved, remaining odontodes nearly straight to slightly curved. Preopercle compact, with short ventral flap and narrow postero-dorsal projection.

*Parurohyal (Fig. 13A)*

Robust, lateral process broad, posterior margin slightly convex, latero-posteriorly directed, extremity truncate; parurohyal head well-developed, with prominent anterolateral paired process; middle foramen small, round; posterior process long, about three fifths of distance between anterior margin of parurohyal and anterior insertion of lateral process.

*Colouration in alcohol (Fig. 1)*

Flank, dorsum and head side pale yellow, with great concentration of small dark brownish grey dots in superficial skin layer, and rounded diffuse pale grey spots, almost inconspicuous, in deeper layer. Venter with paler dots; ventral part of head greyish white. Barbels grey. Fins pale grey with small dark brownish grey dots. In juvenile species, dark grey spots over whole flank.

*Cambeva pericob* n. sp.

(Figs 2, 11B, 12B, 13B; Table 2)

[url:lsid:zoobank.org:act:324271D3-7113-4CE0-8D00-D47AA56C67B7](https://doi.org/10.21203/rs.3.rs-1234567/v1)

MATERIAL EXAMINED. — **Holotype. Brazil** • 1 ex., 97.3 mm SL; Santa Catarina State: São Joaquim Municipality: village of Pericó: Rio Pericó, tributary of Rio Lava-Tudo, Rio Pelotas drainage, Rio Uruguai basin; 28°09'40"S, 49°45'21"W; about 1170 m asl; C. R. M. Feltrin; 14.III.2021; UFRJ 6969.

**Paratypes. Brazil** • 3 ex., 26.7-59.9 mm SL; collected with holotype; UFRJ 6970 • 2 ex., 28.3-52.0 mm SL; Rio Lava-Tudo; 28°08'43"S, 49°42'40"W; about 1210 m asl; C. R. M. Feltrin; 14.III.2021; UFRJ 6971 • 2 ex. (C&S), 65.1-74.4 mm SL; Rio Pericó; 28°09'40"S, 49°45'21"W; about 1170 m asl; C. R. M. Feltrin; 8.II.2021; UFRJ 6972.





FIG. 2. — *Cambeva pericoh* n. sp., UFRJ 6969, holotype, 97.3 mm SL: **A**, left lateral view; **B**, dorsal view; **C**, ventral view.

**DIAGNOSIS.** — *Cambeva pericoh* n. sp. is distinguished from all other species of the *C. balios* complex by the presence of large black blotches irregularly arranged and often partially coalesced on the flank (Fig. 2; vs never a similar colouration, Fig. 1; see also Ferrer & Malabarba, 2013: fig. 1). *Cambeva pericoh* n. sp. is similar to *C. diffusa* n. sp. and distinguished from *C. balios* in having a slightly posteriorly folded extremity of the dorsal process of the opercle (Fig. 12B, vs unfolded), a narrow postero-dorsal projection on the preopercle (Fig. 12A, vs no projection), and eight branchiostegal rays (vs nine). *Cambeva pericoh* n. sp. differs from *C. diffusa* n. sp. in having fewer dorsal procurrent caudal-fin rays (13 or 14, vs 17), more ribs (15, vs 12), and opercular and interopercular postero-dorsal odontodes only slightly wider and more curved than the other odontodes (Fig. 12B; vs opercular and interopercular postero-dorsal odontodes distinctively wider and more curved than the other odontodes, Fig. 12A).

**DISTRIBUTION.** — *Cambeva pericoh* n. sp. occurs in the western open plateau. It is known from three localities in the Rio Pelotas drainage, upper Rio Uruguai basin, in altitudes between about 1170 and 1210 m asl (Fig. 14).

**ETYMOLOGY.** — The name *pericoh* is an allusion to the occurrence of the new species in the Rio Pericó, its type locality. The name probably has a Tupi-Guarani origin, but its meaning is uncertain.

## DESCRIPTION

### *General morphology*

Morphometric data in Table 2. Body moderately slender, subcylindrical anteriorly to compressed posteriorly. Greatest body depth in area just anterior to pelvic-fin base. Dorsal and ventral profiles of head and trunk slightly convex, approximately straight on caudal peduncle. Skin papillae minute. Anus and urogenital papilla in vertical through anterior third of dorsal-fin base. Head trapezoidal in dorsal view, anterior profile of snout convex. Eye small, dorsally positioned in anterior half of head. Posterior nostril located nearer anterior nostril than orbital rim. Tip of maxillary barbel reaching area just anterior to interopercular patch of odontodes; tip of rictal barbel reaching preopercular area in vertical through orbit; tip of nasal barbel posteriorly reaching anterior portion of orbit or area just anterior to it. Mouth subterminal. Jaw teeth slightly pointed to incisiform, slightly curved in premaxilla and strongly curved in dentary, irregularly arranged, 39–43 in premaxilla, 48–50 in dentary. Branchial membrane attached to isthmus only at its anterior point. Branchiostegal rays 8. Cranial fontanels present, posterior fontanel long, anteriorly extending between frontals to reach transverse line close to lateral sphenotic process. Dorsal and anal fins subtriangular,

TABLE 2. — Morphometric data of *Cambeva pericoh* n. sp.

	holotype	paratypes (n = 5)
Standard length (mm)	97.3	52.0-74.4
Percent of standard length		
Body depth	15.8	12.5-15.7
Caudal peduncle depth	11.3	9.1-11.5
Body width	12.4	9.0-12.6
Caudal peduncle width	4.1	3.8-4.2
Pre-dorsal length	64.2	62.6-67.8
Pre-pelvic length	58.2	54.4-61.5
Dorsal-fin base length	11.3	10.1-12.1
Anal-fin base length	9.3	8.2-10.1
Caudal-fin length	13.2	12.3-15.3
Pectoral-fin length	9.6	10.0-11.8
Pelvic-fin length	8.0	7.0-7.9
Head length	20.3	18.8-21.8
Percent of head length		
Head depth	56.3	46.9-53.5
Head width	81.9	77.2-83.5
Snout length	45.2	41.6-43.2
Interorbital length	18.5	19.0-22.7
Preorbital length	15.4	11.9-14.8
Eye diameter	7.6	7.9-9.7

distal margin slightly convex; total dorsal-fin rays 12 (iii + I-II + 7-8), total anal-fin rays 10 (iii + II + 5); anal-fin origin in vertical through middle dorsal-fin base. Dorsal-fin origin in vertical through centrum of 22nd vertebra; anal-fin origin in vertical through centrum of 26th vertebra. Pectoral fin subtriangular in dorsal view, posterior margin slightly convex, first pectoral-fin ray not terminating in filament; total pectoral-fin rays 7 (I + 6). Pelvic fin subtruncate, its extremity in vertical through dorsal-fin origin or just anterior to it; pelvic-fin bases medially in close proximity; total pelvic-fin rays 5 (I + 4). Caudal fin subtruncate, postero-dorsal and postero-ventral extremities rounded; total principal caudal-fin rays 13 (I + 11 + I), total dorsal procurrent rays 13 or 14 (xii-xiii + I), total ventral procurrent rays 10-12 (ix-xi + I). Vertebrae 41. Ribs 15. Single dorsal hypural plate, corresponding to hypurals 4 + 5 + 3; single ventral hypural plate corresponding to hypurals 1 and 2 and parhypural.

#### *Latero-sensory system*

Supraorbital sensory canal continuous, connected to infraorbital sensory canal posteriorly. Supraorbital sensory canal with 3 pores: s1, adjacent to medial margin of anterior nostril; s3, adjacent to medial margin of posterior nostril; and s6, on middle part of dorsal surface of head, in transverse line just posterior to orbit; pore s6 nearer midway between orbit and its paired homologous pore. Infraorbital sensory represented by single segment, with two pores: pore i10, adjacent to ventral margin of orbit, and pore i11, posterior to orbit. Postorbital canal with 2 pores: po1, in vertical line above posterior portion of interopercular patch of odontodes, and po2, in vertical line above posterior portion of opercular patch of odontodes. Lateral line of body short, with 2 pores, posterior-most pore in vertical just posterior to pectoral-fin base.

#### *Mesethmoidal region (Fig. 11B)*

Mesethmoid robust, its anterior margin about straight; mesethmoid cornu subtriangular, extremity slightly pointed; lateral flap on intersection between cornu and main bone axis, posteriorly extending parallel to lateral bone margin. Minute lateral projection on lateral ethmoid margin close to middle portion of sesamoid supraorbital. Antorbital thin, drop-shaped; sesamoid supraorbital flat, its length about twice and half antorbital length, with anterior lateral pointed expansion. Premaxilla sub-trapezoidal in dorsal view, longer than maxilla. Maxilla boomerang-shaped, slender, slightly curved. Autopalatine sub-rectangular in dorsal view, longer than wide, medial margin with deep notch, lateral margin nearly straight to slightly curved near posterolateral process; autopalatine posterolateral process subtriangular in dorsal view, short, its length shorter than osseus portion of autopalatine length excluding posterolateral process.

#### *Cheek region (Fig. 12B)*

Metapterygoid thin, subtriangular, large, its largest length slightly longer than horizontal length of quadrate excluding dorsal process; short process just anterior to articular cartilaginous block. Quadrate slender, dorsal process with constricted base, dorsoposterior margin in contact with from hyomandibula outgrowth. Hyomandibula long, with well-developed anterior outgrowth; middle portion of dorsal margin of hyomandibula slightly concave. Opercle broad, opercular odontode patch depth about two thirds of dorsal hyomandibula articular facet, with 12-15 odontodes; odontodes pointed, straight to slightly curved, arranged in irregular transverse rows; dorsal process of opercle short, extremity slightly posteriorly folded; opercular articular facet for hyomandibula with small, subtrapezoidal flap, articular facet for preopercle minute. Interopercle moderate, about two thirds hyomandibula length, anterior margin deeply concave, ventrally terminating in anteriorly directed prominent process; interopercular odontode patch with 23-25 odontodes; odontodes pointed, relatively short, arranged in irregular longitudinal rows. Preopercle compact, with short ventral flap and narrow postero-dorsal projection.

#### *Parurohyal (Fig. 13B)*

Robust, lateral process broad, posterior margin slightly convex, latero-posteriorly directed, extremity truncate; parurohyal head well-developed, with anterolateral paired process; middle foramen small, oval; posterior process relatively long, about six tenths of distance between anterior margin of parurohyal and anterior insertion of lateral process.

#### *Colouration in alcohol (Fig. 2)*

Flank, dorsum and head side pale yellow, with large black blotches irregularly arranged and often partially coalesced on flank, and small dark brown dots in more superficial skin layer, frequently overlapping black blotches. Venter and ventral part of head greyish white. Barbels black. Fins pale grey with black spots on basal portion.



FIG. 3. — *Cambeva imaruhy* n. sp., UFRJ 6939, holotype, 60.6 mm SL: **A**, left lateral view; **B**, dorsal view; **C**, ventral view.

*Cambeva barbosa* complex

*Cambeva imaruhy* n. sp.  
(Figs 3, 11C, 12C, 13C; Table 3)

[urn:lsid:zoobank.org:act:15E30D5C-5407-4905-A2F6-BA2F3FF76730](https://doi.org/10.11646/zootaxa.4905.2.1)

**MATERIAL EXAMINED.** — **Holotype.** Brazil • 1 ex., 60.6 mm SL; Santa Catarina state: Orleans municipality: Rio Minador, Rio Laranjeiras drainage, village of Brusque do Sul; 28°14'33"S, 49°24'13"W; about 250 m asl; 26.I.2021; UFRJ 6939.

**Paratypes.** Brazil • 6 ex., 23.8–36.7 mm SL; collected with holotype; UFRJ 6964 • 1 ex., 55.8 mm SL; upper Rio Laranjeiras, Rio Tubarão basin, Caminho dos Tropeiros da Serra do Imaruí; 28°13'30"S, 49°29'06"W; about 440 m asl; C. R. M. Feltrin; 9.III.2020 • 7 ex., 25.6–40.8 mm SL; Lauro Muller municipality: upper Rio Rocinha, Novo Horizonte; 28°23'42"S, 49°28'06"W; about 315 m asl; C. R. M. Feltrin; 22.X.2020; UFRJ 6940 • 5 ex., 30.0–36.4 mm SL; same data as UFRJ 6940; CICC AA 04113 • 5 ex., 32.3–38.8 mm SL (C&S); same data as UFRJ 6940; UFRJ 6941.

**ADDITIONAL MATERIAL (NON-TYPE SPECIMENS).** — **Brazil** • 1 ex.; Santa Catarina State: Grão Pará Municipality: Rio Braço Esquerdo subdrainage, Rio Braço do Norte drainage, Rio Tubarão basin; 28°08'37"S, 49°23'25"W; about 450 m asl; C. R. M. Feltrin; 17.II.2021; UFRJ 6959 • 4 ex.; same area as UFRJ 6959; 28°08'29"S, 49°23'37"W; about 460 m asl; C. R. M. Feltrin; 17.II.2021; UFRJ 6960 • 2 ex. (C&S); same data as precedent; UFRJ 6961.

**DIAGNOSIS.** — *Cambeva imaruhy* n. sp. differs from *C. barbosa* and *C. cubataonis* in having 15–17 ribs (vs 11–13) and posterior margin of the parurohyal lateral process concave (Fig. 13C; vs straight, Costa *et al.* 2021a: fig. 4C); from *C. barbosa* in having seven pectoral-fin rays (vs six), fewer interopercular odontodes (19–22 vs 30–36), and fewer jaw teeth (32–35 in the premaxilla, 26–30 in the dentary, vs 40–52 and 42–45, respectively), and from *C. cubataonis* in having 38–40 vertebrae (vs 36–37), the dorsal-fin origin in a vertical through the centrum of the 20th or 21st vertebra (vs 18th vertebra), and the anal-fin origin in a vertical through the centrum of the 24th or 25th vertebra (vs 23rd vertebra), as well as a different colour pattern, consisting of a high concentration of small rounded dark grey spots on the flank (Fig. 3; vs large brownish spots on the dorsal portion of the flank, Katz & Barbosa 2014: figs 1–2).



TABLE 3. — Morphometric data of *Cambeva imaruhy* n. sp.

	holotype	paratypes (n = 6)
Standard length (mm)	60.6	36.2-55.8
Percent of standard length		
Body depth	14.0	12.8-16.9
Caudal peduncle depth	11.3	11.4-12.6
Body width	9.8	10.4-12.5
Caudal peduncle width	4.1	2.4-4.0
Pre-dorsal length	62.6	63.3-65.9
Pre-pelvic length	57.7	58.2-60.0
Dorsal-fin base length	12.5	11.3-13.0
Anal-fin base length	9.9	8.6-9.5
Caudal-fin length	14.2	15.2-17.7
Pectoral-fin length	11.4	12.0-13.6
Pelvic-fin length	8.2	8.4-10.5
Head length	17.9	19.1-20.5
Percent of head length		
Head depth	45.3	46.8-52.0
Head width	82.7	82.3-86.7
Snout length	45.9	43.3-46.6
Interorbital length	22.3	20.2-24.0
Preorbital length	15.9	12.0-13.5
Eye diameter	9.3	8.3-11.9

DISTRIBUTION. — *Cambeva imaruhy* n. sp. occurs in the eastern forested slope. It is only known from the Rio Tubarão basin, in altitudes between about 250 and 440 m asl (Fig. 14).

ETYMOLOGY. — The name *imaruhy* is an allusion to the occurrence of the species in the Caminho dos Tropeiros da Serra do Imaruí (formerly Imaruhy), an old track used to cross the Serra Geral during the 19th century, in a land previously inhabited by the Xokleng people. The word *imaruhy* is possibly derived from the Tupi-Guarani, meaning water mosquito.

DESCRIPTION

*General morphology*

Morphometric data in Table 3. Body slender, subcylindrical and slightly depressed anteriorly, compressed posteriorly. Greatest body depth in area just anterior to pelvic-fin base. Dorsal and ventral profiles of head and trunk slightly convex, approximately straight on caudal peduncle. Skin papillae minute. Anus and urogenital papilla in vertical through anterior portion of dorsal-fin base. Head trapezoidal in dorsal view, anterior profile of snout convex. Eye small, dorsally positioned in head, on anterior half of head. Posterior nostril located nearer anterior nostril than orbital rim. Tip of maxillary barbel reaching between posterior portion of interopercular patch of odontodes and middle portion of pectoral-fin base; tip of rictal barbel reaching between middle portion of interopercular patch of odontodes and pectoral-fin base; tip of nasal barbel reaching opercular patch of odontodes. Mouth subterminal. Jaw teeth pointed, slightly curved, irregularly arranged; premaxillary teeth 32-35, dentary teeth 26-30. Branchial membrane attached to isthmus only at its anterior point. Branchiostegal rays 7 or 8. Cranial fontanels present, posterior fontanel long, anteriorly extending between frontals to reach transverse line close to lateral sphenotic process. Dorsal and anal fins subtriangular, distal margin slightly convex; total dorsal-fin rays 11-12 (iii + II + 7-8), total anal-fin rays 9 (ii + II + 5); anal-fin origin in

vertical through posterior half of dorsal-fin base. Dorsal-fin origin in vertical through centrum of 20th or 21st vertebra; anal-fin origin in vertical through centrum of 24th or 25th vertebra. Pectoral fin subtriangular in dorsal view, posterior margin slightly convex, tip of first pectoral-fin ray slightly projecting beyond fin, forming minute filament; total pectoral-fin rays 7 (I + 6). Pelvic fin subtruncate, its extremity in vertical through anterior portion of dorsal-fin base; pelvic-fin bases medially separated by minute interspace; total pelvic-fin rays 5 (I + 4). Caudal fin subtruncate, postero-dorsal and postero-ventral extremities rounded; total principal caudal-fin rays 13 (I + 11 + I), total dorsal procurrent rays 20-21 (xix-xx + I), total ventral procurrent rays 12-15 (xi-xiv + I). Vertebrae 38-40. Ribs 15-17. Two dorsal hypural plates, corresponding to hypurals 4 + 5 and 3, respectively, sometimes coalesced to form single plate; single ventral hypural plate corresponding to hypurals 1 and 2 and parhypural.

*Latero-sensory system*

Supraorbital sensory canal continuous, connected to posterior section of infraorbital canal posteriorly. Supraorbital sensory canal with 3 pores: s1, adjacent to medial margin of anterior nostril; s3, adjacent and just posterior to medial margin of posterior nostril; and s6, in transverse line through posterior half of orbit; pore s6 nearer orbit than its paired homologous pore. Single infraorbital sensory canal segment, with two pores, corresponding to pore i10, adjacent to ventral margin of orbit, and pore i11, posterior to orbit; anterior segment of infraorbital canal absent. Postorbital canal with 2 pores: po1, in vertical line above posterior portion of interopercular patch of odontodes, and po2, in vertical line above posterior portion of opercular patch of odontodes. Lateral line of body short, with 2 pores, posterior-most pore in vertical just posterior to pectoral-fin base.

*Mesethmoidal region (Fig. 11C)*

Mesethmoid relatively thin, its anterior margin slightly concave; mesethmoid cornu narrow, extremity slightly pointed. No lateral projection on lateral ethmoid margin. Antorbital thin, drop-shaped; sesamoid supraorbital very slender, rod-shaped, without processes, its length about three times antorbital length. Premaxilla sub-trapezoidal in dorsal view, laterally narrowing, moderate in length, slightly longer than maxilla. Maxilla boomerang-shaped, slender, slightly curved. Autopalatine sub-rectangular in dorsal view, medial margin sinuous, lateral margin slightly concave; autopalatine posterolateral process well-developed, narrow, its length about two thirds autopalatine length excluding posterolateral.

*Cheek region (Fig. 12C)*

Metapterygoid thin, subtriangular, large, its largest length slightly shorter than horizontal length of quadrate excluding dorsal process; minute marginal process just posterior to cartilage articulating metapterygoid and quadrate. Quadrate slender, dorsal process with constricted base, dorsoposterior margin separated from hyomandibula outgrowth by small interspace. Hyomandibula long, with well-developed anterior

outgrowth; middle portion of dorsal margin of hyomandibula concave. Opercle compact, opercular odontode patch depth about equal length of dorsal hyomandibula articular facet, with 15-17 odontodes; odontodes pointed, nearly straight to slightly curved, arranged in irregular transverse rows; dorsal process of opercle short and pointed; opercular articular facet for hyomandibula with prominent flap, articular facet for preopercle well-developed, subtriangular, in close proximity to articular facet for hyomandibula. Interopercle moderate, about three fifths of thirds hyomandibula length, with 19-22 odontodes; odontodes pointed, arranged in irregular longitudinal rows. Preopercle compact, with short ventral flap.

#### *Parurohyal* (Fig. 13C)

Parurohyal robust, lateral process sub-triangular, slightly curved, latero-posteriorly directed, extremity pointed; parurohyal head well-developed, with distinctive anterolateral paired process; middle foramen broad, oval; posterior process long, about half length distance between anterior margin of parurohyal and anterior insertion of posterior process.

#### Colouration in alcohol (Fig. 3)

Flank, dorsum and head side pale yellowish brown. Dorsum and flank with high concentration of small rounded dark grey spots, variable in size in different species, usually smaller than orbit, sometimes three or four times orbit, rarely very small almost imperceptible, often darker on flank midline and on procurent caudal-fin rays, sometimes inconspicuous below midline. Dark pigment concentrated between anterior nostril and orbit, and on nasal barbel base. Venter and ventral surface of head light yellowish white. Unpaired fins hyaline with finely dark brown pigmented rays. Paired fins whiteish hyaline.

#### *Cambeva botuvera* complex

*Cambeva orbitofrontalis* n. sp.  
(Figs 4, 11D, 12D, 13D; Table 4)

[urn:lsid:zoobank.org:act:45F25566-C30E-43A4-8523-F77BEC7A5111](http://urn:lsid:zoobank.org:act:45F25566-C30E-43A4-8523-F77BEC7A5111)

**MATERIAL EXAMINED.** — **Holotype.** Brazil • 1 ex., 56.2 mm SL; Santa Catarina State: Treviso Municipality: village of Santo Antônio: Cascata do Salto Branco, Rio Pio, Rio Mãe Luzia drainage, Rio Araranguá basin; 28°29'23"S, 49°31'22"W; about 385 m asl; C. R. M. Feltrin; 20.I.2021; UFRJ 6953.

**Paratypes.** Brazil • 2 ex., 44.5-56.5 mm SL; collected with holotype; UFRJ 6954 • 3 ex. (C&S), 43.6-55.2 mm SL; collected with holotype; UFRJ 6955 • 2 ex., 43.6-45.5 mm SL; collected with holotype; CICC AA 04114 • 1 ex., 22.5 mm SL; same area as anterior; 28°29'32"S, 49°31'26"W; C. R. M. Feltrin; 29.IX.2018; UFRJ 6956 • 1 ex. (C&S), 47.3 mm SL; same area as anterior; 28°29'17"S, 49°30'45"W; about 300 m asl; C. R. M. Feltrin; 30.XI.2020; UFRJ 6957 • 2 ex., 21.8-29.7 mm SL; Siderópolis Municipality: village of Costão da Serra, Rio da Serra, about 100 from its confluence with Rio da Mina; 28°33'16"S, 49°34'53"W; about 230 m asl; C. R. M. Feltrin; 20.I.2021; UFRJ 6958 • 1 ex., 51.3 mm SL; Siderópolis Municipality: upper Rio São Bento, Costão da Serra; 28°35'06"S, 49°33'54"W; about 160 m asl; C. R. M.

Feltrin; 22.II.2021; UFRJ 6987 • 9 ex., 13.5-31.0 mm SL; Nova Veneza Municipality: stream tributary of Rio São Bento, São Bento Alto; 28°37'38"S, 49°34'11"W; about 125 m asl; C. R. M. Feltrin; 24.II.2021; UFRJ 6988.

**DIAGNOSIS.** — *Cambeva orbitofrontalis* n. sp. differs from other species of the *C. botuvera* complex in having more ribs (16, vs 12 or 13 in *C. botuvera* and 14 in *C. panthera* n. sp.), seven branchiostegal rays (vs 8), fewer teeth in the premaxilla (36-38, vs 40-42 in *C. botuvera* and 44-46 in *C. panthera* n. sp.) and dentary (31-34, vs 40-42 in *C. botuvera* and 38-43 in *C. panthera* n. sp.), a rounded caudal fin (vs subtruncate) and a long sesamoid supraorbital, longer than the autopalatine (vs shorter). Also distinguished from *C. botuvera* in having a shorter pectoral fin (pectoral-fin length 7.6-9.1 % SL, vs 12.1-15.1 % SL) and a shorter space between orbit and anterior nostril (pre-orbital length 10.7-12.7 % of the head length, vs 13.6-16.7 %); and from *C. panthera* n. sp. in having fewer dorsal procurent caudal-fin rays (18, vs 20-24), more vertebrae (39-40, vs 37), the dorsal-fin origin in a vertical through the centrum of the 21st vertebra (vs 18th or 19th), more opercular (13-15, vs 10 or 11) and interopercular odontodes (30-35, vs 23-25), a shorter caudal fin (caudal-fin length 13.0-15.2 % SL, vs 17.8-20.2 % SL), and shorter pelvic-fins (pelvic-fin length 7.6-9.1 % SL, vs 9.7-12.6 % SL).

**DISTRIBUTION.** — *Cambeva orbitofrontalis* n. sp. occurs in the eastern forested slope. It is found in the Rio Araranguá basin, in altitudes between about 130 and 390 m (Fig. 14).

**ETYMOLOGY.** — From the Latin *orbita* (orbit, referring to the eye socket) and *frontalis* (frontal), in allusion to the unique long sesamoid supraorbital bone, with posterior extremity firmly attached to the frontal bone.

#### DESCRIPTION

##### *General morphology*

Morphometric data in Table 4. Body moderately slender, subcylindrical anteriorly to compressed posteriorly. Greatest body depth in area just anterior to pelvic-fin base. Dorsal and ventral profiles of head and trunk slightly convex, approximately straight on caudal peduncle. Skin papillae minute. Anus and urogenital papilla in vertical through anterior third of dorsal-fin base. Head trapezoidal in dorsal view, anterior profile of snout convex. Eye small, dorsally positioned in anterior half of head. Posterior nostril located nearer anterior nostril than orbital rim. Tip of maxillary barbel reaching middle portion of interopercular patch of odontodes; tip of rictal barbel reaching anterior part of interopercular patch of odontodes; tip of nasal barbel slightly posteriorly surpassing orbit. Mouth subterminal. Jaw teeth slightly pointed to incisiform in outer areas, slightly curved, irregularly arranged, 36-38 in premaxilla, 31-34 in dentary. Branchial membrane attached to isthmus only at its anterior point. Branchiostegal rays 7. Cranial fontanelles present, posterior fontanel long, anteriorly extending between frontals to reach transverse line close to lateral sphenotic process. Dorsal fin short, subrectangular, anal fin subtriangular, distal margin slightly convex in both; total dorsal-fin rays 11 (ii + I-II + 7-8), total anal-fin rays 9 (ii + II + 5); anal-fin origin in vertical through last third of dorsal-fin base. Dorsal-fin origin in vertical through centrum of 21st vertebra; anal-fin origin in vertical through centrum of 24th or 25th vertebra. Pectoral fin subtriangular in dorsal view, posterior margin slightly convex, first pectoral-fin ray not terminating in filament; total pectoral-fin rays 7 (I + 6). Pelvic

TABLE 4. — Morphometric data of *Cambeva orbitofrontalis* n. sp.

	holotype	paratypes (n = 8)
Standard length (mm)	56.2	43.3-56.5
Percent of standard length		
Body depth	14.7	13.0-15.9
Caudal peduncle depth	11.3	10.0-11.7
Body width	10.0	9.2-11.0
Caudal peduncle width	2.1	3.0-4.3
Pre-dorsal length	64.4	61.4-65.6
Pre-pelvic length	57.4	55.2-57.7
Dorsal-fin base length	11.7	10.7-11.9
Anal-fin base length	8.9	8.1-9.0
Caudal-fin length	13.5	13.0-15.2
Pectoral-fin length	10.6	10.1-11.5
Pelvic-fin length	8.1	7.6-9.1
Head length	18.2	18.0-19.9
Percent of head length		
Head depth	49.2	47.9-52.8
Head width	83.3	77.9-84.6
Snout length	44.8	39.5-45.6
Interorbital length	23.1	21.2-24.7
Preorbital length	12.4	10.7-12.7
Eye diameter	9.7	8.4-9.5

fin subtruncate, its extremity in vertical anterior to dorsal-fin base; pelvic-fin bases medially in close proximity; total pelvic-fin rays 5 (I + 4). Caudal fin rounded; total principal caudal-fin rays 13 (I + 11 + I), total dorsal procurrent rays 18 (xvii + I), total ventral procurrent rays 13 (xii + I). Vertebrae 39-40. Ribs 16. Two dorsal hypural plates, corresponding to hypurals 4 + 5 and 3, respectively; single ventral hypural plate corresponding to hypurals 1 and 2 and parhypural.

*Latero-sensory system*

Supraorbital sensory canal continuous, connected to infraorbital sensory canal posteriorly. Supraorbital sensory canal with 3 pores: s1, adjacent to medial margin of anterior nostril; s3, adjacent to medial margin of posterior nostril; and s6, on middle part of dorsal surface of head, in transverse line just posterior to orbit; pore s6 nearer orbit than its paired homologous pore. Infraorbital sensory canal represented by single segment, with two pores: pore i10, adjacent to ventral margin of orbit, and pore i11, posterior to orbit. Postorbital canal with 2 pores: po1, in vertical line above posterior portion of interopercular patch of odontodes, and po2, in vertical line above posterior portion of opercular patch of odontodes. Lateral line of body short, with 2 pores, posterior-most pore in vertical just posterior to pectoral-fin base.

*Mesethmoidal region (Fig. 11D)*

Mesethmoid robust, its anterior margin about straight; mesethmoid cornu subtriangular, extremity pointed; narrow lateral flap on intersection between cornu and main bone axis, posteriorly extending parallel to lateral bone margin. Minute lateral projection on lateral ethmoid margin close to middle portion of sesamoid supraorbital, often absent. Antorbital thin, drop-shaped; sesamoid supraorbital slender, long and slightly curved, its length about three and half times antorbital length, without lateral projections, its posterior portion firmly attached to neu-

rocranium. Premaxilla sub-trapezoidal in dorsal view, slightly laterally narrowing, longer than maxilla. Maxilla boomerang-shaped, slender, curved. Autopalatine sub-rectangular in dorsal view, moderate in width, slightly longer than wide when excluding posterolateral process, medial margin sinuous, lateral margin nearly straight to slightly curved near posterolateral process; autopalatine posterolateral process subtriangular in dorsal view, with sharp extremity, short, its length shorter than osseous portion of autopalatine length excluding posterolateral process.

*Cheek region (Fig. 12D)*

Metapterygoid thin, subtriangular, large, its largest length slightly longer than horizontal length of quadrate excluding dorsal process; minute projection on anteroventral bone margin, close to articulatory cartilage block. Quadrate slender, dorsal process with constricted base, dorsoposterior margin in contact with from hyomandibula outgrowth; small process close and anterior to cartilage articulating quadrate and metapterygoid. Hyomandibula long, with well-developed anterior outgrowth; deep notch on dorsal margin of hyomandibula outgrowth. Opercle slender, abruptly widening on odontode patch, its depth about three fifths of dorsal hyomandibula articular facet, 13-15 odontodes; odontodes pointed, straight to slightly curved, arranged in irregular transverse rows; dorsal process of opercle short and truncate; opercular articular facet for hyomandibula with small, rounded flap, articular facet for preopercle indistinct. Interopercle moderate, about two thirds hyomandibula length, anterior margin slightly concave; interopercular odontode patch with 30-35 pointed odontodes, arranged in irregular longitudinal rows. Preopercle compact, with short ventral flap.

*Parurohyal (Fig. 13D)*

Robust, lateral process sub-triangular, weakly curved, latero-posteriorly directed, extremity pointed, posterior margin slightly sinuous; parurohyal head well-developed, with anterolateral paired process; middle foramen small, round; posterior process relatively long, about half distance between anterior margin of parurohyal and anterior insertion of lateral process.

*Colouration in alcohol (Fig. 4)*

Flank, dorsum and head side pale yellowish grey, with small, rounded dark grey spots, larger on dorsal portion of flank; spots irregularly arranged, except forming horizontal row on longitudinal midlateral line of flank. Venter and ventral part of flank yellowish white. Barbels dark grey. Fins hyaline with grey rays on basal portion.

*Cambeva panthera* n. sp.

(Figs 5, 11E, 12E, 13E; Table 5)

[urn:lsid:zoobank.org:act:96329D84-8A60-4849-A1D4-17BCB13401A1](https://doi.org/10.21203/rs.3.rs-1111111/v1)

MATERIAL EXAMINED. — **Holotype**. Brazil • 1 ex., 66.5 mm SL; Santa Catarina State: Pedras Grandes Municipality: village of Azambuja, stream tributary of Rio Pedras Grandes, Rio Tubarão basin; 28°28'37"S, 49°11'41"W; about 245 m asl; C. R. M. Feltrin; 22.III.2021; UFRJ 6984.





FIG. 4. — *Cambeva orbitofrontalis* n. sp., UFRJ 6953, holotype, 56.2 mm SL: **A**, left lateral view; **B**, dorsal view; **C**, ventral view.

**Paratypes.** Brazil • 6 ex., 18.7-63.6 mm SL; collected with holotype; UFRJ 6985 • 4 ex. (C&S), 30.9-55.5 mm SL; collected with holotype; UFRJ 6986 • 3 ex., 46.2-57.0 mm SL; collected with holotype; CICCAA 04108.

**DIAGNOSIS.** — *Cambeva panthera* n. sp. is distinguished from other species of the *C. botuvera* complex in having a longer maxillary barbel, its tip reaching the middle of the pectoral-fin base (vs reaching area between interopercular patch of odontodes and pectoral-fin base), fewer vertebrae (37, vs 39 or 40), the dorsal-fin origin in a vertical through the centrum of the 18th or 19th vertebra (vs 21st or 22nd), fewer opercular odontodes (10 or 11, vs 13-18), more premaxillary teeth (44-46, vs 36-42), and by the presence of rounded brown spots with dark brown to black margin on the flank in adult specimens (vs uniformly pigmented spots). *Cambeva panthera* n. sp. is also distinguished from *C. orbitofrontalis* n. sp. in having fewer ribs (14, vs 16), a subtruncate caudal fin (vs rounded), more dorsal-procurrent caudal-fin rays (20-24, vs 18), fewer interopercular odontodes (23-25, vs 30-35), a longer caudal fin (caudal-fin length 17.8-20.2 % SL, vs 13.0-15.2 % SL), and longer pelvic-fins (pelvic-fin length 9.7-12.6 % SL, vs 7.6-9.1 % SL).

**DISTRIBUTION.** — *Cambeva panthera* n. sp. occurs in the eastern forested slope. It is only known from the type locality, a stream tributary of the Rio Pedras Grandes, Rio Tubarão basin, altitude about 250 m (Fig. 14).

**ETYMOLOGY.** — The name *panthera* (panther), derived from the Greek, is an allusion to the colour pattern of larger specimens that exhibit a colour pattern similar to that occurring in species of the felid genus *Panthera* Oken, 1816.

#### DESCRIPTION

##### *General morphology*

Morphometric data in Table 5. Body moderately slender, subcylindrical anteriorly to compressed posteriorly. Greatest body depth in area between pectoral and pelvic fins. Dorsal and ventral profiles of head and trunk slightly convex, slightly convex on caudal peduncle. Skin papillae minute. Anus and urogenital papilla in vertical through middle portion of dorsal-fin base. Head trapezoidal in dorsal view, anterior profile of snout slightly convex. Eye small, dorsally positioned in middle portion of head. Posterior nostril located nearer anterior nostril than orbital rim. Tip of maxillary barbel reaching middle of pectoral-fin base; tip of rictal reaching between interopercular patch of odontodes and pectoral-fin base; tip of nasal barbel reaching middle of opercular patch of odontodes. Mouth subterminal. Jaw teeth pointed, slightly curved, irregularly

TABLE 5. — Morphometric data of *Cambeva panthera* n. sp.

	holotype	paratypes (n = 9)
Standard length (mm)	66.5	40.3-63.6
Percent of standard length		
Body depth	14.4	12.8-16.9
Caudal peduncle depth	11.7	13.8-15.0
Body width	12.0	11.1-12.4
Caudal peduncle width	4.0	3.6-4.3
Pre-dorsal length	64.7	62.1-66.0
Pre-pelvic length	59.3	57.7-61.2
Dorsal-fin base length	11.3	11.1-12.4
Anal-fin base length	7.4	7.5-9.3
Caudal-fin length	18.8	17.8-20.2
Pectoral-fin length	13.8	11.9-15.0
Pelvic-fin length	11.7	9.7-12.6
Head length	21.0	19.6-23.2
Percent of head length		
Head depth	47.7	48.0-54.3
Head width	82.0	81.1-86.2
Snout length	44.2	43.2-46.6
Interorbital length	25.6	23.3-26.0
Preorbital length	12.9	11.4-13.6
Eye diameter	9.2	8.4-10.5

arranged, 44-46 in premaxilla, 38-43 in dentary. Branchial membrane attached to isthmus only at its anterior point. Branchiostegal rays 8. Cranial fontanels present, posterior fontanel long, anteriorly extending between frontals to reach transverse line close to lateral sphenotic process. Dorsal and anal fins subtriangular, distal margin slightly convex; total dorsal-fin rays 11-12 (ii-iii + II + 7), total anal-fin rays 9-10 (ii-iii + I-II + 5-6); anal-fin origin in vertical just anterior to posterior dorsal-fin base end. Dorsal-fin origin in vertical through centrum of 18th or 19th vertebra; anal-fin origin in vertical through centrum of 23rd or 24th vertebra. Pectoral fin subtriangular in dorsal view, posterior margin slightly convex, first pectoral-fin ray terminating in short filament, about 10-15 % of pectoral-fin length; total pectoral-fin rays 7 (I + 6). Pelvic fin subtruncate, its extremity in vertical through middle of dorsal-fin base; pelvic-fin bases medially in close proximity; total pelvic-fin rays 5 (I + 4). Caudal fin subtruncate, postero-dorsal and postero-ventral extremities rounded; total principal caudal-fin rays 13 (I + 11 + I), total dorsal procurrent rays 20-23 (xix-xxii + I), total ventral procurrent rays 13-14 (xii-xiii + I-II). Vertebrae 37. Ribs 14. Two dorsal hypural plates, corresponding to hypurals 4 + 5 and 3, respectively; single ventral hypural plate corresponding to hypurals 1 and 2 and parhypural.

*Latero-sensory system*

Supraorbital sensory canal continuous, connected to infraorbital sensory canal posteriorly. Supraorbital sensory canal with 3 pores: s1, adjacent to medial margin of anterior nostril; s3, adjacent to medial margin of posterior nostril; and s6, on middle part of dorsal surface of head, in transverse line just posterior to orbit; pore s6 nearer orbit than its paired homologous pore. Anterior segment of infraorbital sensory canal absent; posterior segment with pore i10, adjacent to ventral margin of orbit, and pore i11, posterior to orbit. Postorbital

canal with 2 pores: po1, in vertical line above posterior portion of interopercular patch of odontodes, and po2, in vertical line above posterior portion of opercular patch of odontodes. Lateral line of body short, with 2 pores, posterior-most pore in vertical just posterior to pectoral-fin base.

*Mesethmoidal region (Fig. 11E)*

Mesethmoid robust, its anterior margin about straight; mesethmoid cornu subtriangular in dorsal view, extremity pointed; narrow lateral flap on intersection between cornu and main bone axis. Small lateral projection on lateral ethmoid margin close to posterior portion of sesamoid supraorbital. Antorbital thin, drop-shaped; sesamoid supraorbital slender, its length about thrice or slightly more antorbital length. Premaxilla subtrapezoidal in dorsal view, anterior margin convex, laterally narrowing, longer than maxilla. Maxilla boomerang-shaped, slender, slightly curved. Autopalatine sub-rectangular in dorsal view, broad, about so long as wide, with concavity on medial margin, lateral margins slightly concave; autopalatine posterolateral process subtriangular in dorsal view, short, its length shorter than osseus portion of autopalatine length excluding posterolateral process.

*Cheek region (Fig. 12E)*

Metapterygoid thin, subtriangular, large, its largest length longer than horizontal length of quadrate excluding dorsal process; minute projection on anteroventral bone margin, close to articulatory cartilage block. Quadrate slender, dorsal process with constricted base, dorsoposterior margin in contact with from hyomandibula outgrowth. Hyomandibula long, with well-developed anterior outgrowth, with deep dorsal concavity. Opercle relatively slender, opercular odontode patch depth about half dorsal hyomandibula articular facet, with 10 or 11 odontodes; odontodes pointed, straight to slightly curved, arranged in irregular transverse rows; dorsal process of opercle short; opercular articular facet for hyomandibula with small, rounded flap, articular facet for preopercle rounded, close to opercular facet. Interopercle moderate, about two thirds hyomandibula length, anterior margin concave; interopercular odontode patch with 23-25 pointed odontodes, arranged in irregular longitudinal rows. Preopercle compact, with short ventral flap.

*Parurohyal (Fig. 13E)*

Robust, lateral process sub-triangular, posterior margin slightly convex, latero-posteriorly directed, extremity pointed; parurohyal head well-developed, with prominent anterolateral paired process; middle foramen small, rounded; posterior process long, about three fifths of distance between anterior margin of parurohyal and anterior insertion of lateral process.

*Colouration in alcohol (Fig. 5)*

Flank, dorsum and head side pale yellow, with rounded brown spots with dark brown to black margin; flank spots irregularly arranged and variable in size, largest spots slightly larger than opercular patch of odontodes. Venter and ventral part of head yellowish white. Barbels brown, with dark



FIG. 5. — *Cambeva panthera* n. sp., UFRJ 6984, holotype, 66.5 mm SL: **A**, left lateral view; **B**, dorsal view; **C**, ventral view.

brown dots. Fins pale grey with small brownish grey spots on basal portion. In juveniles, spots dark brown without distinct margin colour; spots slightly darker along longitudinal midline of flank.

#### *Cambeva brachykechenos* complex

##### *Cambeva grisea* n. sp.

(Figs 6, 11F, 12F, 13F; Table 6)

[urn:lsid:zoobank.org:act:A5CFD65E-416F-4722-AE0B-9335C766E27F](https://doi.org/10.21203/rs.3.rs-1000000/v1)

**MATERIAL EXAMINED.** — **Holotype.** Brazil • 1 ex., 43.1 mm SL; Santa Catarina State: Treviso Municipality: village of Santo Antônio: Rio Pio, Rio Mãe Luzia drainage, Rio Araranguá basin;  $28^{\circ}29'17''\text{S}$ ,  $49^{\circ}30'45''\text{W}$ ; about 300 m asl; C. R. M. Feltrin; 30.XI.2020; UFRJ 6936.

**Paratypes.** Brazil • 2 ex., 38.4–39.3 mm SL; collected with holotype; UFRJ 6937 • 4 ex., 29.1–40.9 mm SL (C&S); collected with holotype; UFRJ 6938 • 4 ex., 24.1–45.9 mm SL; same area as holotype,  $28^{\circ}29'32''\text{S}$ ,  $49^{\circ}31'26''\text{W}$ ; C. R. M. Feltrin; 29.IX.2018; UFRJ 1219 • 2 ex., 48.1–66.4 mm SL; same data as UFRJ 1219; CIC-CAA 04112 • 1 ex. (C&S), 52.3 mm SL; Siderópolis Municipality: stream tributary to Rio São Bento, village of São Pedro, Aguá

Santuário Ecológico;  $28^{\circ}36'52''\text{S}$ ,  $49^{\circ}33'40''\text{W}$ ; about 155 m asl; C. R. M. Feltrin; 26.VIII.2020; UFRJ 6962 • 4 ex. (C&S), 21.5–34.8 mm SL; Siderópolis Municipality: Rio da Serra, about 100 m from the confluence with the Rio da Mina to form Rio São Bento, village of Costão da Serra;  $28^{\circ}33'16''\text{S}$ ,  $49^{\circ}34'53''\text{W}$ ; about 230 m asl; C. R. M. Feltrin; 1.IX.2015; UFRJ 10698.

**DIAGNOSIS.** — *Cambeva grisea* n. sp. is distinguished from *C. brachykechenos*, the only other species of the *C. brachykechenos* complex, in having more pleural ribs (13–15, vs 12), anal and dorsal fins more posteriorly placed relatively to vertebrae (dorsal-fin origin in a vertical through centrum of the 20th or 21st vertebra, vs 19th; anal-fin origin in vertical through centrum of 23rd or 24th vertebra, vs 21st or 22nd), and a different colouration on the flank (pale brownish grey, sometimes with dark grey pigment irregularly distributed, vs dark brown with small light brownish grey spots). *Cambeva grisea* n. sp. also seems to be smaller than *C. brachykechenos*, with the largest specimen found reaching only 52.3 mm SL (vs 70.9 mm SL recorded for *C. brachykechenos* by Ferrer & Malabarba 2013).

**DISTRIBUTION.** — *Cambeva grisea* n. sp. occurs in the eastern forested slope. It is known from the Rio Araranguá basin, in altitudes about 160–300 m asl (Fig. 14).

**ETYMOLOGY.** — From the Latin *grisea* (grey), referring to the predominant colouration of this new species.



TABLE 6. — Morphometric data of *Cambeva grisea* n. sp.

	holotype	paratypes (n = 6)
Standard length (mm)	43.1	35.5-45.9
Percent of standard length		
Body depth	17.1	13.7-17.0
Caudal peduncle depth	11.3	11.0-12.5
Body width	10.8	8.5-10.5
Caudal peduncle width	3.5	3.4-4.5
Pre-dorsal length	63.6	65.3-67.9
Pre-pelvic length	56.3	57.3-59.1
Dorsal-fin base length	11.9	10.8-11.7
Anal-fin base length	8.2	8.3-9.5
Caudal-fin length	16.8	16.5-18.0
Pectoral-fin length	12.0	12.2-13.4
Pelvic-fin length	8.4	8.8-9.6
Head length	20.5	19.9-22.5
Percent of head length		
Head depth	47.3	45.8-52.0
Head width	80.3	72.2-83.5
Snout length	38.4	39.3-41.1
Interorbital length	17.3	16.7-25.6
Preorbital length	12.0	9.5-10.6
Eye diameter	8.6	7.7-11.0

## DESCRIPTION

*General morphology*

Morphometric data in Table 6. Body slender, subcylindrical and slightly depressed anteriorly, compressed posteriorly. Greatest body depth in area just anterior to pelvic-fin base. Dorsal profile of head and trunk slightly convex, approximately straight on caudal peduncle; ventral profile straight to slightly convex between lower jaw and end of anal-fin base, straight on caudal peduncle. Skin papillae minute. Anus and urogenital papilla in vertical just posterior to dorsal-fin origin. Head subtrapezoidal in dorsal view, almost rectangular, with anterior profile of snout slightly convex. Eye small, dorsally positioned in head, on its anterior half. Posterior nostril located nearer anterior nostril than orbital rim. Tip of maxillary and rictal barbels reaching area between interopercular patch of odontodes and pectoral-fin base; tip of nasal barbel reaching area between eye and opercular patch of odontodes. Mouth subterminal. Jaw teeth 26-35 in both jaws, incisiform in specimens above about 35 mm SL, pointed in smaller specimens, always irregularly distributed. Branchial membrane attached to isthmus only at its anterior point. Branchiostegal rays 8. Anterior cranial fontanel absent, posterior fontanel restricted to parieto-supraoccipital, sometimes slightly anteriorly advancing between frontals. Dorsal and anal fins subtriangular, distal margin slightly convex; total dorsal-fin rays 11 (ii + II + 7), total anal-fin rays 9 (ii + II + 5); anal-fin origin in vertical through anterior third of dorsal-fin base. Dorsal-fin origin in vertical through centrum of 20th or 21st vertebra; anal-fin origin in vertical through centrum of 23rd or 24th vertebra. Pectoral fin subtriangular in dorsal view, posterior margin slightly convex, first pectoral-fin ray not terminating in filament; total pectoral-fin rays 6 (I + 5). Pelvic fin subtruncate, its extremity in vertical anterior to dorsal-fin base; pelvic-fin bases medially in contact; total pelvic-fin rays 5 (I + 4). Caudal fin subtruncate, postero-dorsal and postero-ventral extremi-

ties rounded; total principal caudal-fin rays 13 (I + 11 + I), total dorsal procurent rays 14-16 (xiii-xv + I), total ventral procurent rays 8-12 (vii-xi + I). Vertebrae 38-39. Ribs 13-15. Single dorsal hypural plate, corresponding to hypurals 3 + 4 + 5, single ventral hypural plate corresponding to hypurals 1 + 2 and parhypural.

*Latero-sensory system*

Supraorbital sensory canal continuous, connected to posterior section of infraorbital canal posteriorly. Supraorbital sensory canal with 3 pores: s1, adjacent to medial margin of anterior nostril; s3, adjacent and just posterior to medial margin of posterior nostril; and s6, in transverse line through posterior half of orbit; pore s6 nearer orbit than its paired homologous pore. Single infraorbital sensory canal segment, with two pores, corresponding to pore i10, adjacent to ventral margin of orbit, and pore i11, posterior to orbit; anterior segment of infraorbital canal absent. Postorbital canal with 2 pores: po1, in vertical line above posterior portion of interopercular patch of odontodes, and po2, in vertical line above posterior portion of opercular patch of odontodes. Lateral line of body short, with 2 pores, posterior-most pore in vertical just posterior to pectoral-fin base.

*Mesethmoidal region (Fig. 11F)*

Mesethmoid robust, its anterior margin about straight; mesethmoid cornu subtriangular in dorsal view, extremity pointed; narrow lateral flap on intersection between cornu and main bone axis. Small lateral projection on lateral ethmoid margin close to middle portion of sesamoid supraorbital. Antorbital thin, drop-shaped; sesamoid supraorbital short and slender, slightly longer than antorbital, without processes. Premaxilla sub-trapezoidal in dorsal view, laterally narrowing, moderate in length, slightly longer than maxilla. Maxilla boomerang-shaped, slender, slightly curved. Autopalatine sub-rectangular in dorsal view, medial margin slightly concave, lateral margin approximately straight; autopalatine posterolateral process short, subtriangular.

*Cheek region (Fig. 12F)*

Metapterygoid thin, subtrapezoidal, large, slightly longer than deep, its largest length about equal to horizontal length of quadrate excluding dorsal process. Quadrate slender, dorsal process with constricted base, dorsoposterior margin separated from hyomandibula outgrowth by small interspace. Hyomandibula long, with well-developed anterior outgrowth; middle portion of dorsal margin of hyomandibula slightly concave. Opercle relatively slender, opercular odontode patch depth about half length of dorsal hyomandibula articular facet, with 10-16 odontodes; odontodes pointed, nearly straight to slightly curved, arranged in irregular transverse rows; dorsal process of opercle short and pointed; opercular articular facet for hyomandibula with prominent trapezoidal flap, articular facet for preopercle inconspicuous. Interopercle moderate, its length about equal to hyomandibular outgrowth length, with 23-26 odontodes; odontodes pointed, arranged in irregular longitudinal rows. Preopercle compact, with short ventral flap.



FIG. 6. — *Cambeva grisea* n. sp., UFRJ 6936, holotype, 43.1 mm SL: **A**, left lateral view; **B**, dorsal view; **C**, ventral view.

*Parurohyal* (Fig. 13F)

Parurohyal robust, lateral process sub-triangular, slightly curved, latero-posteriorly directed, extremity pointed; parurohyal head well-developed, with anterolateral paired process; middle foramen oval; posterior process short, about one third of distance between anterior margin of parurohyal and anterior insertion of posterior process.

*Colouration in alcohol* (Fig. 6)

Flank pale brownish grey, sometimes with dark grey pigment irregularly distributed; dorsum greyish brown with small light grey vermiculate spots, venter light yellowish grey. Head pale brownish grey to brown on nape, with darker pigmentation concentrated between orbit and anterior nostril; small dark grey spots along lateral extremity of head and basal portion of barbels. Fins whit-

ish hyaline, with minute grey dots along rays of unpaired fins and small dark grey spot close to dorsal-fin origin and pectoral-fin base.

*Cambeva tropeira* complex

*Cambeva duplimaculata* n. sp.  
(Figs 7, 11G, 12G, 13G; Table 7)

[urn:lsid:zoobank.org:act:17CCE793-8B84-41C6-B304-CD44C46747FE](https://doi.org/10.12010/zoobank.org/act:17CCE793-8B84-41C6-B304-CD44C46747FE)

MATERIAL EXAMINED. — **Holotype**. Brazil • 1 ex., 83.4 mm SL; Santa Catarina State: Bom Jardim da Serra Municipality: Rio Barrinha, a tributary of the upper Rio Pelotas, Rio Uruguai basin, 28°20'24"S, 49°36'59"W; about 1245 m asl; C. R. M. Feltrin; 8.II.2021; UFRJ 6949.

TABLE 7. — Morphometric data of *Cambeva duplimaculata* n. sp.

	holotype	paratypes (n = 6)
Standard length (mm)	83.4	33.5-61.5
Percent of standard length		
Body depth	13.9	14.7-16.7
Caudal peduncle depth	10.8	10.8-11.8
Body width	10.3	10.3-12.4
Caudal peduncle width	4.1	2.6-4.1
Pre-dorsal length	63.5	63.9-68.2
Pre-pelvic length	56.6	60.4-63.2
Dorsal-fin base length	11.0	10.6-12.2
Anal-fin base length	9.0	7.5-9.6
Caudal-fin length	15.5	13.5-16.5
Pectoral-fin length	10.9	11.2-12.9
Pelvic-fin length	7.5	7.0-8.6
Head length	19.6	21.1-23.4
Percent of head length		
Head depth	47.0	48.1-53.0
Head width	82.8	73.9-82.0
Snout length	43.3	39.7-44.3
Interorbital length	21.4	22.0-23.7
Preorbital length	13.1	13.0-16.4
Eye diameter	9.7	10.5-14.0

**Paratypes.** Brazil • 2 ex., 29.6-61.5 mm SL; upper Rio Pelotas, Rio Uruguai basin, 28°20'07"S, 49°40'43"W; about 1190 m asl; C. R. M. Feltrin; 8.II.2021; UFRJ 6950 • 2 ex., 37.4-38.0 mm SL; same locality as UFRJ 6950; C. R. M. Feltrin; 16.VII.2020; UFRJ 6951 • 3 ex. (C&S), 33.5-41.1 mm SL; same data as UFRJ 6951; UFRJ 6952.

**DIAGNOSIS.** — *Cambeva duplimaculata* n. sp. is distinguished from all other species of the *C. tropeira* complex in having more dorsal procurrent caudal-fin rays (16 or 17, vs 12-15) and a colour pattern in adult specimens (above about 50 mm SL) consisting of flank with rounded black spots arranged in three irregular longitudinal rows, overlapped by a high concentration of minute dark brown spots that are placed at a more superficial skin layer (Fig. 7; vs never a similar colour pattern, Figs 8-10; see also Ferrer & Malabarba 2011: fig. 1). Also distinguished from *C. longipalata* n. sp. in having fewer vertebrae (39 or 40, vs 41 or 42), the dorsal-fin origin in vertical through centrum of 20th or 21st vertebrae (vs 23rd or 24th) and the anal-origin in vertical through centrum of 24th or 25th vertebrae (vs 26th), and a wider body (body width 10.8-11.8 % SL, vs 8.0-9.7 % SL); from *C. notabilis* n. sp. in having a shorter pelvic fin (pelvic-fin length 7.0-8.6 % SL, vs 9.0-10.4 % SL); from *C. tropeira* in having a well-developed pelvic fin (vs pelvic fin absent); from *C. urubici* n. sp. in having fewer teeth on premaxilla (38-41, vs 46-51) and dentary (35-39, vs 46-51); from *C. notabilis* n. sp., *C. tropeira* and *C. urubici* n. sp. in having more ventral procurrent caudal-fin rays (12-15, vs 10-11); and from *C. notabilis* n. sp. and *C. urubici* n. sp. in having fewer opercular odontodes (11-13, vs 15 or 16).

**DISTRIBUTION.** — *Cambeva duplimaculata* n. sp. occurs in the western open plateau. It is only known from two localities in the upper Rio Pelotas drainage, upper Rio Uruguai basin, in altitudes between about 1190 and 1250 m asl (Fig. 14).

**ETYMOLOGY.** — The name *duplimaculata*, from the Latin (doubly maculated) refers to its colour pattern in the flank, consisting of two overlapped spotted patterns in different skin layers, comprising inner large black spots and outer small brown spots.

## DESCRIPTION

*General morphology*

Morphometric data in Table 7. Body moderately slender, subcylindrical anteriorly to compressed posteriorly. Greatest body depth in area just anterior to pelvic-fin base. Dorsal and ventral profiles of head and trunk slightly convex, approximately straight on caudal peduncle. Skin papillae minute. Anus and urogenital papilla in vertical through anterior third of dorsal-fin base. Head trapezoidal in dorsal view, anterior profile of snout convex. Eye small, dorsally positioned in anterior half of head. Posterior nostril located nearer anterior nostril than orbital rim. Tip of maxillary barbel reaching middle of interopercular patch of odontodes; tip of rictal and nasal barbels reaching anterior portion of interopercular patch of odontodes. Mouth subterminal. Jaw teeth pointed, slightly curved, irregularly arranged, 38-41 in premaxilla, 35-39 in dentary. Branchial membrane attached to isthmus only at its anterior point. Branchiostegal rays 9. Cranial fontanels present, posterior fontanel long, anteriorly extending between frontals to reach transverse line close to lateral sphenotic process. Dorsal and anal fins subtriangular, distal margin slightly convex; total dorsal-fin rays 12-13 (iii-iv + II + 7), total anal-fin rays 10-11 (iii-iv + II + 5); anal-fin origin in vertical through just anterior to posterior dorsal-fin base end. Dorsal-fin origin in vertical through centrum of 20th or 21st vertebra; anal-fin origin in vertical through centrum of 24th or 25th vertebra. Pectoral fin subtriangular in dorsal view, posterior margin slightly convex, first pectoral-fin ray not terminating in filament; total pectoral-fin rays 7 (I + 6). Pelvic fin subtruncate, its extremity in vertical through anterior-most portion of dorsal-fin base; pelvic-fin bases medially in contact; total pelvic-fin rays 5 (I + 4). Caudal fin subtruncate, postero-dorsal and postero-ventral extremities rounded; total principal caudal-fin rays 13 (I + 11 + I), total dorsal procurrent rays 16-17 (xv-xvi + I), total ventral procurrent rays 12-15 (xi-xiv + I). Vertebrae 39-40. Ribs 14 or 15. Two dorsal hypural plates, corresponding to hypurals 4 + 5 and 3, respectively; single ventral hypural plate corresponding to hypurals 1 and 2 and parhypural.

*Latero-sensory system*

Supraorbital sensory canal continuous, connected to infraorbital sensory canal posteriorly. Supraorbital sensory canal with 3 pores: s1, adjacent to medial margin of anterior nostril; s3, adjacent to medial margin of posterior nostril; and s6, on middle part of dorsal surface of head, in transverse line just posterior to orbit; pore s6 nearer orbit than its paired homologous pore. Infraorbital sensory canal arranged in 2 segments, each with two pores; anterior segment with pore i1, in transverse line through anterior nostril, and pore i3, in transverse line just anterior to posterior nostril; posterior segment with pore i10, adjacent to ventral margin of orbit, and pore i11, posterior to orbit. Postorbital canal with 2 pores: po1, in vertical line above posterior portion of interopercular patch of odontodes, and po2, in vertical line above posterior portion of opercular patch of odontodes. Lateral line of body short, with 2 pores, posterior-most pore in vertical just posterior to pectoral-fin base.





FIG. 7. — *Cambeva duplimaculata* n. sp., UFRJ 6949, holotype, 83.4 mm SL: **A**, left lateral view; **B**, dorsal view; **C**, ventral view.

*Mesethmoidal region* (Fig. 11G)

Mesethmoid robust, its anterior margin about straight; mesethmoid cornu narrow, extremity slightly pointed; narrow lateral flap on intersection between cornu and main bone axis, posteriorly extending parallel to lateral bone margin. Minute lateral projection on lateral ethmoid margin close to posterior portion of sesamoid supraorbital. Antorbital thin, posteriorly supporting anterior infraorbital canal; sesamoid supraorbital slender, its length about twice or slightly more antorbital length, sometimes with minute lateral process. Premaxilla sub-trapezoidal in dorsal view, slightly laterally narrowing, longer than maxilla. Maxilla boomerang-shaped, slender, slightly curved. Autopalatine sub-rectangular in dorsal view, moderate in width, longer than wide, lateral and medial margins slightly concave; autopalatine posterolateral process subtriangular in dorsal view, with sharp extremity, short, its length shorter than osseous portion of autopalatine length excluding posterolateral process.

*Cheek region* (Fig. 12G)

Metapterygoid thin, subtriangular, large, its largest length about equal horizontal length of quadrate excluding dorsal

process. Quadrate slender, dorsal process with constricted base, dorsoposterior margin in contact with from hyomandibula outgrowth. Hyomandibula long, with well-developed anterior outgrowth; middle portion of dorsal margin of hyomandibula slightly concave. Opercle relatively slender, with deep transverse constriction just anterior to opercular odontode patch; opercular odontode patch depth about three fifths of dorsal hyomandibula articular facet, with 11-13 odontodes; odontodes pointed, straight to slightly curved, arranged in irregular transverse rows; dorsal process of opercle short and truncate; opercular articular facet for hyomandibula with small, rounded flap, articular facet for preopercle almost indistinct. Interopercle moderate, about two thirds hyomandibula length, anterior margin concave; interopercular odontode patch with 16-18 pointed odontodes, arranged in irregular longitudinal rows. Preopercle compact, with short ventral flap.

*Parurohyal* (Fig. 13G)

Robust, lateral process sub-triangular, posterior margin slightly convex, latero-posteriorly directed, extremity pointed; parurohyal head well-developed, with prominent anterolateral

TABLE 8. — Morphometric data of *Cambeva longipalata* n. sp.

	holotype	paratypes (n = 6)
Standard length (mm)	86.0	46.4–53.9
Percent of standard length		
Body depth	12.2	14.8–15.8
Caudal peduncle depth	10.1	10.8–11.8
Body width	8.1	8.0–9.7
Caudal peduncle width	2.7	2.6–3.5
Pre-dorsal length	60.7	62.0–66.9
Pre-pelvic length	54.9	56.5–60.9
Dorsal-fin base length	9.1	10.5–12.0
Anal-fin base length	8.2	8.9–9.9
Caudal-fin length	13.2	14.1–15.3
Pectoral-fin length	10.3	10.1–11.0
Pelvic-fin length	6.6	6.5–7.5
Head length	18.5	20.0–22.1
Percent of head length		
Head depth	45.2	44.0–51.4
Head width	79.9	75.2–84.4
Snout length	43.7	41.8–44.7
Interorbital length	20.9	20.0–23.2
Preorbital length	15.1	12.0–14.5
Eye diameter	8.5	8.4–10.6

paired process; middle foramen small, round; posterior process long, about three fifths of distance between anterior margin of parurohyal and anterior insertion of lateral process.

#### Colouration in alcohol (Fig. 7)

Flank, dorsum and head side pale yellow, with rounded black spots, flank spots larger than interopercular patch of odontodes, head spots equal or slightly larger than orbit; flank spots arranged in three irregular longitudinal rows. Small pale brown spots in superficial skin layer, scattered over flank and dorsum, overlapping dark grey spots, their diameter equal or smaller than posterior nostril. Venter and ventral part of head greyish white. Barbels grey with dark grey margin. Fins pale grey with small black spots on basal portion.

#### *Cambeva longipalata* n. sp. (Figs 8, 11H, 12H, 13H; Table 8)

[urn:lsid:zoobank.org:act:F938318C-424E-490E-B187-3CBEED09F201](https://doi.org/10.3896/BI.2021.187-3CBEED09F201)

**MATERIAL EXAMINED.** — **Holotype.** Brazil • 1 ex., 86.0 mm SL; Santa Catarina State: Bom Jardim da Serra Municipality: Rio Mantiqueira, tributary of Rio Pelotas, Rio Uruguai basin; 28°15'47"S, 49°45'46"W; about 1325 m asl; C. R. M. Feltrin; 8.II.2021; UFRJ 6944.

**Paratypes.** Brazil • 6 ex., 26.5–53.9 mm SL; collected with holotype; UFRJ 6945 • 1 ex. (C&S), 52.4 mm SL; collected with holotype; UFRJ 6947 • 2 ex., 46.4–52.9 mm SL; collected with holotype; CICC AA 04109 • 11 ex., 28.5–37.03 mm SL; same area as holotype, 28°16'08"S, 49°45'40"W; about 1325 m asl; C. R. M. Feltrin; 16.VII.2020; UFRJ 6946 • 4 ex. (C&S), 28.9–36.9 mm SL; same data as UFRJ 6946; UFRJ 6948.

**DIAGNOSIS.** — *Cambeva longipalata* n. sp. differs from all other congeners of the *C. tropeira* complex in having more vertebrae (41 or 42, vs 37–40), dorsal-fin origin in a vertical between the centrum of the 23rd or 24th vertebra (vs 19th–21st) and anal-fin origin in a vertical between the centrum of the 26th vertebra (vs 22nd–25th),

a narrower body (body width 8.0–9.7 % SL, vs 10.0–12.8 % SL); and a long posterolateral process of the autopalatine, its length about equal to the osseus portion of the autopalatine length excluding the posterolateral process (Fig. 11H, vs smaller, Figs 11G, I–K). *Cambeva longipalata* n. sp. is distinguished from all other congeners of the *C. tropeira* complex, except *C. tropeira*, in having rounded black spots and dots irregularly arranged on the flank (never a similar colour pattern), and the presence of a lateral projection on the lateral ethmoid, close to the middle portion of the sesamoid supraorbital (Figs 11H, J; vs projection absent or close to posterior portion of the sesamoid supraorbital when present, Figs 11 G, I, K) and posterior portion of the antorbital slightly laterally bowed (Fig. 11H, J; vs straight, Figs 11 G, I, K); *C. longipalata* n. sp. is readily distinguished from *C. tropeira* in having a well-developed pelvic fin (vs pelvic fin absent). *Cambeva longipalata* n. sp. is also distinguished from *C. duplimaculata* n. sp. in having fewer dorsal procurrent caudal-fin rays (12–14, vs 16 or 17); from *C. urubici* n. sp. in having fewer teeth in the premaxilla (39–41, vs 46–51) and dentary (35–38, vs 46–51); and from *C. notabilis* n. sp. and *C. urubici* n. sp. in having fewer opercular odontodes (10 or 11, vs 14–16).

**DISTRIBUTION.** — *Cambeva longipalata* n. sp. occurs in the western open plateau. It is only known from the Rio Mantiqueira, a tributary of the upper Rio Pelotas, upper Rio Uruguai basin, about 1330 m asl (Fig. 14).

**ETYMOLOGY.** — From the Latin, the name *longipalata* (long palate) is an allusion to the peculiar morphology of the autopalatine of the new species, with a long posterolateral process.

#### DESCRIPTION

##### General morphology

Morphometric data in Table 8. Body moderately slender, subcylindrical anteriorly to compressed posteriorly. Greatest body depth in area just anterior to pelvic-fin base. Dorsal and ventral profiles of head and trunk slightly convex, approximately straight on caudal peduncle. Skin papillae minute. Anus and urogenital papilla in vertical just posterior to dorsal-fin origin. Head trapezoidal in dorsal view, anterior profile of snout convex. Eye small, dorsally positioned in anterior half of head. Posterior nostril located nearer anterior nostril than orbital rim. Tip of maxillary barbel reaching between interopercular and opercular patch of odontodes; tip of nasal and rictal barbels reaching interopercular patch of odontodes. Mouth subterminal. Jaw teeth pointed, slightly curved, irregularly arranged, 39–41 in premaxilla, 35–38 in dentary. Branchial membrane attached to isthmus only at its anterior point. Branchiostegal rays 8. Cranial fontanels present, posterior fontanel long, anteriorly extending between frontals to reach transverse line close to lateral sphenotic process. Dorsal and anal fins subtriangular, distal margin slightly convex; total dorsal-fin rays 12 (iii + II + 7), total anal-fin rays 10 (iii + I–II + 5–6); anal-fin origin in vertical through middle of dorsal-fin base or just posterior to it. Dorsal-fin origin in vertical through centrum of 23rd or 24th vertebra; anal-fin origin in vertical through centrum of 26th vertebra. Pectoral fin subtriangular in dorsal view, posterior margin slightly convex, first pectoral-fin ray not terminating in filament; total pectoral-fin rays 7 (I + 6). Pelvic fin subtruncate, its extremity in vertical anterior to dorsal-fin base; pelvic-fin bases medially in close proximity; total pelvic-fin rays 5 (I +



FIG. 8. — *Cambeva longipalata* n. sp., UFRJ 6944, holotype, 86.0 mm SL: **A**, left lateral view; **B**, dorsal view; **C**, ventral view.

4). Caudal fin truncate, postero-dorsal and postero-ventral extremities rounded; total principal caudal-fin rays 13 (I + 11 + I), total dorsal procurrent rays 12-14 (x-xiii + I-II), total ventral procurrent rays 10-12 (xi-xv + I). Vertebrae 41-42. Ribs 13 or 14. Two dorsal hypural plates, corresponding to hypurals 4 + 5 and 3, respectively, often coalesced to form single plate; single ventral hypural plate corresponding to hypurals 1 and 2 and parhypural.

#### *Latero-sensory system*

Supraorbital sensory canal continuous, connected to infraorbital sensory canal posteriorly. Supraorbital sensory canal with 3 pores: s1, adjacent to medial margin of anterior nostril; s3, adjacent to medial margin of posterior nostril; and s6, on middle part of dorsal surface of head, in transverse line just posterior to orbit; pore s6 nearer orbit than its paired homologous pore. Infraorbital sensory canal arranged in 2 segments, each with two pores; anterior segment with pore i1, in transverse line through anterior nostril, and pore i3, in transverse line just anterior to posterior nostril; posterior segment with pore i10, adjacent to ventral margin of orbit, and pore i11, posterior to orbit. Postorbital canal with 2 pores: po1, in vertical line above posterior portion of interopercular patch of odontodes, and po2, in vertical line above posterior portion of opercular patch of odontodes. Lateral line of body short, with 2 pores, posterior-most pore in vertical just posterior to pectoral-fin base.

#### *Mesethmoidal region (Fig. 11H)*

Mesethmoid robust, its anterior margin about straight; mesethmoid cornu narrow, extremity pointed; narrow lateral flap on intersection between cornu and main bone axis, posteriorly extending parallel to lateral bone margin. Minute lateral projection on lateral ethmoid margin close to middle portion of sesamoid supraorbital. Antorbital thin, posterior portion slightly laterally bowed, posteriorly supporting anterior infraorbital canal; sesamoid supraorbital slender, its length about twice or slightly less antorbital length, with weak lateral projection. Premaxilla sub-trapezoidal in dorsal view, slightly laterally narrowing, longer than maxilla. Maxilla boomerang-shaped, slender, slightly curved. Autopalatine sub-rectangular in dorsal view, slender, longer than wide, with posterior portion of medial margin expanded, lateral margin nearly straight to slightly curved near posterolateral process; autopalatine posterolateral process subtriangular in dorsal view, with sharp extremity, long, its length about equal to osseus portion of autopalatine length excluding posterolateral process.

#### *Cheek region (Fig. 12H)*

Metapterygoid thin, subtriangular, large, its largest length slightly longer than horizontal length of quadrate excluding dorsal process; minute process just anterior to articular cartilaginous block. Quadrate slender, dorsal process with constricted base, dorsoposterior margin in contact with



TABLE 9. — Morphometric data of *Cambeva notabilis* n. sp.

	holotype	paratypes (n = 2)
Standard length (mm)	71.7	39.3-65.1
Percent of standard length		
Body depth	15.5	16.3-16.4
Caudal peduncle depth	10.6	10.7-11.7
Body width	12.1	10.4-10.9
Caudal peduncle width	4.3	3.4-4.1
Pre-dorsal length	65.3	64.8-65.6
Pre-pelvic length	57.4	58.7-58.8
Dorsal-fin base length	10.6	11.1-12.1
Anal-fin base length	8.2	8.9-9.6
Caudal-fin length	16.7	16.5-18.0
Pectoral-fin length	13.0	12.6-14.4
Pelvic-fin length	9.0	9.9-10.4
Head length	21.6	22.2-24.0
Percent of head length		
Head depth	51.0	49.9-51.1
Head width	81.4	74.9-83.6
Snout length	43.3	43.6-48.9
Interorbital length	21.2	23.2-23.5
Preorbital length	13.7	13.7-15.4
Eye diameter	8.4	8.8-9.0

from hyomandibula outgrowth. Hyomandibula long, with well-developed anterior outgrowth; middle portion of dorsal margin of hyomandibula slightly concave. Opercle relatively slender, with deep transverse constriction just anterior to opercular odontode patch; opercular odontode patch depth about three fifths of dorsal hyomandibula articular facet, with 10 or 11 odontodes; odontodes pointed, straight to slightly curved, arranged in irregular transverse rows; dorsal process of opercle short and truncate; opercular articular facet for hyomandibula with small, rounded flap, articular facet for preopercle indistinct. Interopercle moderate, about two thirds hyomandibula length, anterior margin slightly concave; interopercular odontode patch with 18-20 pointed odontodes, arranged in irregular longitudinal rows. Preopercle compact, with short ventral flap.

*Parurohyal* (Fig. 13H)

Robust, lateral process sub-triangular, posterior margin slightly sinuous, latero-posteriorly directed, extremity pointed; parurohyal head well-developed, with anterolateral paired process; middle foramen small, round; posterior process relatively long, about six tenths of distance between anterior margin of parurohyal and anterior insertion of lateral process.

*Colouration in alcohol* (Fig. 8)

Flank, dorsum and head side pale yellow, with rounded black spots and small dots; most flank spots larger than interopercular patch of odontodes, head spots equal or slightly larger than orbit; spots and dots irregularly arranged on flank. Venter and ventral part of flank greyish white. Barbels dark grey. Fins pale grey with small, dark greyish brown spots on basal portion.

*Cambeva notabilis* n. sp.  
(Figs 9, 11I, 12I, 13I; Table 9)

[urn:lsid:zoobank.org:act:7495C863-9AB2-4B1B-9822-CD30FE954F10](http://urn:lsid:zoobank.org:act:7495C863-9AB2-4B1B-9822-CD30FE954F10)

MATERIAL EXAMINED. — **Holotype.** Brazil • 1 ex., 71.7 mm SL; Santa Catarina State: Grão Pará Municipality: upper Rio Braço Esquerdo, Rio Braço do Norte drainage, Rio Tubarão basin; 28°08'02"S, 49°24'54"W; about 610 m asl; C. R. M. Feltrin; 17.II.2021; UFRJ 6965.

**Paratypes.** Brazil • 1 ex. (C&S), 39.4 mm SL; collected with holotype; UFRJ 6966 • 1 ex., 65.1 mm SL; same locality as holotype; C. R. M. Feltrin; 2.III.2015; UFRJ 10513.

DIAGNOSIS. — *Cambeva notabilis* n. sp. is distinguished from all other species of the *C. tropeira* complex, except *C. urubici* n. sp., in the presence of a black stripe along flank longitudinal midline during some life stage (vs black stripe along flank longitudinal midline always absent); in *C. notabilis* n. sp., the stripe is interrupted in the largest specimen (71.7 mm SL), forming a distinctive series of horizontally elongated black spots (Fig. 9), a colouration not seen in any specimen of other species of the *C. tropeira* complex (Figs 7, 8, 10). *Cambeva notabilis* n. sp. differs from *C. urubici* n. sp. in having fewer teeth in the premaxilla (39, vs 46-51) and dentary (31, vs 46-51), and by the presence of round black spots irregularly arranged on dorsum (Fig. 9B; vs arranged in two dorsolateral longitudinal rows, often coalesced and forming stripes, Fig. 10B). *Cambeva notabilis* n. sp. is also distinguished from *C. duplimaculata* n. sp. in having fewer dorsal procurrent caudal-fin rays (13, vs 16 or 17); from *C. longipalata* n. sp. in having fewer vertebrae (39, vs 41 or 42), more opercular odontodes (14, vs 10 or 11), dorsal fin origin in a vertical through the centrum of the 21st vertebra (vs between 23rd and 24th vertebrae) anal fin origin in a vertical through the centrum of the 24th vertebra (vs 26th vertebra), and a wider body (10.4-12.4 % SL, vs 8.0-9.7 % SL); and from *C. tropeira* in having a well-developed pelvic fin (vs pelvic fin absent). Examination of a single cleared and stained paratype for bone and cartilage, indicates that *C. notabilis* n. sp. also differs from all other species of the *C. tropeira* complex by the possession of a long antorbital, about three fourths of the sesamoid supraorbital length (Fig. 11I, vs about half length of less, Figs 11G, H, J, K), and the absence of a dorsal constriction close to the opercular patch of odontodes (Fig. 12I), vs presence (Figs 12G, H, J).

DISTRIBUTION. — *Cambeva notabilis* n. sp. occurs in the eastern forested slope. It is only known from the upper Rio Braço Esquerdo, Rio Braço do Norte drainage, Rio Tubarão basin, altitude about 610 m asl (Fig. 14).

ETYMOLOGY. — From the Latin, the name *notabilis* (notable) refers to the unique colouration of this new species.

DESCRIPTION

*General morphology*

Morphometric data in Table 9. Body moderately slender, subcylindrical anteriorly to compressed posteriorly. Greatest body depth in area just anterior to pelvic-fin base. Dorsal and ventral profiles of head and trunk slightly convex, approximately straight on caudal peduncle. Skin papillae minute. Anus and urogenital papilla in vertical through middle of dorsal-fin origin. Head trapezoidal in dorsal view, anterior profile of snout convex. Eye small, dorsally positioned in anterior half of head. Posterior nostril located nearer ante-



FIG. 9. — *Cambeva notabilis* n. sp., UFRJ 6965, holotype, 71.7 mm SL: **A**, left lateral view; **B**, dorsal view; **C**, ventral view.

rior nostril than orbital rim. Tip of maxillary barbel reaching middle part of interopercular patch of odontodes; tip of rictal barbel reaching anterior margin of interopercular patch of odontodes; tip of nasal barbel slightly posteriorly surpassing posterior margin of orbit. Mouth subterminal. Jaw teeth pointed, slightly curved, irregularly arranged, premaxillary teeth 39, dentary teeth 31. Branchial membrane attached to isthmus only at its anterior point. Branchiostegal rays 8. Cranial fontanels present, posterior fontanel long, anteriorly extending between frontals to reach transverse line close to lateral sphenotic process. Dorsal and anal fins short, subtriangular, distal margin slightly convex; total dorsal-fin rays 12 (iii + II + 7), total anal-fin rays 10 (iii + I-II + 5-6); anal-fin origin in vertical just anterior to dorsal-fin base posterior end. Dorsal-fin origin in vertical through centrum of 21st vertebra; anal-fin origin in vertical through centrum of 24th vertebra. Pectoral fin subtriangular in dorsal view, posterior margin slightly convex, first pectoral-fin ray not terminating in filament; total pectoral-fin rays 7 (I + 6). Pelvic fin subtruncate, its extremity in vertical through dorsal-fin origin, or slightly anterior to it; pelvic-fin bases

medially in close proximity; total pelvic-fin rays 5 (I + 4). Caudal fin truncate, postero-dorsal and postero-ventral extremities rounded; total principal caudal-fin rays 13 (I + 11 + I), total dorsal procurent rays 13 (xii + I), total ventral procurent rays 12 (xi + I). Vertebrae 39. Ribs 14. Single dorsal hypural plate, corresponding to hypurals 3 + 4 + 5; single ventral hypural plate corresponding to hypurals 1 and 2 and parhypural.

#### *Latero-sensory system*

Supraorbital sensory canal continuous, connected to infraorbital sensory canal posteriorly. Supraorbital sensory canal with 3 pores: s1, adjacent to medial margin of anterior nostril; s3, adjacent to medial margin of posterior nostril; and s6, on middle part of dorsal surface of head, in transverse line just posterior to orbit; pore s6 nearer its paired homologous pore than orbit or slightly nearer orbit than its paired homologous. Infraorbital sensory canal arranged in 2 segments, each with two pores; anterior segment with pore i1, in transverse line through anterior nostril, and pore i3, in transverse line just anterior to posterior nostril; posterior segment with pore

i10, adjacent to ventral margin of orbit, and pore i11, posterior to orbit. Postorbital canal with 2 pores: po1, in vertical line above posterior portion of interopercular patch of odontodes, and po2, in vertical line above posterior portion of opercular patch of odontodes. Lateral line of body short, with 2 pores, posterior-most pore in vertical just posterior to pectoral-fin base.

*Mesethmoidal region (Fig. 11I)*

Mesethmoid robust, its anterior margin about straight; mesethmoid cornu narrow, extremity rounded; narrow lateral flap on intersection between cornu and main bone axis, posteriorly extending parallel to lateral bone margin. Minute lateral projection on lateral ethmoid margin close to middle portion of sesamoid supraorbital. Antorbital thin, relatively long, posteriorly supporting anterior infraorbital canal, its posterior extremity near anterior extremity of sesamoid supraorbital; sesamoid supraorbital flat and slender, without processes. Premaxilla sub-trapezoidal in dorsal view, longer than maxilla. Maxilla boomerang-shaped, slender, slightly curved. Autopalatine sub-rectangular in dorsal view, compact, slightly longer than wide when excluding postero-lateral process, medial margin straight, lateral margin nearly straight to slightly curved near posterolateral process; autopalatine posterolateral process subtriangular in dorsal view, with sharp extremity, short, its length shorter than osseus portion of autopalatine length excluding posterolateral process.

*Cheek region (Fig. 12I)*

Metapterygoid thin, subtriangular, large, its largest length slightly shorter than horizontal length of quadrate excluding dorsal process. Quadrate slender, dorsal process with constricted base, dorsoposterior margin slightly separated from hyomandibula outgrowth. Hyomandibula long, with well-developed anterior outgrowth; middle portion of dorsal margin of hyomandibula slightly concave. Opercle relatively slender; opercular odontode patch depth about three fifths of dorsal hyomandibula articular facet, with 14 odontodes; odontodes pointed, straight to slightly curved, arranged in irregular transverse rows; dorsal process of opercle short and truncate; opercular articular facet for hyomandibula with small, rounded flap, articular facet for preopercle indistinct. Interopercle moderate, about two thirds hyomandibula length, anterior margin slightly concave; interopercular odontode patch with 20 pointed odontodes, arranged in irregular longitudinal rows. Preopercle compact, with short ventral flap.

*Parurohyal (Fig. 13I)*

Robust, lateral process sub-triangular, posterior margin slightly sinuous, latero-posteriorly directed, extremity pointed; parurohyal head well-developed, with prominent anterolateral paired process; middle foramen small, round; posterior process relatively long, about three quarters of distance between anterior margin of parurohyal and anterior insertion of lateral process.

*Colouration in alcohol (based on holotype, 71.1 mm SL, Fig. 9)*  
Flank, dorsum and head side pale yellow, with rounded black spots; spots distinctively larger on row through longitudinal midlateral line of flank; spots irregularly arranged on dorsum and head. Venter and ventral part of flank greyish white. Barbels dark grey. Fins pale grey. Paratypes, 39.3 and 65.1 mm SL, differing only by spots on longitudinal midlateral line of flank being longitudinally coalesced, forming broad black stripe.

*Cambeva urubici* n. sp.

(Figs 10, 11K, 12J, 13J; Table 10)

[urn:lsid:zoobank.org:act:4F7C0D5A-4EC1-4D1D-9AFA-CEFE1973A810](https://doi.org/10.21203/rs.3.rs-1111111/v1)

**MATERIAL EXAMINED.** — **Holotype.** Brazil • 1 ex., 65.6 mm SL; Santa Catarina state: Urubici Municipality: Rio Urubici, Rio Canoas drainage, upper Rio Uruguai basin; 28°01'37"S, 49°35'21"W; about 935 m asl; C. R. M. Feltrin; 14.III.2021; UFRJ 6967.

**Paratypes.** Brazil • 4 ex., 23.0-51.0 mm SL; collected with holotype; UFRJ 6973 • 2 ex., 28.3-61.0 mm SL; same locality and collector as holotype; 8.II.2021; UFRJ 6975 • 3 ex. (C&S), 31.2-47.3 mm SL, same data as for precedent; UFRJ 6976 • 4 ex., 19.1-32.0 mm SL; upper Rio Canoas, road between Urubici and Rio dos Bugres, 27°59'24"S, 49°32'39"W; about 905 m asl; C. R. M. Feltrin; 14.III.2021; UFRJ 6983 • 2 ex., 33.5-38.0 mm SL; same data as for precedent; CICCAA 04110.

**DIAGNOSIS.** — *Cambeva urubici* n. sp. differs from all other species of the *C. tropeira* complex in having more opercular odontodes (15 or 16, vs 10 – 14), more teeth in the premaxilla and dentary (46-51 in both, vs 38-41 in the premaxilla and 31-39 in the dentary), a unique colour pattern, comprising three longitudinal rows of black spots on the flank in juveniles, with spots of the median row coalescing to form a black stripe along lateral midline (vs never a similar colour pattern), a robust autopalatine with a nearly straight medial margin (Fig. 11K; vs autopalatine more slender, with concave medial margin, Figs G-J), and the presence of a pronounced lateral process on the sesamoid supraorbital (Fig. 11K; vs absence, Figs G-J). *Cambeva urubici* n. sp. is also distinguished from *C. duplimaculata* n. sp. in having fewer dorsal procurrent caudal-fin rays (13-15, vs 16 or 17); and from *C. longipalata* n. sp. in having fewer vertebrae (40, vs 41 – 42), dorsal-fin origin in a vertical through the centrum of the 21st vertebra (vs 23rd or 24th) and anal-fin origin in a vertical through the centrum of the 25th vertebra (vs 26th).

**DISTRIBUTION.** — *Cambeva urubici* n. sp. occurs in the western open plateau. It is known from two localities in the upper Rio Canoas drainage, Rio Uruguai basin, in altitudes between about 910 and 940 m asl (Fig. 14).

**ETYMOLOGY.** — The name *urubici* is an allusion to the occurrence of the species in the Rio Urubici, Rio Uruguai basin, southern Brazil, where is its type locality. This name is derived from the Tupi-Guarani, but its meaning is unclear.

**DESCRIPTION**

*General morphology*

Morphometric data in Table 10. Body moderately slender, subcylindrical anteriorly to compressed posteriorly. Greatest body depth in area just anterior to pelvic-fin base. Dorsal





FIG. 10. — *Cambeva urubici* n. sp., UFRJ 6967, holotype, 65.6 mm SL: **A**, left lateral view; **B**, dorsal view; **C**, ventral view.

and ventral profiles of head and trunk slightly convex, approximately straight on caudal peduncle. Skin papillae minute. Anus and urogenital papilla in vertical trough anterior portion of dorsal-fin origin. Head trapezoidal in dorsal view, anterior profile of snout convex. Eye small, dorsally positioned in anterior half of head. Posterior nostril located nearer anterior nostril than orbital rim. Tip of maxillary barbel reaching anterior part of interopercular patch of odontodes; tip of rictal barbel reaching anterior margin of interopercular patch of odontodes, sometimes shorter, not reaching; tip of nasal barbel reaching posterior margin of orbit, or little beyond it. Mouth subterminal.

Jaw teeth pointed, slightly curved, irregularly arranged, 46–51 in both jaws. Branchial membrane attached to isthmus only at its anterior point. Branchiostegal rays 8 or 9. Cranial fontanels present, posterior fontanel long, anteriorly extending between frontals to reach transverse line close to lateral sphenotic process. Dorsal and anal fins short, subtriangular, distal margin slightly convex; total dorsal-fin rays 12 (iii + II + 7), total anal-fin rays 10 (iii + I-II + 5-6); anal-fin origin in vertical just anterior to dorsal-fin base posterior end. Dorsal-fin origin in vertical through centrum of 21st or 22nd vertebra; anal-fin origin in vertical through centrum of 25th or 26th vertebra. Pectoral

TABLE 10. — Morphometric data of *Cambeva urubici* n. sp.

	holotype	paratypes (n = 6)
Standard length (mm)	65.6	37.0-61.0
Percent of standard length		
Body depth	14.0	13.4-16.0
Caudal peduncle depth	9.4	10.0-11.2
Body width	11.5	10.0-12.8
Caudal peduncle width	4.9	3.5-4.5
Pre-dorsal length	62.4	63.8-67.4
Pre-pelvic length	56.8	56.9-60.9
Dorsal-fin base length	11.4	11.2-12.4
Anal-fin base length	8.9	8.2-10.5
Caudal-fin length	15.0	14.3-17.1
Pectoral-fin length	11.9	11.9-14.2
Pelvic-fin length	8.5	8.7-9.4
Head length	20.2	21.3-23.4
Percent of head length		
Head depth	54.1	47.0-51.2
Head width	78.0	74.1-80.1
Snout length	42.0	41.8-43.0
Interorbital length	20.4	20.4-24.0
Preorbital length	12.8	12.1-14.7
Eye diameter	9.4	10.0-11.1

fin subtriangular in dorsal view, posterior margin slightly convex, first pectoral-fin ray not terminating in filament; total pectoral-fin rays 7 (I + 6). Pelvic fin subtruncate, its extremity in vertical through dorsal-fin origin; pelvic-fin bases medially in close proximity; total pelvic-fin rays 5 (I + 4). Caudal fin truncate, postero-dorsal and postero-ventral extremities rounded; total principal caudal-fin rays 13 (I + 11 + I), total dorsal procurrent rays 13-15 (xii-xiv + I), total ventral procurrent rays 10-11 (ix-x + I). Vertebrae 38-40. Ribs 15 or 16. Two dorsal hypural plates, corresponding to hypurals 4 + 5 and 3, respectively; single ventral hypural plate corresponding to hypurals 1 and 2 and parhypural.

*Latero-sensory system*

Supraorbital sensory canal continuous, connected to infraorbital sensory canal posteriorly. Supraorbital sensory canal with 3 pores: s1, adjacent to medial margin of anterior nostril; s3, adjacent to medial margin of posterior nostril; and s6, on middle part of dorsal surface of head, in transverse line just posterior to orbit; pore s6 nearer orbit than its paired homologous pore, near its paired homologous pore than orbit in larger specimens, above about 60 mm SL or more. Infraorbital sensory canal arranged in 2 segments, each with two pores; anterior segment with pore i1, in transverse line through anterior nostril, and pore i3, in transverse line just anterior to posterior nostril; posterior segment with pore i10, adjacent to ventral margin of orbit, and pore i11, posterior to orbit. Postorbital canal with 2 pores: po1, in vertical line above posterior portion of interopercular patch of odontodes, and po2, in vertical line above posterior portion of opercular patch of odontodes. Lateral line of body short, with 2 pores, posterior-most pore in vertical just posterior to pectoral-fin base.

*Mesethmoidal region (Fig. 11K)*

Mesethmoid robust, its anterior margin about straight; mesethmoid cornu narrow, extremity rounded; narrow lateral flap on intersection between cornu and main bone axis, posteriorly extending parallel to lateral bone margin. Minute lateral projection on lateral ethmoid margin close to middle portion of sesamoid supraorbital. Antorbital thin, posteriorly supporting anterior infraorbital canal; sesamoid supraorbital flat, slender anteriorly, widening posteriorly, its length about twice or slightly less antorbital length, with pronounced lateral process postero-laterally directed. Premaxilla sub-trapezoidal in dorsal view, longer than maxilla. Maxilla boomerang-shaped, slender, slightly curved. Autopalatine sub-rectangular in dorsal view, robust, about so wide as long when excluding posterolateral process, medial margin straight to slightly concave, lateral margin nearly straight to slightly curved near posterolateral process; autopalatine posterolateral process subtriangular in dorsal view, with sharp extremity, short, its length shorter than osseous portion of autopalatine length excluding posterolateral process.

*Cheek region (Fig. 12J)*

Metapterygoid thin, subtriangular, large, its largest length slightly longer than horizontal length of quadrate excluding dorsal process; short process just anterior to articulatory cartilaginous block. Quadrate slender, dorsal process with constricted base, dorsoposterior margin in contact with from hyomandibula outgrowth. Hyomandibula long, with well-developed anterior outgrowth; middle portion of dorsal margin of hyomandibula slightly concave. Opercle relatively slender, with deep transverse constriction just anterior to opercular odontode patch; opercular odontode patch depth about three fifths of dorsal hyomandibula articular facet, with 15 or 16 odontodes; odontodes pointed, straight to slightly curved, arranged in irregular transverse rows; dorsal process of opercle short and truncate; opercular articular facet for hyomandibula with small, rounded flap, articular facet for preopercle indistinct. Interopercle moderate, about two thirds hyomandibula length, anterior margin slightly concave; interopercular odontode patch with 18-20 pointed odontodes, arranged in irregular longitudinal rows. Preopercle compact, with short ventral flap.

*Parurohyal (Fig. 13J)*

Robust, lateral process sub-triangular, posterior margin slightly sinuous, latero-posteriorly directed, extremity slightly pointed; parurohyal head well-developed, with prominent anterolateral paired process; middle foramen small, round; posterior process relatively long, about six tenths of distance between anterior margin of parurohyal and anterior insertion of lateral process.

*Colouration in alcohol (Fig. 10)*

Flank, dorsum and head side pale yellowish grey, with rounded dark brown spots; spots larger than interopercular patch of odontodes, arranged in three longitudinal series

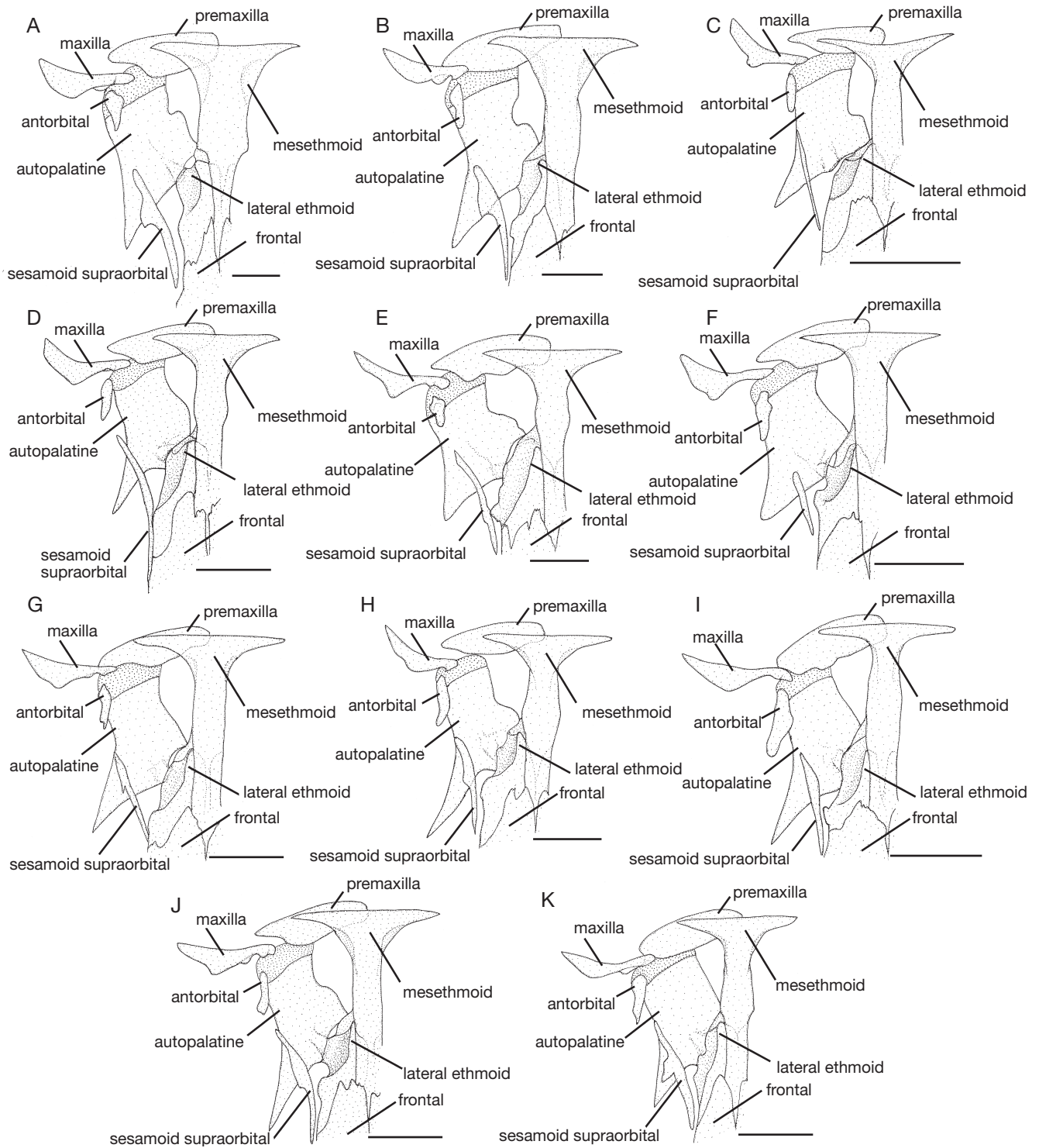


FIG. 11. — Mesethmoidal region and adjacent structures, left and middle portions, dorsal view: **A**, *Cambeva diffusa* n. sp.; **B**, *Cambeva pericoh* n. sp.; **C**, *Cambeva imaruy* n. sp.; **D**, *Cambeva orbitofrontalis* n. sp.; **E**, *Cambeva panthera* n. sp.; **F**, *Cambeva grisea* n. sp.; **G**, *Cambeva duplimaculata* n. sp.; **H**, *Cambeva longipalata* n. sp.; **I**, *Cambeva notabilis* n. sp.; **J**, *Cambeva tropeira*; **K**, *Cambeva urubici* n. sp. Larger stippling represents cartilaginous areas.

on flank; spots of two dorsal-most rows longitudinally coalesced with neighbouring spots in specimens about 50 mm SL or larger, forming stripe on longitudinal mid-lateral line of flank. Venter and ventral part of flank greyish

white. Barbels dark grey. Fins pale grey. Smaller juvenile specimens, 23 mm SL or less, with homogeneous brownish grey flank; faint spots in juvenile specimens 25 mm SL or slightly larger.



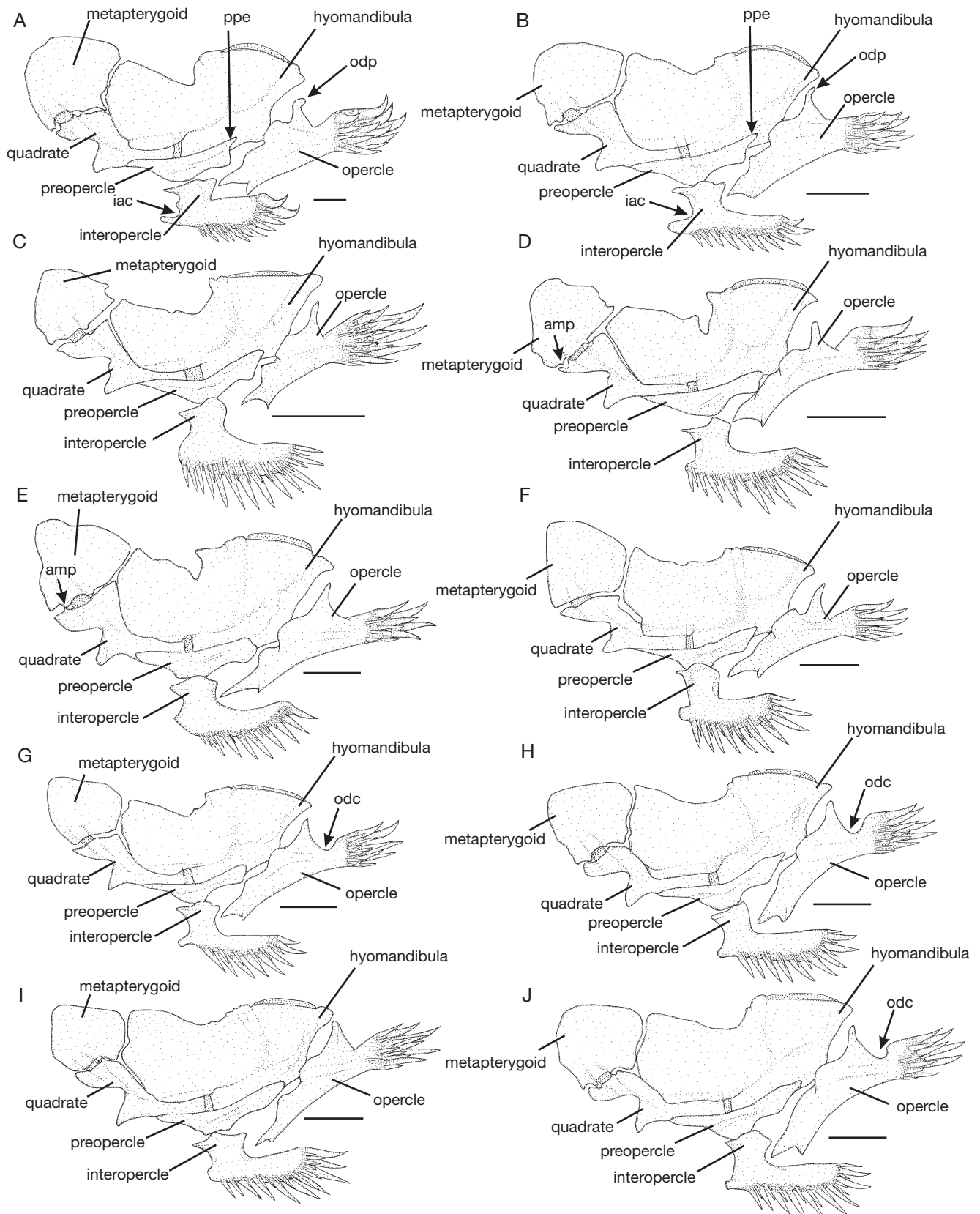


FIG. 12. — Left suspensorium and opercular series, lateral view: **A**, *Cambeva diffusa* n. sp.; **B**, *Cambeva pericoh* n. sp.; **C**, *Cambeva imaruhy* n. sp.; **D**, *Cambeva orbitofrontalis* n. sp.; **E**, *Cambeva panthera* n. sp.; **F**, *Cambeva grisea* n. sp.; **G**, *Cambeva duplimaculata* n. sp.; **H**, *Cambeva longipalata* n. sp.; **I**, *Cambeva notabilis* n. sp.; **J**, *Cambeva urubici* n. sp. Abbreviations of structures indicated by arrows are: **iac**, interopercular anterior concavity; **ppe**, preopercular postero-dorsal expansion; **odc**, opercular dorsal constriction; **odp**, opercular dorsal process; **ppp**, parurohyal posterior process. Larger stippling represents cartilaginous areas.

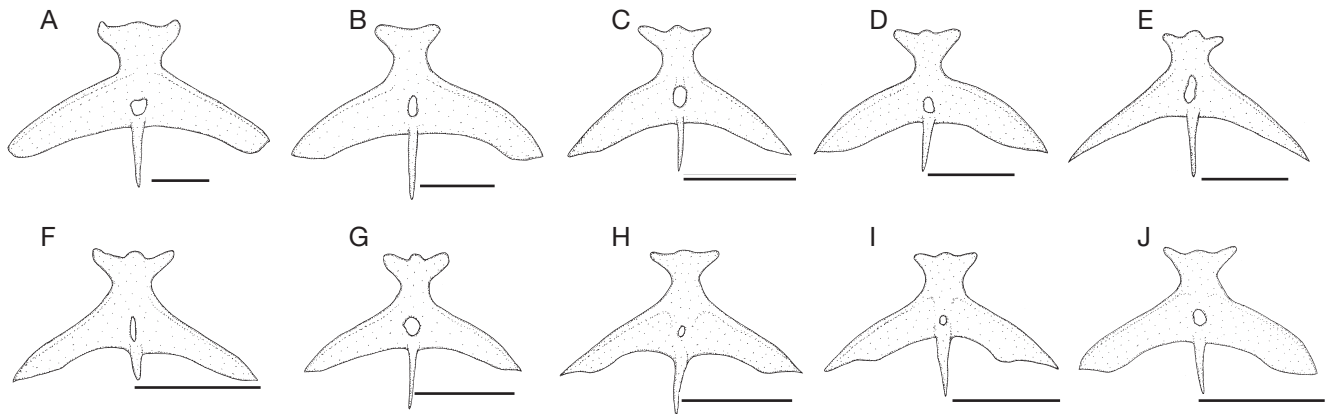


FIG. 13. — Urohyal, ventral view. **A**, *Cambeva diffusa* n. sp.; **B**, *Cambeva pericoh* n. sp.; **C**, *Cambeva imaruhy* n. sp.; **D**, *Cambeva orbitofrontalis* n. sp.; **E**, *Cambeva panthera* n. sp.; **F**, *Cambeva grisea* n. sp.; **G**, *Cambeva duplimaculata* n. sp.; **H**, *Cambeva longipalata* n. sp.; **I**, *Cambeva notabilis* n. sp.; **J**, *Cambeva urubici* n. sp.

## DISCUSSION

### DISTRIBUTION PATTERNS

According to our data, all the five new species reported to occur in the western open plateau of SESG, *C. diffusa* n. sp., *C. duplimaculata* n. sp., *C. longipalata* n. sp., *C. pericoh* n. sp., and *C. urubici* n. sp., are confined to small areas in altitudes above 900 m asl, thus contrasting with three of the five species occurring in the eastern forested plateau, *C. grisea* n. sp., *C. imaruhy* n. sp., and *C. orbitofrontalis* n. sp., which occupy larger areas in lower altitudes, between 125 and 500 m asl. This result is similar to that found by Ferrer & Malabarba (2011) when describing *C. tropeira* from a small area of the upper Rio das Antas drainages, Lagoa dos Patos system, in the western open plateau of southern Serra Geral, which was only found above 1000 m asl. However, the occurrence in small high-altitude areas of the SESG western open plateau is not restrict to trichomycterines. For example, the loricariids *Eurycheilichthys pantherinus* (Reis & Schaefer, 1992) and *Paraeiorhaphis vestigipinnis* (Pereira & Reis, 1992) are only found in small areas of the upper Rio Uruguai basin in altitudes above 1000 m asl (Pereira & Reis 1992; Reis & Schaefer 1992).

It is possible that some species complexes, as herein delimited, are adapted to live in specific altitudinal zones. For example, the four species of the *C. tropeira* complex sharing a derived distinctive constriction on the dorsal margin of the opercle (Figs 12G, H, J), *C. duplimaculata* n. sp., *C. longipalata* n. sp., *C. tropeira*, and *C. urubici* n. sp., were found in altitudes between 905 and 1325 m, suggesting that species of this putative clade are only found in higher altitudes. On the other hand, *C. grisea* n. sp. is here reported to occur between 155 and 300 m asl, whereas the closely related *C. brachykechenos* was reported to occur between 110 and 265 m asl (Ferrer & Malabarba 2013), suggesting that members of this peculiar group diagnosed by the unique morphology of the cranial roof (see results above), are only found in lower altitudes. However, phylogenetic analyses involving larger samples of species of *Cambeva* are still necessary to test this hypothesis.

### SPECIES DIVERSITY

The high concentration of species still unknown by scientists in a relatively small area of the Serra Geral, as herein firstly reported, is mainly a result of our still incomplete knowledge on the Neotropical mountain biota. This is particularly reinforced considering that the organisms herein reported are member of a group of small vertebrates that have been studied since the nineteenth century (e.g. Costa *et al.* 2020c). Furthermore, this high concentration of species cannot be interpreted as a local isolated phenomenon, but a widespread evolutionary process possibly associated to mountain building (e.g. Antonelli *et al.* 2018), also occurring in trichomycterines inhabiting other South American highlands. For example, seven different species of *Cambeva* have been reported for a small area of the Rio Jordão, which drains the northern portion of the Serra Geral in the middle Rio Iguaçu basin, southern Brazil (Wosiacki & Garavello 2004; Wosiacki & de Pinna 2008a, b) and at least 12 trichomycterine species have been recorded for a small area of the Río Magdalena in the Departamento de Santander, north-eastern Colombian Andes (Castellanos-Morales *et al.* 2011), but our knowledge on these species is mainly limited to brief taxonomical notes, not allowing more detailed comparisons.

The area encompassing the rivers draining the Maciço de Itatiaia nucleus of the Serra da Mantiqueira in south-eastern Brazil (hereafter MIN), a high massif with peaks reaching about 2900 m asl, is presently the best studied region for trichomycterine taxonomy and distribution in eastern South America (A. Miranda Ribeiro 1906; P. Miranda Ribeiro 1949; Costa 1992; Barbosa & Costa 2008, 2010; Costa *et al.* 2020a, c, 2021a), thus providing a fine comparative basis for our preliminary data on SESG. Field inventories have been concentrated in an area about 440 km<sup>2</sup>, where a total of eleven species of the genus *Trichomycterus* Valenciennes, 1832 have been recorded: two endemic to the headwaters of the Rio Grande, Rio Paraná basin, four to the upper Rio Preto drainage, middle Rio Paraíba do Sul basin, four to small neighbouring tributaries of the upper Rio Paraíba do



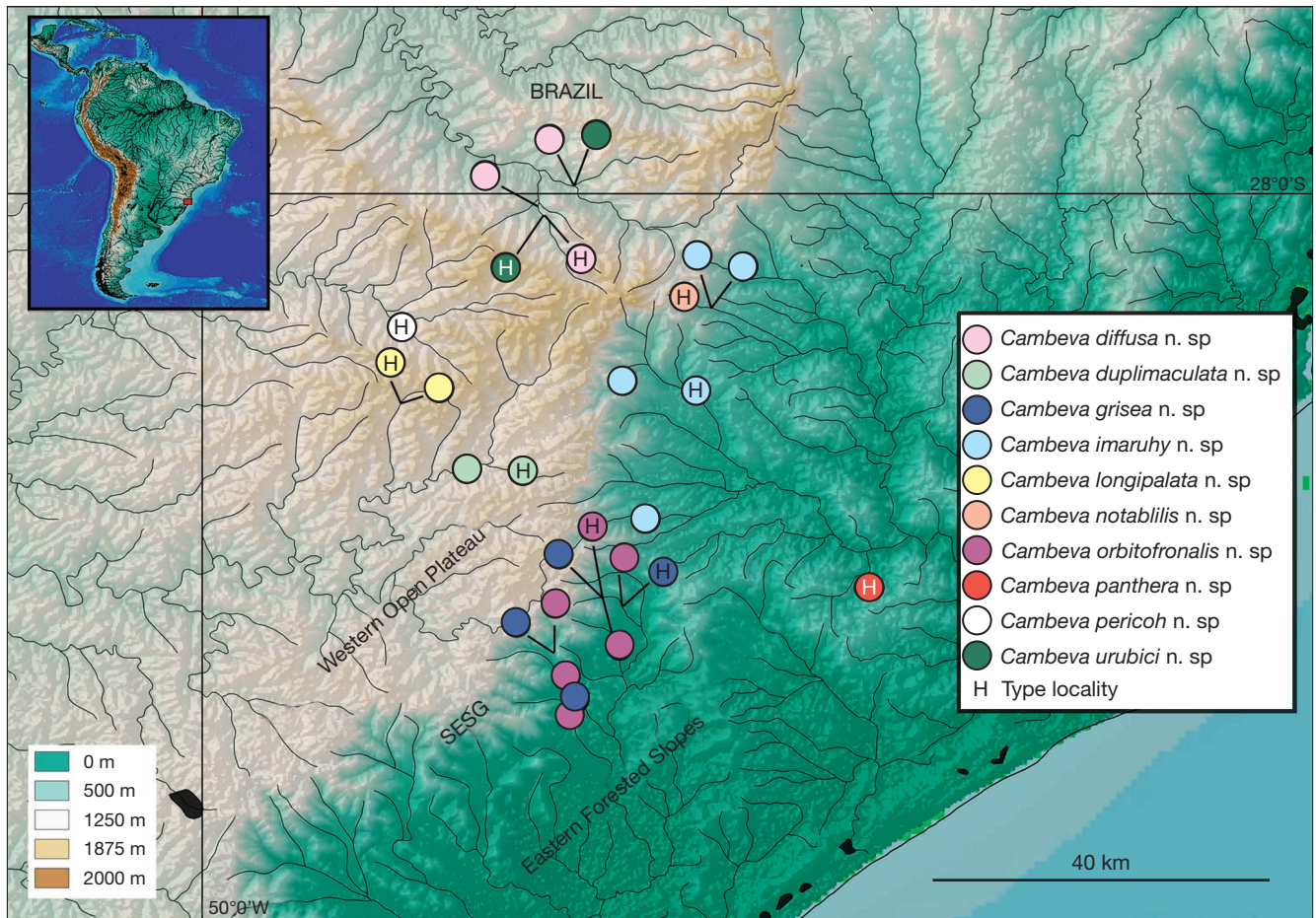


FIG. 14. — Map of geographical distribution of *Cambeva* Katz, Barbosa, Mattos & Costa, 2018 in the southeastern nucleus of the Serra Geral (SESG), southern Brazil.

Sul, besides one species widespread in the Rio Paraíba do Sul basin (Costa 1992; Barbosa & Costa 2008, 2010; Costa *et al.* 2020a, c). Therefore, the MIN studied area is about six times smaller than the SESG studied area (about 2800 km<sup>2</sup>), whereas the number of species is approximately the same (10 in SESG, vs 11 in MIN).

The occurrence of 11 species in an area of MIN that is significantly smaller than the SESG area here analysed may indicate a greater species concentration in MIN. However, trichomycterines in these areas greatly differ in two main aspects. Firstly, the maximum number of species found to be sympatric in SESG was two: *C. diffusa* n. sp. and *C. urubici* n. sp. in the upper Rio Uruguai basin, and *C. grisea* n. sp. and *C. orbitofronalis* n. sp. in the Rio Araranguá basin, whereas four or five species are often sympatric in MIN, for example: *T. albinotatus* Costa, 1992, *T. auroguttatus* Costa, 1992, *T. immaculatus* (Eigenmann & Eigenmann, 1889), *T. mirissumba* Costa, 1992, and *T. quintus* Costa, 2020 in the upper Rio Preto drainage, middle Rio Paraíba do Sul basin (Costa 1992; Costa *et al.* 2020a, c); and *T. immaculatus*, *T. itatiayae* Miranda Ribeiro 1906, *T. nigroauratus* Barbosa & Costa, 2008, *T. mariamole* Barbosa & Costa, 2010, and *T. travassosi* Miranda Ribeiro 1949, in the Rio Alambari drainage, upper Rio Paraíba do Sul basin (P. Miranda Ribeiro 1949; Barbosa &

Costa 2008, 2010). Secondly, no evidence was found about ecological divergent specializations among sympatric species in SESG, but in MIN, high levels of divergence have been recorded (Costa 1992; Costa *et al.* 2020a, c). For example, in SESG, sympatric species were found exactly at the same place (Feltrin, pers. obs.), whereas during daylight collections in the upper Rio Preto drainage, *T. albinotatus* was found actively swimming above gravel substratum, *T. auroguttatus* was found swimming close or buried in sandy substratum, *T. immaculatus* was found below large rocks in the middle of rivers, *T. mirissumba* was found deeply buried in riverbanks, and *T. quintus* was only found buried in leaf litter deposits on the middle part of rivers (Costa 1992; Costa *et al.* 2020a, c).

Differences found in number of sympatric species and their ecological specializations may be explained by different estimated ages for the groups occurring in these areas. According to Ochoa *et al.* (2017), the estimated age for initial diversification of *Cambeva* is about 12 mya, whereas diversification in *Trichomycterus* is estimated to start at about 18 mya, that is considerably older. In fact, still according to Ochoa *et al.* (2017), some different lineages of *Trichomycterus* with representatives in MIN have their estimated origin between about 13 and 18 mya, thus older than the whole *Cambeva* clade. In fact, some intrageneric lineages of *Trichomycterus*



seems to be as old as the whole genus *Cambeva*. For example, the lineage that includes the *T. brasiliensis* species group and some closely related species (Barbosa & Costa 2010; Vilar do et al. 2020), and represented in MIN by four species (Costa 1992; Barbosa & Costa 2010), has an estimated origin at about 12.5 mya (Ochoa et al. 2017). However, further time-calibrated phylogenetic analyses are needed to infer the specific age of taxa inhabiting these regions.

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