

Article

A Riverine Species Flock? A Remarkably High Diversity of Endemic Fossorial Catfishes, Genus *Cambeva* (Siluriformes: Trichomycteridae), in a Small Mountain Drainage of Southern Brazil

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Abstract

A field inventory in the Rio Chapecó drainage, southern Brazil, about 11,120 km², revealed an unexpected diversity of endemic small fossorial catfishes, genus *Cambeva*, comprising 2 species recently described and 11 undescribed. They were found in different habitats, including sediment types and altitudes, and exhibited great morphological diversity, suggesting them to be a species flock. The objectives of this study were to analyse criteria (monophyly, endemism, species richness, ecomorphological diversity) used to recognise species flocks and to describe the new species, which were diagnosed using external morphology and osteological characters. The phylogenetic analyses using *COI*, *CYTb* and *RAG2* (2305 bp) for 64 species of *Cambeva* and 4 outgroups did not support that species assemblage as a single monophyletic group but supported a clade with 3 species, the *C. alphabelardense* clade, and a clade with 10 species, the *C. betabelardense* clade. The latter clade was recognised as a putative species flock based on those criteria. A time-calibrated analysis indicated the origin and diversification of both clades during the Miocene, a time-frame coinciding with the emergence and persistence of the Paranean Sea, which may have isolated adjacent river drainages, favouring the high species diversification of *Cambeva*, besides diversification of the *Crenicichla missioneira* complex from the same region.

Keywords: Araucaria forest plateau; mountain biodiversity; Paranean Sea; Rio Chapecó drainage; Rio Uruguai basin; Serra Geral



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1. Introduction

Mountains and high plateaus of tropical and subtropical regions are known to harbour a great diversity of endemic species [1], often receiving the status of biodiversity hotspots [2]. Most studies delineating mountain biodiversity hotspots rely on data regarding terrestrial organisms, for example the violets from the Eastern Arc Mountains of Africa [3] and the Canela-de-Ema from the Brazilian Campos Rupestres of the Serra do Espinhaço [4]. On the other hand, some classic comparative biology studies have focused on highly diverse groups of teleost fishes occurring in highland areas, such as the poeciliids of the Guatemalan highland basins, a landmark in biogeography and species delimitation [5], and the cichlids of the Great Lakes on the East African plateau, a milestone in studies of adaptive radiation and evolution of species flocks [6–8]. However, the study of teleost

fish diversity in certain mountainous regions has been largely neglected for decades, as evidenced by recent research on trichomycterine catfishes, a group exhibiting high species diversity in South American mountain rivers and lakes [9,10]. This is the case of the basins draining the mountains and plateaus of eastern South America, where recent studies across various areas have consistently revealed a wide diversity of previously undescribed species belonging to the genus *Cambeva* Katz, Barbosa, Mattos & Costa, 2018 [10].

With an area of approximately 11,120 km² and the main river course measuring about 250 km, the Rio Chapecó drainage (hereafter RCD) is the largest tributary of the Rio Uruguai, one of the major watercourses in southern Brazil. This drainage system, ranging from headwaters at approximately 1320 m asl to its lowest point at approximately 225 m asl, is situated across the plateau and mountainous areas of the Serra do Espigão, part of the extensive Serra Geral of southern Brazil, in the Araucaria Forest Plateau. Much of RCD consists of fast-flowing rivers and streams, the typical habitat of trichomycterine catfishes. However, the first record of this fish group in RCD occurred only in 2022 with the descriptions of *Cambeva alphabelardense* Costa, Feltrin & Katz, 2022 and *Cambeva betabelardense* Costa, Feltrin & Katz, 2022 [11], immediately followed by the description of a third species, *Cambeva gamabelardense* Costa, Feltrin & Katz 2022 [12]. All these three species belong to the *Cambeva* beta clade, a diverse group widely distributed across southern Brazilian basins [10].

Cambeva alphabelardense and *C. betabelardense* are small species, reaching between about 45 and 60 mm of standard length (SL), and exhibit unusual morphology, including the eye situated close to the posterior nostril, a characteristic typical of species with fossorial habits, such as those belonging to the subgenus *Cryptocambeva* Costa, 2021 of the genus *Trichomycterus* Valenciennes, 1832 and *Ituglanis* Costa & Bockmann, 1993 (e.g., [13,14]), besides species of the *Cambeva taroba* clade. Concordantly, *Cambeva alphabelardense* was found buried in vegetal debris and *C. betabelardense* in gravel bottom associated with vegetal remnants [11]. Additionally, *C. alphabelardense* and *C. betabelardense* also share some characteristics that are rare among southeastern South American trichomycterines, such as a broad and short autopalatine with small or rudimentary postero-lateral process, which is also found in species of other trichomycterid groups with fossorial habits [15].

During a recent detailed ichthyofaunal survey of all the river basins from the highlands of southern Brazil conducted by one of us (CRMF), comprising 66 collecting trips, each during three to eight days between January 2022 and June 2026, an unexpected diversity of undescribed species of *Cambeva* was found in RCD. Eleven of these new species were small-sized and shared specialised morphological characteristics typical of fossorial species occurring in *C. alphabelardense* and *C. betabelardense*, suggesting that all these species form a monophyletic group. The new species were found in different types of fossorial habitats, making some species rare and geographically restricted to places with those habitats. In addition, the species exhibited striking divergent morphological structures, including bones associated with the upper jaw and the anterior portion of the jaw suspensorium. Field collections in all neighbouring drainages did not reveal other species sharing these characteristics.

The presence of a high concentration of supposed closely related species occurring in sympatry or parapatry of the same well-delimited confined aquatic system and exhibiting considerable diversification in feeding-related morphological characters and subtle habitat preferences suggest the existence of species flocks. Although there are inaccuracies in the definition of the species flock concept [16,17], some authors have proposed criteria to recognise species flocks, among which are monophyly, endemism, species richness and morphological and ecological diversity [16–19]. The objectives of the present study are to test monophyly of fossorial *Cambeva* from RCD and possible close relationships with the

Cambeva taroba clade through a molecular phylogenetic analysis using a comprehensive intrageneric species sample; to estimate the time of origin and species diversification of lineages endemic to RCD through a time-calibrated phylogenetic analysis; to describe the new fossorial species; and to evaluate the existence of a *Cambeva* species flock based on criteria used to recognise species flocks.

2. Materials and Methods

2.1. Specimens and Morphological Data

Methods used in field collections are the same described in all our recent studies on trichomycterids (e.g., [20], using collecting permits given by ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade; permit number: 38553-13) in accordance with methods approved by CEUA-CCS-UFRJ (Ethics Committee for Animal Use of Federal University of Rio de Janeiro; permit number: 084/23). Methods for morphological studies and morphological terminology followed Costa [10]. Most material used in this study, including type series of new species, was deposited in the fish collection of the Instituto de Biologia, Universidade Federal do Rio de Janeiro (UFRJ), whereas some additional paratypes, when available, were deposited in the Centro de Ciências Agrárias e Ambientais, Universidade Federal do Maranhão (CICCAA). In list of specimens, the abbreviation C&S indicates cleared and stained specimens for osteological observation and DNA indicates specimens fixed and preserved in absolute ethanol for molecular analyses; geographical names correspond to Portuguese names used in the region. Species description texts follow the same standard used in our previous trichomycterine taxonomic studies to make possible direct comparison. Comparative morphological analyses and descriptions focused on characters taken from both the external morphology and osseous structures commonly used to diagnose trichomycterine taxa. Comparative material is listed in Costa [10]. Species were delimited using a diagnosability criterion [21,22], following a hierarchical order of monophyletic groups established in the resulting molecular phylogenetic tree.

2.2. DNA Extraction, Amplification and Sequencing

DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) was used for DNA purification of muscle tissue from the right side of the caudal peduncle, according to the manufacturer instructions. DNA extract quality was visually evaluated by agarose gel electrophoresis. The sampled loci included two mitochondrial and one nuclear genes, which were amplified by polymerase chain reactions (PCR) using the primers Cox1F [23] and H7271 [24] for *cytochrome c oxidase subunit 1* (COI); Gludg-L and CB3-H [25] for *cytochrome b* (CYTB); and RAG2 TRICHO F and RAG2 TRICHO R [26] for *recombination activating protein 2* (RAG2). The reactions were performed in 50 µL reaction mixtures containing 5× Green GoTaq Reaction Buffer (Promega, Madison, WI, USA), 3.2 mM MgCl₂, 1 µM of each primer, 75 ng of total genomic DNA, 0.2 mM of each dNTP and 1 U of Taq polymerase. The thermocycling profile was (1) 1 cycle of 4 min at 94 °C; (2) 35 cycles of 1 min at 92 °C, 1 min at 50–64 °C and 1 min and 30 s at 72 °C; and (3) 1 cycle of 4 min at 72 °C. Negative controls without DNA were used to check contamination in all PCR reactions. The purification of the amplified PCR products was performed using the Wizard SV Gel and PCR Clean-Up System (Promega). The BigDye Terminator Cycle Sequencing Mix (Applied Biosystems, Foster City, CA, USA) was used for the sequencing reactions. Cycle sequencing reactions were performed in 10 µL reaction volumes containing 1 µL BigDye 2.5, 1.55 µL 5× sequencing buffer (Applied Biosystems), 2 µL of the amplified products (10–40 ng) and 2 µL primer. The thermocycling profile was (1) 35 cycles of 10 s at 96 °C, 5 s at 54 °C and 4 min at 60 °C. The sequencing reactions were purified and denatured and the samples were analysed on an ABI 3130 Genetic Analyzer. Sequence edition was performed in MEGA 12 [27], where

forward and reverse reads were assembled into consensus sequences. Low-quality regions at the ends of chromatograms were removed based on visual inspection. To check the quality of the sequences and the absence of premature stop codons or indels, all the DNA sequences were translated into amino acids residues in MEGA 12. The list with the sampled species and the GenBank accession numbers of the DNA sequences used in the current analyses are presented in Appendix A.

2.3. Phylogenetic Analyses

The concatenated molecular dataset comprised 2305 bp (COI 723 bp, CYTB 787 bp, RAG2 795 bp). Sequence alignments were performed separately for each gene in MEGA 12 using the ClustalW algorithm [28]. Few indels were observed only in the RAG2 alignment, and alignment gaps were treated as missing data in all analyses. Substitution saturation was assessed using Xia's index (Iss) implemented in DAMBE v7 [29]. Alignment statistics and substitution saturation for each gene were provided in Appendix B. The concatenated dataset was initially partitioned by gene and codon position, and the optimal partitioning scheme and best-fitting nucleotide substitution models were subsequently determined in IQ-TREE v2.4.0 [30], using ModelFinder [31] with partition merging enabled. Model selection was based on the corrected Akaike Information Criterion (AICc [32]). The optimal partitioning scheme and substitution models are presented in Appendix C. Phylogenetic relationships were inferred using both Bayesian Inference (BI) and Maximum Likelihood (ML). BI was conducted using BEAST v1.10.4 [33] under a Yule speciation prior for tree reconstruction [34]. Two independent Markov chain Monte Carlo (MCMC) analyses were run with 100 million generations and sampling every 10,000. Convergence of the MCMC runs and effective sample size (ESS) values were assessed in Tracer v1.7.1 [35], and all estimated parameters achieved ESS values >200. The independent runs were combined in LogCombiner v1.10.4 [33] after discarding the first 10% of samples from each run as burn-in. A maximum clade credibility (MCC) tree with posterior probabilities was generated in TreeAnnotator v1.10.4 [33]. ML was conducted in IQ-TREE v2.4.0 [30]. Branch support was assessed using the SH-like approximate likelihood ratio test (SH-aLRT [36]) and ultrafast bootstrap [37], each with 1000 replicates. ML trees for each gene were inferred to assess topological congruence among molecular markers (Appendices D–F). Terminal ingroup taxa comprised 64 species of *Cambeva*, including all species from RCD and congeners representing all intrageneric lineages. Outgroup taxa comprised representatives of closely related genera within the TL clade [10].

2.4. Divergence-Time Estimation

The same dataset, partitioning scheme, substitution models, tree prior, MCMC settings, and burn-in strategy described above were used for the divergence time analysis conducted in BEAST v1.10.4. Phylogenetic topology and divergence times were estimated simultaneously under an uncorrelated lognormal relaxed clock model, with unlinked relaxed clocks assigned to the mitochondrial and nuclear partitions. Two calibration points were established as follows: a secondary calibration point applied to the Trichomycteridae crown following Betancur-R et al. [38] assigned a normal prior distribution with a mean of 106.0 Ma and standard deviation (SD) of 1.2; and a fossil calibration point applied to the stem age of genus *Hoplisoma* within Callichthyidae, based on the oldest known fossil assigned to *Hoplisoma* Swainson, 1838 [39], *Hoplisoma revelatus* (Cockerell, 1925) from the Late Paleocene of the Maíz Gordo Formation in Salta, Argentina, about 58 Ma. This prior was modeled using a lognormal prior with the fossil age as a hard minimum bound, as fossils indicate minimum ages but generally do not provide reliable maximum age constraints for the lineage (mean = 0.8, SD = 0.6, Offset = 58.0 Ma). To represent the diversification of

Callichthyidae associated with the fossil calibration, *Hoplisoma panda* (Nijssen & Isbrücker, 1971), *Hoplisoma nattereri* (Steindachner, 1876), *Corydoras stenocephalus* Eigenmann & Allen, 1942, and *Callichthys callichthys* Linnaeus, 1758 were included in the dataset. Other siluriform taxa representing deeper phylogenetic divergences were also included to improve the temporal framework for divergence-time estimation: *Diplomystes nahuelbutaensis* Arratia, 1987, *Nematogenys inermis* (Guichenot, 1848), *Trichogenes longipinnis* Britski & Ortega, 1983, *Microcambeva ribeirae* Costa, Lima & Bizerril, 2004, and *Eremophilus mutisii* Humboldt, 1805. Posterior median age of lineage origin, 95% HPD intervals, and posterior probabilities for the main recovered clades were summarized in Appendix G and Appendix H, respectively.

3. Results

3.1. Phylogenetic Relationships

The phylogenetic analyses generated similar topologies, where the fossorial taxa endemic to RCD are supported as members of the diverse *Cambeva* beta clade, but together do not form a monophyletic group (Figure 1). They comprise two well supported clades, the first one containing *C. alphabelardense* and two new species (hereafter the *C. alphabelardense* clade, CAC) and the second one comprising *C. betabelardense* and nine new species (hereafter the *C. betabelardense* clade, CBC). CBC includes two subclades, the *Cambeva betabelardense* subclade 1 (CBS1) and the *Cambeva betabelardense* subclade 2 (CBS2). The time-calibrated analyses indicated the origin and diversification of both CAC and CBC during the Miocene (Figure 2).

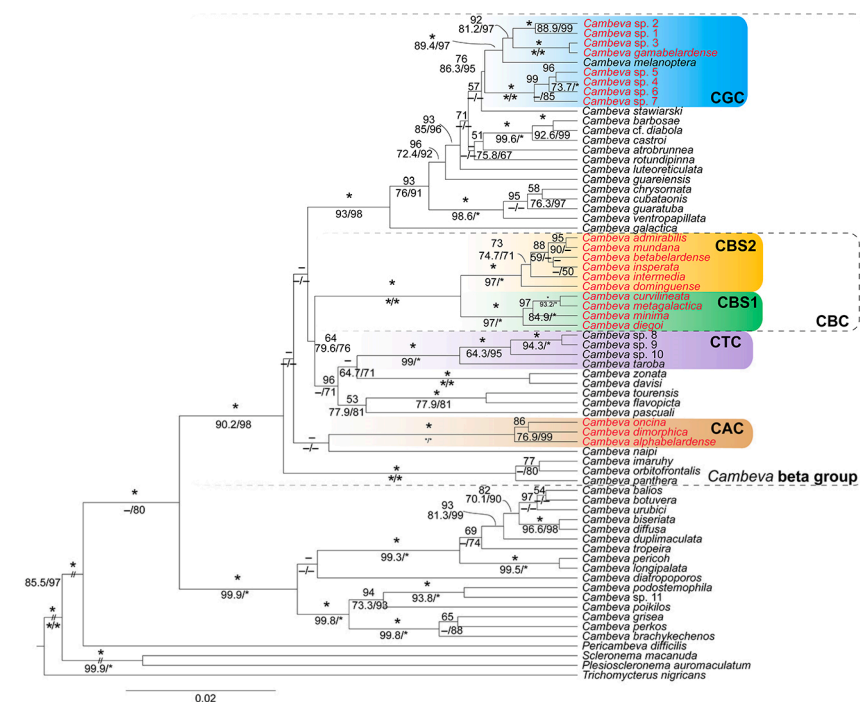


Figure 1. Bayesian inference phylogenetic tree inferred in BEAST v1.10.4 from a concatenated molecular dataset comprising *COI*, *CYTb*, and *RAG2* sequences (2305 bp) for 64 species of *Cambeva*, and 4 outgroup species representing closely related genera within the *Trichomycterus* clade. Numbers above branches indicate Bayesian posterior probabilities. Numbers below branches, separated by slashes (/), indicate ultrafast bootstrap (UFBoot) and SH-like approximate likelihood ratio test (SH-aLRT) support values, respectively. Asterisks (*) indicate maximum support values, and dashes (–) indicate support values below 50. CAC, *Cambeva alphabelardense* clade; CBC, *Cambeva betabelardense* clade; CBS1, *Cambeva betabelardense* subclade 1; CBS2, *Cambeva betabelardense* subclade 2; CGC, *Cambeva gamabelardense* clade; CTC, *Cambeva taroba* clade. Species names written in red are species endemic to the Rio Chapecó drainage.

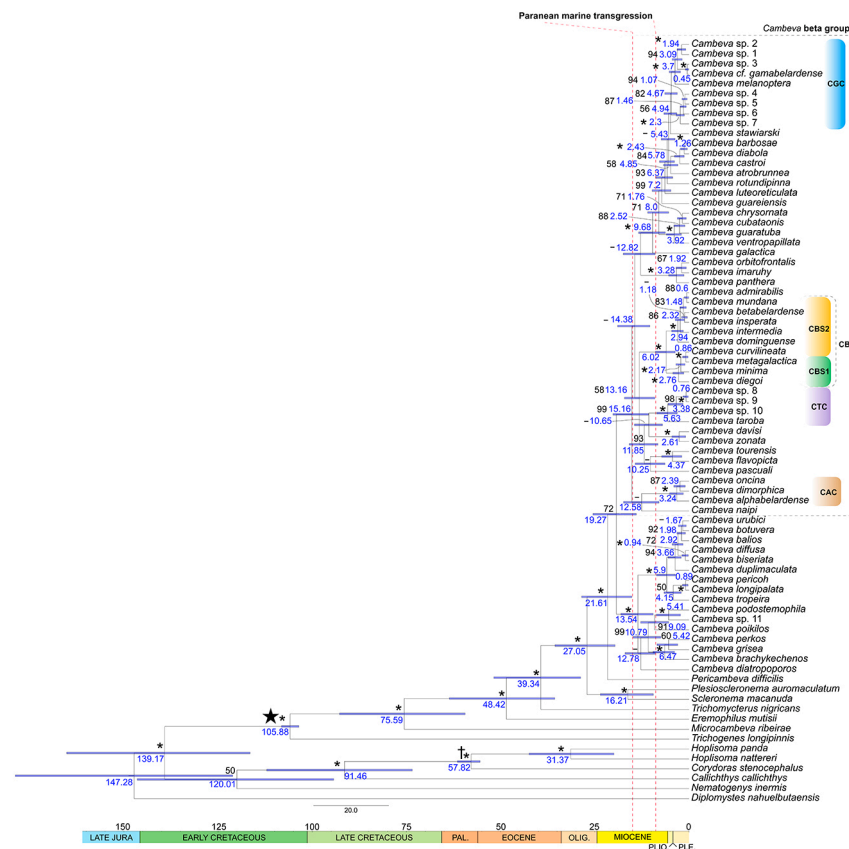


Figure 2. Time-calibrated phylogenetic tree inferred in BEAST v1.10.4. Numbers and symbols in black above branches indicate Bayesian posterior probabilities (asterisks (*) indicate maximum support values, and dashes (-) indicate support values below 50). Numbers in blue indicate estimated node ages (Ma), and blue bars represent the 95% highest posterior density (HPD) intervals. Black star indicates the Trichomycteridae calibration point, black cross indicates the *Hoplisoma* fossil calibration point. Red dashed lines indicate the approximate time interval of the Paranean Sea. CAC, *Cambeva alphabelardense* clade; CBC, *Cambeva betabelardense* clade; CBS1, *Cambeva betabelardense* subclade 1; CBS2, *Cambeva betabelardense* subclade 2; CGC, *Cambeva gamabelardense* clade; CTC, *Cambeva taroba* clade.

3.2. The *Cambeva alphabelardense* Clade (CAC)

Diagnosis. Species of CAC differ from other fossorial congeners endemic to RCD by the presence of a long nerve canal, positioned obliquely along the dorsal surface of the autopalatine (Figure 3A–C; vs. nerve canal when present restricted to the area adjacent to articulatory area for lateral ethmoid, Figure 3D–M). Species of CAC also differ from other taxa here analysed by having a narrow opercular odontode patch with six to nine odontodes (Figure 4A–C; vs. relatively broad opercular patch, with 11–14 odontodes in CBS2, Figure 5A–F); anterior infraorbital section always present and not attached to the lacrimal (vs. always absent in CBS2); and absence of a ligament between an antero-medial process on the sesamoid supraorbital and a prominent lateral process on the lateral ethmoid (Figure 3A–C; vs. presence, Figure 3D–G).

Included species. *Cambeva alphabelardense*, Costa, Feltrin & Katz 2022, *Cambeva dimorpha* sp. nov., and *Cambeva oncina* sp. nov.

Habitat. Headwaters of short brooks with diverse bottom sediment. The brooks are associated with the middle channel of the Rio Chapecó and with the upper section of the Rio Chapecozinho, which is the main tributary of the Rio Chapecó, in altitudes between about 800 and 1300 m asl.

Cambeva alphabelardense Costa, Feltrin & Katz, 2022.

urn:lsid:zoobank.org:act:13FDAD9A-CEDC-4027-A79D-FCC3E09CF166.

Figures 3A, 4A, 6A and 7.

Cambeva alphabelardense Costa, Feltrin & Katz [11]: 142 (original description; type locality: Brazil: Santa Catarina State: Abelardo Luz Municipality: stream tributary to middle Rio Chapecó, Rio Uruguai basin, 26°32'19" S, 52°25'17" W, 805 m asl; holotype: UFRJ 6990, 43.4 mm SL).

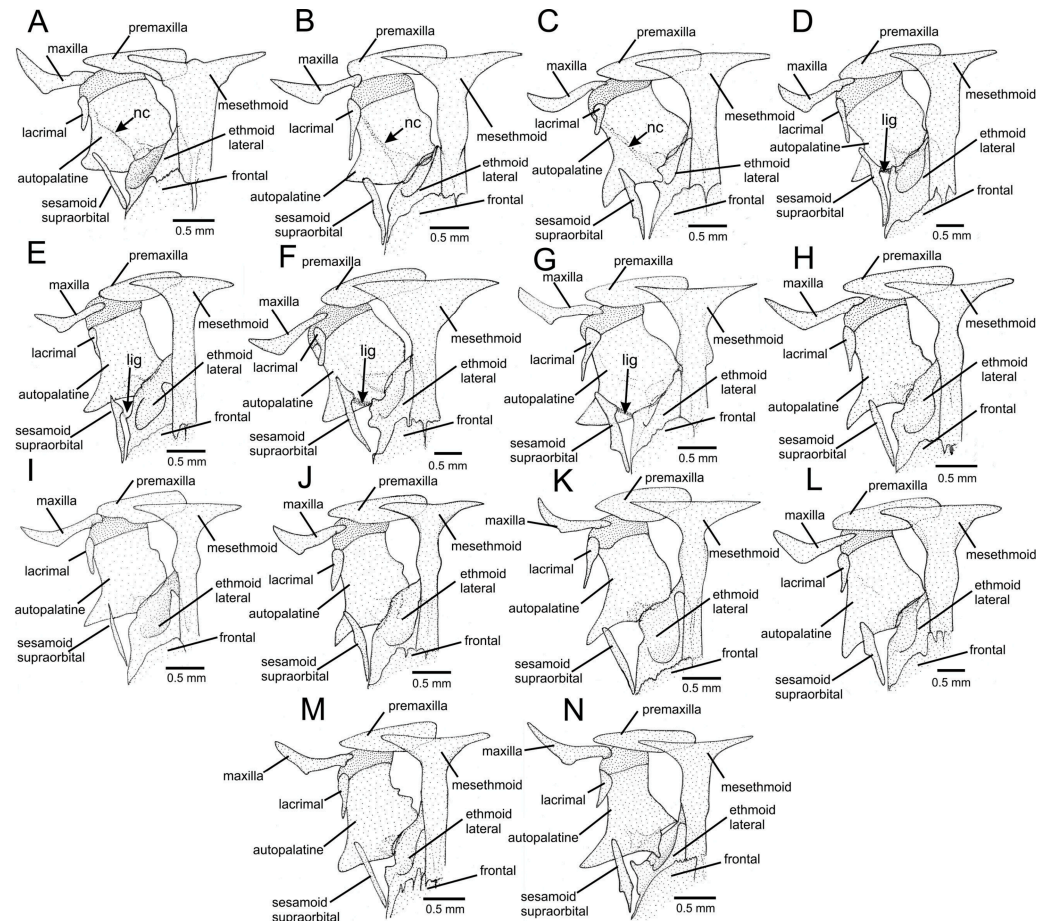


Figure 3. Mesethmoidal region, middle and left portions, dorsal view: (A) *Cambeva alphabelardense*; (B) *Cambeva dimorphica* sp. nov.; (C) *Cambeva oncina* sp. nov.; (D) *Cambeva curvilineata* sp. nov.; (E) *Cambeva diegoi* sp. nov.; (F) *Cambeva metagalactica* sp. nov.; (G) *Cambeva minima* sp. nov.; (H) *Cambeva admirabilis* sp. nov.; (I) *Cambeva betabelardense*; (J) *Cambeva dominguense* sp. nov.; (K) *Cambeva insperata* sp. nov.; (L) *Cambeva intermedia* sp. nov.; (M) *Cambeva mundana* sp. nov.; (N) *Cambeva taroba*. Larger stippling represents cartilage; lig, ligament connecting sesamoid supraorbital and lateral ethmoid; nc, nerve canal.

Diagnosis. *Cambeva alphabelardense* is distinguished from all other congeners by having four pelvic-fin rays (vs. five, when the pelvic fin is present). *Cambeva alphabelardense* also differs from other species of CAC by having 20 or 21 interopercular odontodes (vs. 28–33 in *C. dimorphica* sp. nov. and 24–26 in *C. oncina* sp. nov.); 20–23 premaxillary teeth (vs. 29–38); the dorsal-fin origin at a vertical posterior to the middle of the dorsal-fin base (vs. anterior in *C. dimorphica* sp. nov.); the pectoral-fin filament about 10–20% of the pectoral-fin length (vs. 5% or rudimentary in *C. oncina* sp. nov.); anterior portion of the mesethmoid relatively broad, cornua anterolaterally directed (Figure 3A; vs. anterior portion of the mesethmoid relatively narrow, cornua laterally directed, Figure 3B,C); metapterygoid subrectangular (Figure 4A; vs. subtriangular, Figure 4B,C); and a single colour pattern in adult specimens (two distinct colour patterns in *C. dimorphica* sp. nov.). For a full description, see [11].

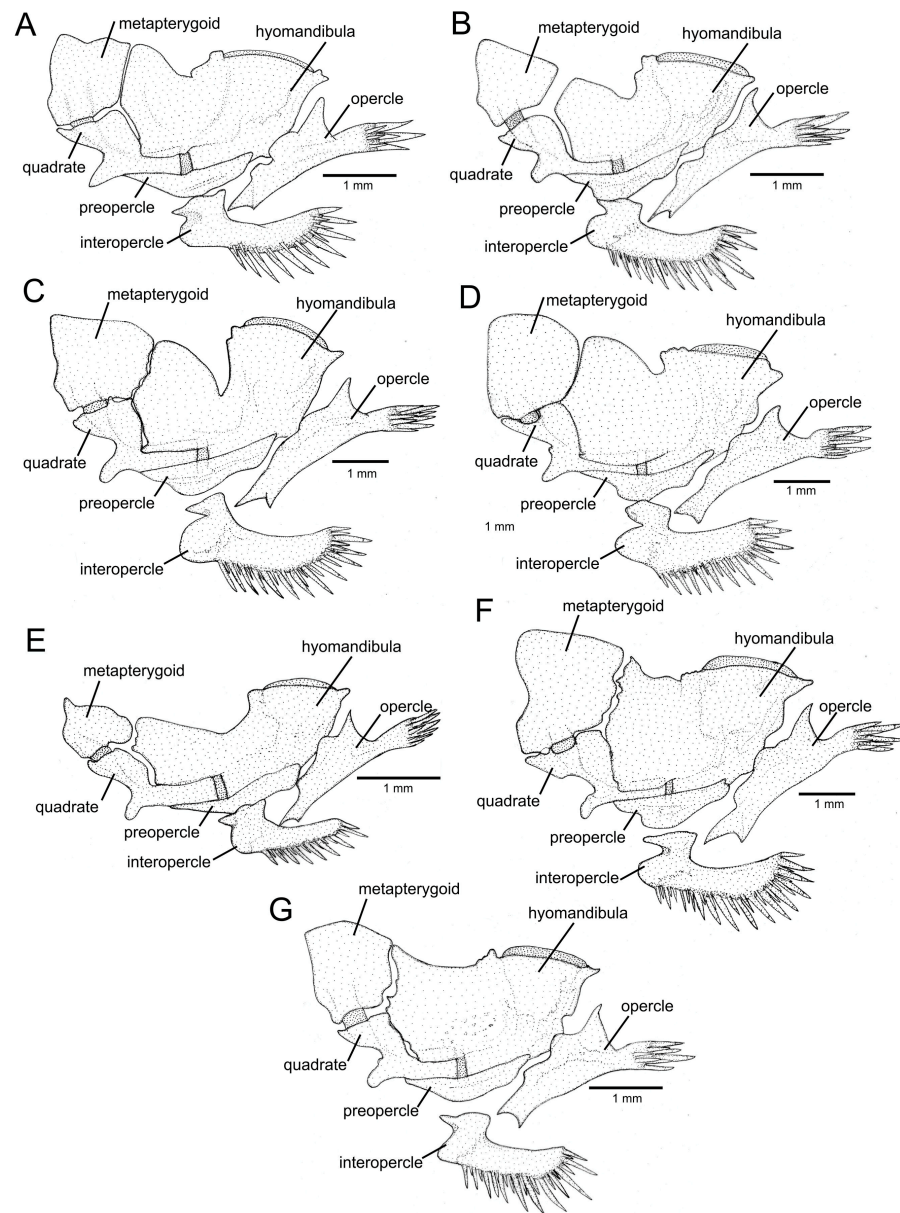


Figure 4. Left jaw suspensorium and opercular series, lateral view: (A) *Cambeva alphabelardense*; (B) *Cambeva dimorphica* sp. nov.; (C) *Cambeva oncina* sp. nov.; (D) *Cambeva curvilineata* sp. nov.; (E) *Cambeva diegoi* sp. nov.; (F) *Cambeva metagalactica* sp. nov.; (G) *Cambeva minima* sp. nov. Larger stippling represents cartilage.

Distribution. Middle Rio Chapecó drainage (Figure 8A).

Habitat. Headwaters of a small brook, altitude about 805 m asl, with dense marginal vegetation and great concentration of ferns. Specimens found buried in vegetal debris, mostly tree ferns, on the bottom of brook banks.

Material examined. UFRJ 6990, holotype, 43.4 mm SL; UFRJ 6991, one paratype (C&S), 41.8 mm SL; UFRJ 6992, three paratypes, 34.1–39.7 mm SL; Brazil: Estado de Santa Catarina: Município de Abelardo Luz: stream tributary of the middle Rio Chapecó, Rio Uruguai basin, 26°32′19″ S, 52°25′17″ W, 805 m asl; C.R.M. Feltrin, 20 March 2021. UFRJ 6993, two paratypes (C&S), 34.3–39.5 mm SL; CICCAA 12706, four paratypes, 29.8–46.4 mm SL; same locality as for holotype; A. Bianco, F.H. Llanos and C.R.M. Feltrin, 15 July 2020. UFRJ 14098, 3 ex. (DNA), 31.0–44.7 mm SL; same locality and collector as holotype, 20 May 2024.

Cambeva dimorphica sp. nov.

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Figures 3B, 4B, 6B, 9 and 10; Table 1.

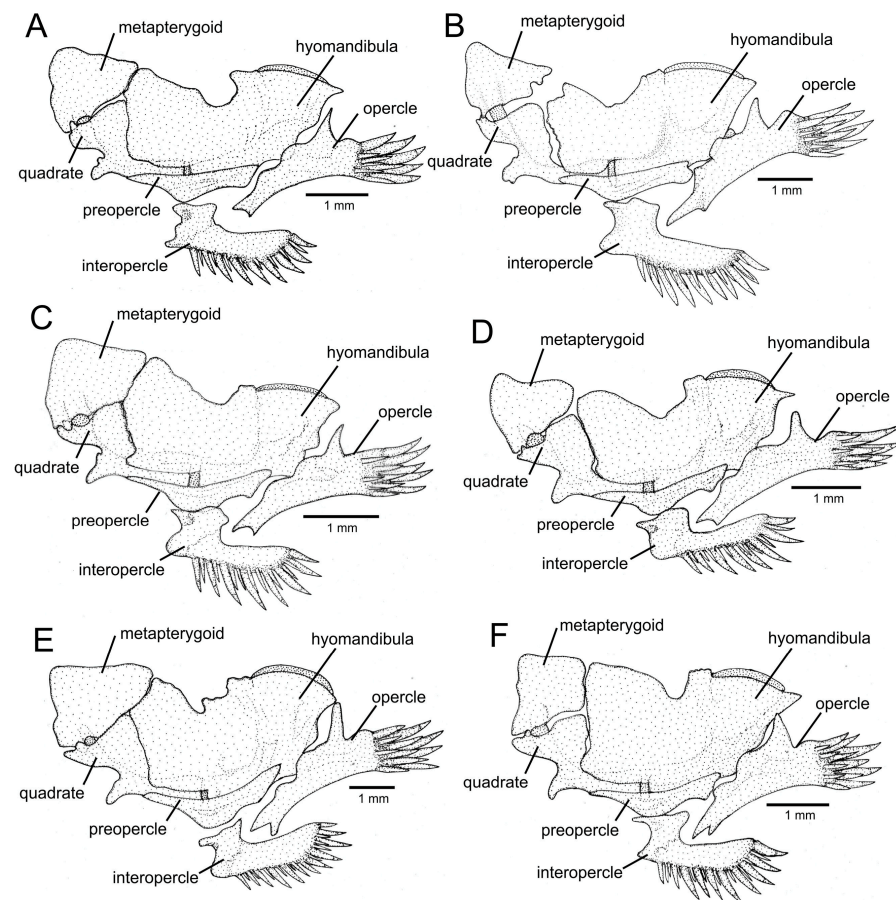


Figure 5. Left jaw suspensorium and opercular series, lateral view: (A) *Cambeva admirabilis* sp. nov.; (B) *Cambeva betabelardense*; (C) *Cambeva dominguense* sp. nov.; (D) *Cambeva insperata* sp. nov.; (E) *Cambeva intermedia* sp. nov.; (F) *Cambeva mundana* sp. nov. Larger stippling represents cartilage.

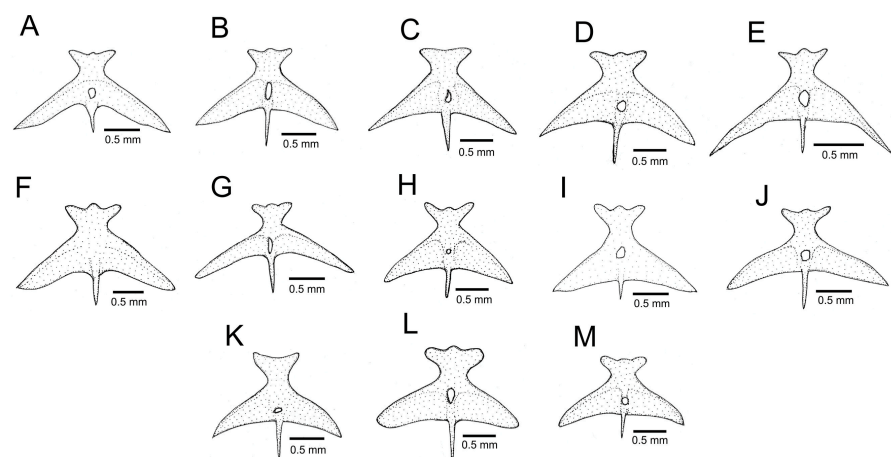


Figure 6. Parurohyal, ventral view: (A) *Cambeva alphabelardense*; (B) *Cambeva dimorphica* sp. nov.; (C) *Cambeva oncina* sp. nov.; (D) *Cambeva curvilineata* sp. nov.; (E) *Cambeva diegoi* sp. nov.; (F) *Cambeva metagalactica* sp. nov.; (G) *Cambeva minima* sp. nov.; (H) *Cambeva admirabilis* sp. nov.; (I) *Cambeva betabelardense*; (J) *Cambeva dominguense* sp. nov.; (K) *Cambeva insperata* sp. nov.; (L) *Cambeva intermedia* sp. nov.; (M) *Cambeva mundana* sp. nov.



Figure 7. *Cambeva alphabelardense*, UFRJ 6990, holotype, 43.4 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

Holotype. UFRJ 15075, 35.7 mm SL; Brazil: Estado de Santa Catarina: Município de Água Doce: Linha Limoeiro: small stream tributary of upper Rio Chapecozinho, Rio Chapecó drainage, Rio Uruguai basin, 26°46'06" S 51°40'23" W, about 1230 m asl; C.R.M. Feltrin, 9 February 2026.

Paratypes. All from Brazil: Estado de Santa Catarina: Município de Água Doce: Linha Limoeiro: upper Rio Chapecozinho, Rio Chapecó drainage, Rio Uruguai basin. UFRJ 15058, 5 ex., 19.9–40.1 mm SL; UFRJ 15059, 4 ex. (C&S), 26.3–33.6 mm SL; UFRJ 14976, 2 ex. (DNA), 28.4–30.9 mm SL; CICCAA 13602, 3 ex., 28.0–37.0 mm SL; collected with holotype. UFRJ 15017, 5 ex., 21.9–44.3 mm SL; same locality as holotype; same locality and collector as holotype, 2 April 2026. UFRJ 15018, 4 ex., 26.7–42.7 mm SL; UFRJ 15076, 1 ex. (DNA), 29.4 mm SL; stream near type locality, 26°45'39" S 51°39'50" W, about 1215 m asl; C.R.M. Feltrin, 2 April 2026. UFRJ 15061, 4 ex., 26.0–27.8 mm SL; same locality as holotype; C.R.M. Feltrin, 15 April 2026.

Diagnosis. *Cambeva dimorphica* is distinguished from all other congeners by having two distinct flank colour patterns in adult specimens, the first one comprising irregularly shaped dark brown blotches, often coalesced to form large dark brown zones (Figure 9) and the second one comprising small rounded dark brown spots with lighter brown centre (Figure 10) (vs. never simultaneously having these two distinct colour patterns). *Cambeva dimorphica* also differs from all other species of CAC by having the dorsal-fin origin at a vertical anterior to the middle of the dorsal-fin base (vs. posterior); five pelvic-fin rays (vs. four in *C. alphabelardense* and pelvic fin absent in *C. oncina*); 9 opercular and 28–33 interopercular odontodes (vs. 6 or 7 opercular, 20 or 21 interopercular odontodes in *C. alphabelardense*, 7 or 8 opercular, 24–26 interopercular odontodes in *C. oncina*); a long lacrimal, its length about equal to sesamoid supraorbital length (Figure 3B; vs. half-length or less, Figure 3A,C); and mesethmoid cornua sharply pointed (Figure 3B; vs. not pointed, Figure 3A,C).

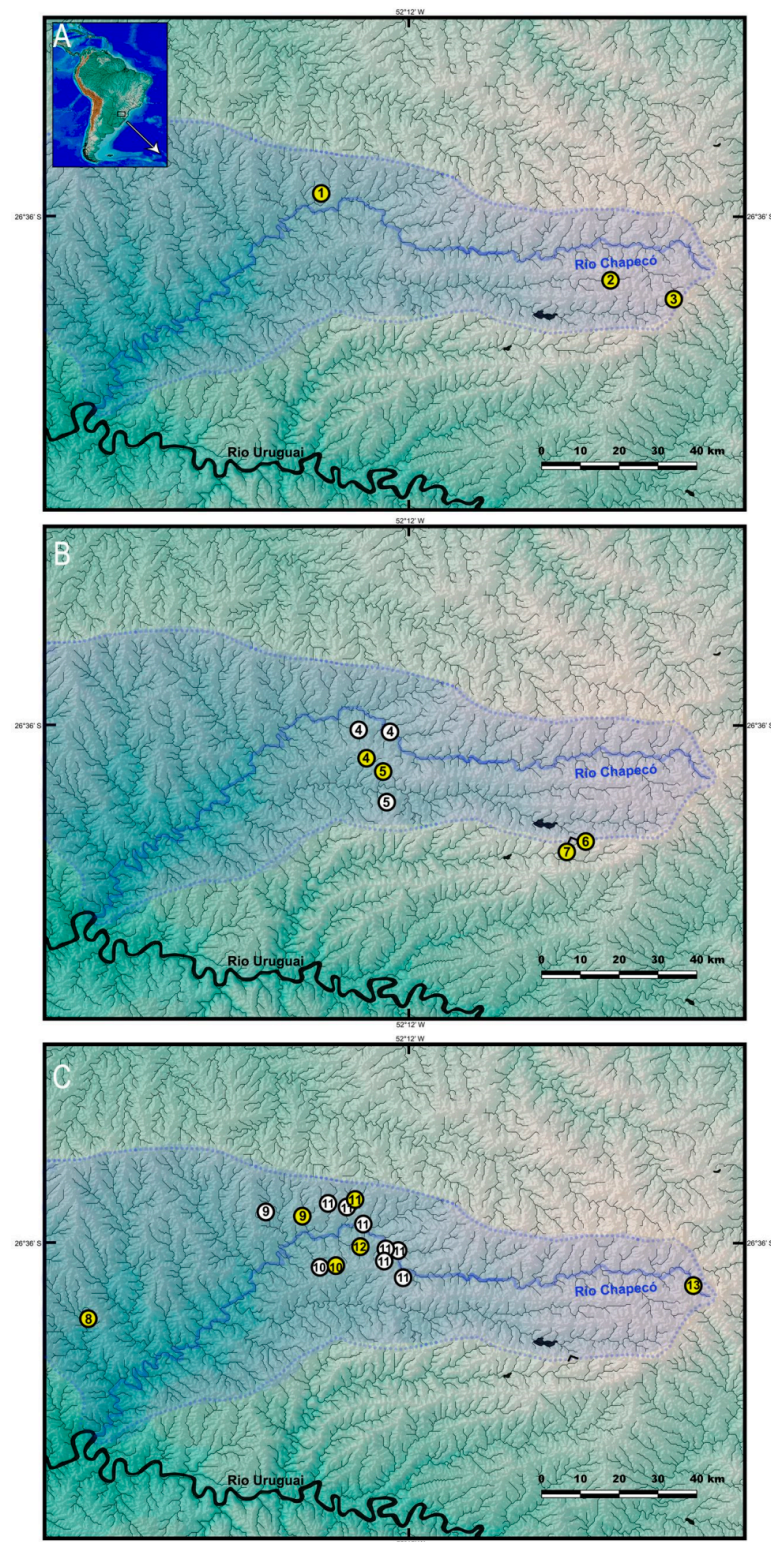


Figure 8. Geographical distribution: (A) *Cambeva alphabelardense* clade (1, *Cambeva alphabelardense*; 2, *Cambeva dimorphica* sp. nov.; 3, *Cambeva oncina* sp. nov.); (B) *Cambeva betabelardense* subclade 1 (4, circle, *Cambeva minima* sp. nov.; 5, *Cambeva curvilineata* sp. nov.; 6, *Cambeva diegoi* sp. nov.; 7, *Cambeva metagalactica* sp. nov.); (C) *Cambeva betabelardense* subclade 2 (8, *Cambeva intermedia* sp. nov.; 9, *Cambeva dominguense* sp. nov.; 10, *Cambeva admirabilis* sp. nov.; 11, *Cambeva betabelardense*; 12, *Cambeva mundana* sp. nov.; 13, *Cambeva insperata* sp. nov.). Yellow symbols are type localities. Map generated using QGIS software v. 3.14, hydrography retrieved from HydroSHEDS database (<https://www.hydrosheds.org>, access on 31 July 2026). All spatial data were projected with WGS 84 datum (EPSG:4326).

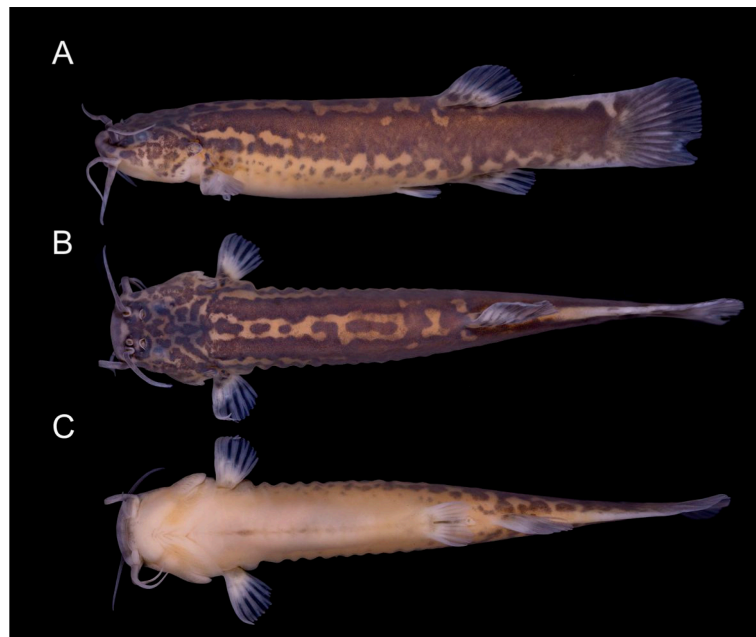


Figure 9. *Cambeva dimorphica* sp. nov., UFRJ 15075, holotype, 35.7 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

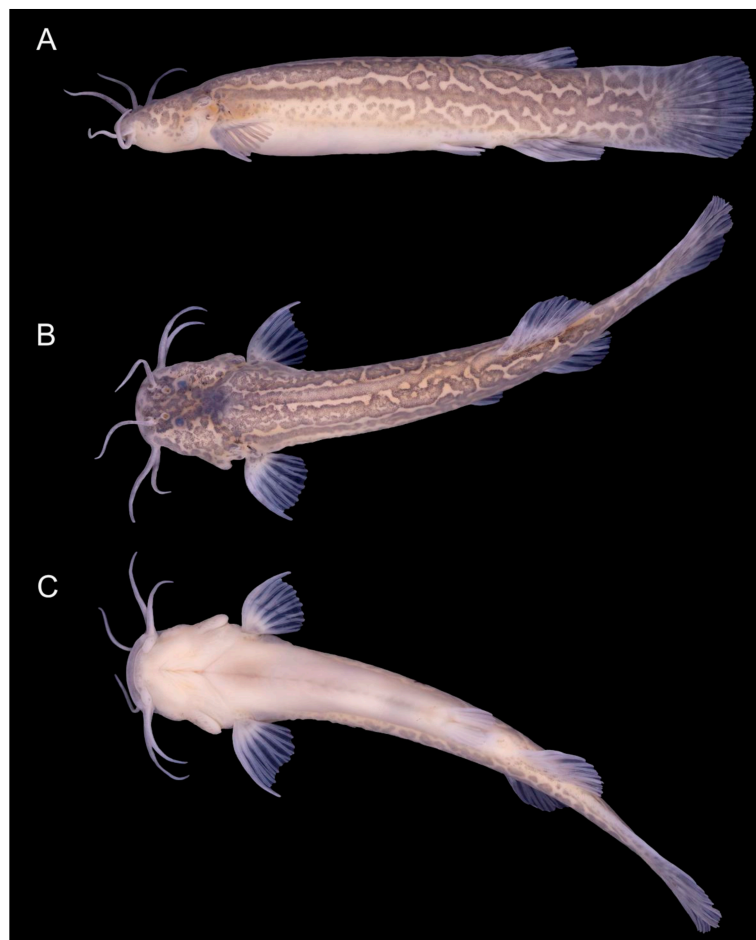


Figure 10. *Cambeva dimorphica* sp. nov., UFRJ 15058, paratype, 40.1 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

Table 1. Morphometric data of *Cambeva dimorphica* sp. nov.

	Holotype	Paratypes (n = 8)
Standard length (SL)	35.7	26.3–44.3
Percentage of standard length		
Body depth	20.1	16.7–20.2
Caudal peduncle depth	14.4	12.6–14.5
Body width	12.9	10.7–12.4
Caudal peduncle width	4.6	3.3–5.7
Pre-dorsal length	65.5	63.5–69.4
Pre-pelvic length	61.4	57.6–65.8
Dorsal-fin base length	12.2	12.0–14.8
Anal-fin base length	10.7	9.5–11.6
Caudal-fin length	19.9	17.0–21.8
Pectoral-fin length	11.7	12.3–14.4
Pelvic-fin length	8.8	8.1–10.0
Head length	21.1	19.6–23.7
Percentage of head length		
Head depth	58.1	50.8–54.5
Head width	89.0	82.3–87.4
Snout length	40.1	38.0–42.8
Interorbital width	29.0	21.5–30.8
Preorbital length	8.2	6.9–10.5
Eye diameter	13.1	9.6–12.4

Description. External morphology: Morphometric data in Table 1. Body relatively moderately deep, greatest body depth at vertical through area midway distance between pectoral and pelvic-fin bases. Trunk subcylindrical on its anterior portion, deeper than broad, compressed posteriorly. Dorsal and ventral profiles of head and trunk weakly convex, dorsal and ventral profiles of caudal peduncle about straight. Anus and urogenital papilla opening located at vertical through anterior portion of dorsal-fin base. Lateral line canal of trunk short, with two pores just posterior to opercular patch of odontodes.

Head sub-trapezoidal in dorsal view, anterior profile of snout slightly convex. Eye moderate in size, round, dorsally positioned on head, nearer snout than posterior margin of opercle. Distance between anterior and posterior nostrils about equal distance between posterior nostril and orbital rim. Tip of nasal barbel reaching opercular patch of odontodes or area just anterior to it, tip of maxillary barbel reaching pectoral-fin base and rictal barbel reaching area just posterior to interopercular patch of odontodes. Mouth subterminal. Lateral fleshy lobe of mouth narrow, moderate in length, its longest length approximately half lower jaw length excluding lobes. Jaw teeth pointed, arranged in irregular rows, 28–33 on premaxilla, 29–38 on dentary. Whole head surface, except branchiostegal region, covered by minute skin papillae. Branchial membrane thickened, attached to isthmus only at its anterior-most point, in ventral midline. Odontodes conical, narrow and approximately straight, nine on opercle, 28–33 on interopercle.

Supraorbital sensory canal continuous, with three paired pores: s1, s3, and s6. Pore s6 about equidistant or slightly nearer to orbit than from its symmetrical homologous pore s6. Infraorbital canal represented by two separate segments, anterior segment delimited by pores io1 and io2, posterior segment with pores io8 and io9. Anterior infraorbital canal totally dermal, separated from lacrimal. Posterior infraorbital, supraorbital and postorbital canals continuous. Postorbital canal with two pores: po1 and po2.

Fins well-developed, dorsal, anal and pectoral fins with thickened bases. Unpaired fins with convex distal margins. Dorsal-fin origin nearer caudal-fin posterior margin than nape, anal-fin origin at vertical through middle of dorsal-fin base, through base of third dorsal-fin

branched ray. Eleven (ii + II + 7) dorsal-fin rays, 9 (ii + II + 5) anal-fin rays. Pectoral fin subtriangular in dorsal view, posterior margin convex, first ray longer than other rays, its distal extremity forming short filament, its length about 5–10% of pectoral-fin length excluding filament. Six (I + 5) pectoral-fin rays. Pelvic fin with rounded posterior margin, reaching vertical through anterior portion of dorsal-fin base, its extremity not reaching anus or barely touching it. Pelvic-fin bases in close proximity. Five (I + 4) pelvic-fin rays. Thirteen (I + 11 + I) principal caudal-fin rays, 20 (xviii + II) dorsal procurrent rays, and 13–15 (xii–xiv + I) ventral procurrent rays.

Osteology (Figures 3B, 4B and 6B): Anterior portion of mesethmoid moderately broad, subtriangular in dorsal view, anterior margin weakly concave in dorsal view, cornu sharply pointed. Lateral ethmoid with minute lateral projection. Lacrimal thin, with narrow and long posterior portion. Sesamoid supraorbital short, about equal in length to lacrimal, without lateral projections. Premaxilla subrectangular in dorsal view, maxilla slender, slightly curved, shorter than premaxilla, without distinct posterior process.

Autopalatine relatively broad and short, subrectangular in dorsal view, with rudimentary postero-lateral process; lateral margin weakly concave, medial margin near mesethmoid, with small rounded expansion. Metapterygoid relatively small, sub-triangular. Quadrate L-shaped, with deep anterior constriction. No laminar expansions articulating metapterygoid and quadrate. Hyomandibula relatively short and slender. Opercle elongate, opercular odontode patch narrow, its depth about one third of hyomandibula articular facet length. Dorsal process of opercle short, pointed, slightly curved. Opercular articular facet for hyomandibula with short rounded laminar projection. Articular facet for preopercle rounded, short. Interopercle relatively long, its longitudinal length slightly shorter than total hyomandibula longitudinal length. Preopercle short, with moderate ventral projection.

Parurohyal thin, lateral process short, pointed. Parurohyal head broad, with prominent anterolateral paired process. Parurohyal middle foramen minute. Parurohyal posterior process moderate in length, about two thirds distance between anterior margin of parurohyal and anterior insertion of posterior process. Branchiostegal rays 7 or 8. Vertebrae 37 or 38. Ribs 13–15. Dorsal-fin origin at vertical between centra of 19th and 21st vertebrae; anal-fin origin at vertical between centra of 23rd and 24th vertebrae. Two dorsal and single ventral hypural plate.

Colouration in alcohol: Two distinct colour patterns. Colour pattern 1 (Figure 9): dorsal and lateral surface of head and trunk pale yellow, with irregularly shaped dark brown blotches, often coalesced on caudal peduncle and longitudinal dorsolateral zone, forming large dark brown zones. Venter white. Nasal and maxillary barbels dark grey, rictal barbel white. Fins hyaline, with brown spots on basal portion of unpaired and pectoral fins.

Colour pattern 2 (Figure 10): dorsal and lateral surface of head and trunk pale yellow, with small rounded dark brown spots with lighter brown centre, often coalesced on longitudinal lateral midline and dorsolateral line. Venter white. Nasal and maxillary barbels dark grey, rictal barbel white. Fins hyaline, with brown spots on basal portion of unpaired and pectoral fins.

Etymology. From the Greek *di* (two) and *morphe* (relative to shape), referring to the two colour patterns of adult specimens.

Distribution. Upper Rio Chapecozinho subdrainage, Rio Chapecó drainage (Figure 8A).

Habitat. Headwaters of small brook, about 1230 m asl, with small pebbles and gravel on the bottom. Most specimens were concentrated within mats of marginal amphibious plants, whereas a few ones were found under small pebbles near marginal amphibious plants.

Remarks. Although the two colour patterns possibly representing a case of sexual dimorphism due to the slightly swollen abdomen of specimens exhibiting the colour pattern 1, which is similar to the common condition in trichomycterine females, developed gonads were not found in dissections to confirm it.

Cambeva oncina sp. nov.
urn:lsid:zoobank.org:act: 52536C1B-F151-482E-82D5-CA43ECF17AA6.
Figures 3C, 4C, 6C and 11; Table 2.



Figure 11. *Cambeva oncina* sp. nov., UFRJ 15060, holotype, 63.5 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

Table 2. Morphometric data of *Cambeva oncina* sp. nov.

	Holotype	Paratypes (n = 9)
Standard length (SL)	63.5	34.7–61.8
Percentage of standard length		
Body depth	17.5	13.3–16.7
Caudal peduncle depth	13.7	11.8–13.8
Body width	11.8	9.7–12.1
Caudal peduncle width	3.9	3.1–4.8
Pre-dorsal length	66.3	64.9–67.5
Dorsal-fin base length	11.0	10.5–12.9
Anal-fin base length	9.1	8.1–11.1
Caudal-fin length	15.2	16.2–18.9
Pectoral-fin length	10.9	10.3–12.7
Head length	19.9	19.6–20.8
Percentage of head length		
Head depth	55.8	49.1–57.9
Head width	90.2	84.2–93.0
Snout length	41.6	39.0–42.5
Interorbital width	29.0	26.4–32.5
Preorbital length	8.6	6.5–9.0
Eye diameter	8.2	8.5–11.4

Holotype. UFRJ 15060, 63.5 mm SL; Brazil: Estado de Santa Catarina: Município de Água Doce: Herciliópolis: brook tributary of upper Rio do Mato, tributary of Rio

Chapecozinho, Rio Chapecó drainage, Rio Uruguai basin, 26°49'00" S 51°30'30" W, about 1300 m asl; C.R.M. Feltrin, 19 April 2026.

Paratypes. UFRJ 15063, 18 ex., 26.4–61.8 mm SL; UFRJ 15062, 4 ex. (C&S), 34.7–52.8 mm SL; UFRJ 15036, 4 ex. (DNA), 15.6–43.0 mm SL; CICCAA 13603, 3 ex., 45.2–50.3 mm SL; collected with holotype.

Diagnosis. *Cambeva oncina* differs from all congeners of CAC by the absence of pelvic fin and support (vs. presence); by having 24–26 interopercular odontodes (vs. 20 or 21 in *C. alphabelardense* and 28–33 in *C. dimorphica*); presence of a short dowel-like process on the lateral margin of the lateral ethmoid (Figure 3C; vs. absence, Figure 3A,B); the presence of a deep cleft on the dorsal margin of the hyomandibular outgrowth (Figure 4C; vs. absence, Figure 4A,B); and a colour pattern consisting of dark brown blotches with lighter central portion on the whole flank (vs. only on the dorsum when present).

Description. External morphology: Morphometric data in Table 2. Body relatively moderately deep, greatest body depth at vertical through area just anterior to dorsal-fin origin. Trunk subcylindrical on its anterior portion, deeper than broad, compressed posteriorly. Dorsal and ventral profiles of head and trunk weakly convex, dorsal and ventral profiles of caudal peduncle about straight. Anus and urogenital papilla opening located at vertical middle portion of dorsal-fin base. Lateral line canal of trunk short, with two pores just posterior to opercular patch of odontodes.

Head sub-trapezoidal in dorsal view, anterior profile of snout convex. Eye moderate in size, round, dorsally positioned on head, nearer snout than posterior margin of opercle. Distance between anterior and posterior nostrils about equal distance between posterior nostril and orbital rim. Tip of nasal barbel reaching area immediately anterior to opercular patch of odontodes, tip of maxillary barbel reaching posterior margin of interopercular patch of odontodes or area just posterior to it and rictal barbel reaching area between middle and posterior portions to interopercular patch of odontodes. Mouth subterminal. Lateral fleshy lobe of mouth narrow and long, its longest length approximately two thirds of lower jaw length excluding lobes. Jaw teeth pointed, arranged in irregular rows, 29–36 on premaxilla, 25–36 on dentary. Whole head surface covered by minute skin papillae, slightly larger on lower jaw. Branchial membrane thickened, attached to isthmus only at its anterior-most point, in ventral midline. Odontodes conical, narrow and approximately straight, 7 or 8 on opercle, 24–26 on interopercle.

Supraorbital sensory canal continuous, with three paired pores: s1, s3, and s6. Pore s6 slightly nearer to orbit than from its symmetrical homologous pore s6. Infraorbital canal represented by two separate segments, anterior segment delimited by pores io1 and io2, posterior segment with pores io8 and io9. Anterior infraorbital canal totally dermal, separated from lacrimal. Posterior infraorbital, supraorbital and postorbital canals continuous. Postorbital canal with two pores: po1 and po2.

Fins well-developed, dorsal, anal and pectoral fins with thickened bases. Unpaired fins with convex distal margins. Dorsal-fin origin nearer caudal-fin posterior margin than nape, anal-fin origin at vertical through middle of dorsal-fin base, through base of fourth dorsal-fin branched ray. Eleven (ii + II + 7) dorsal-fin rays, 9 (ii + II + 5) anal-fin rays. Pectoral fin subtriangular in dorsal view, posterior margin convex, first ray longer than other rays, its distal extremity often forming short filament, its length about 5% of pectoral-fin length excluding filament. Five or six (I + 4–5) pectoral-fin rays. Pelvic fin and support absent. Thirteen (I + 11 + I) principal caudal-fin rays, 19–20 (xviii–xix + II) dorsal procurent rays, and 15 (xiv + I) ventral procurent rays.

Osteology (Figures 3C, 4C and 6C): Anterior portion of mesethmoid moderately broad, subtriangular in dorsal view, anterior margin weakly convex in dorsal view, cornu narrow. Lateral ethmoid with short dowel-like process on its lateral margin. Lacrimal thin, short.

Sesamoid supraorbital short, often with minute lateral projection, its length about two times lacrimal length. Premaxilla narrow, sub-rectangular in dorsal view, slightly tapering laterally; maxilla slender, curved, shorter than premaxilla, without distinct posterior process.

Autopalatine broad and short, subrectangular in dorsal view, with short postero-lateral process; lateral margin about straight, medial margin near weakly sinuous. Metapterygoid relatively large, sub-triangular. Quadrate L-shaped, with deep anterior constriction. Small laminar expansion articulating metapterygoid and quadrate. Hyomandibula relatively short and deep. Opercle elongate, opercular odontode patch narrow, its depth about one third of hyomandibula articular facet length. Dorsal process of opercle short, pointed, slightly curved. Opercular articular facet for hyomandibula with short rounded laminar projection. Articular facet for preopercle rounded, short. Interopercle relatively long, its longitudinal length slightly shorter than total hyomandibula longitudinal length. Preopercle short, with moderate ventral projection.

Parurohyal thin, lateral process short, pointed. Parurohyal head broad, with prominent anterolateral paired process. Parurohyal middle foramen minute. Parurohyal posterior process moderate in length, about two thirds distance between anterior margin of parurohyal and anterior insertion of posterior process. Branchiostegal rays 8 or 9. Vertebrae 38 or 39. Ribs 13–14. Dorsal-fin origin at vertical between centra of 21st vertebrae; anal-fin origin at vertical between centra of 24th and 25th vertebrae. Two dorsal and single ventral hypural plate.

Colouration in alcohol: Dorsal and lateral surface of head and trunk yellowish white, with irregularly shaped dark brown blotches with lighter central portion, interspaces forming reticular pattern with irregularly shaped lines. Venter white. Barbels light grey. Fins hyaline, with brown spots on basal portion of unpaired and pectoral fins.

Etymology. Name derived from the Portuguese *oncinha*, a small *onça*, the popular Brazilian name for the panther *Panthera onca* L. 1758, a reference to the similar colour pattern of the new species.

Distribution. Upper Rio Chapecozinho subdrainage, Rio Chapecó drainage (Figure 8A).

Habitat. Headwaters of a small brook, about 1300 m asl, with small pebbles on silty bottom. Specimens were found concentrated buried in the silty bottom covered by leaf litter, in area with reduced light incidence.

3.3. The *Cambeva betabelardense* Clade (CBC)

CBC is well-supported by molecular data but lacks unique morphological characteristics shared by all species. It includes two subclades with divergent morphological and ecological characteristics, CBS1 and CBS2.

3.4. The *Cambeva betabelardense* Subclade 1 (CBS1)

Diagnosis. Species of CBS1 differ from other congeners by having the lateral ethmoid with a small lateral projection supporting ligament connected to sesamoid supraorbital (Figure 3D–G). Species of CBS1 are also distinguished from other taxa here analysed by having a narrow opercular odontode patch with 7–9 odontodes (Figure 4D–G; vs. relatively broad opercular patch, with 11–14 odontodes in CBS2, Figure 5A–F); anterior infraorbital section usually present and not attached to the lacrimal (vs. always absent in CBS2); and absence of a long nerve canal, positioned obliquely along the dorsal surface of the bone (Figure 3D–G; vs. presence in CAC, Figure 3A–C).

Included species. *Cambeva curvilineata* sp. nov., *Cambeva diegoi* sp. nov., *Cambeva metagalactica* sp. nov. and *Cambeva minima* sp. nov.

Habitat. Headwaters of short brooks and streams with diverse bottom sediment. The brooks are associated both with the main channel of the Rio Chapecó and with its main tributary, the Rio Chapecozinho, in altitudes between about 740 and 1075 m asl.

Cambeva curvilineata sp. nov.

urn:lsid:zoobank.org:act: F7449AEC-1CDF-489E-9014-473D5A0057CB.

Figures 3D, 4D, 6D, 12 and 13; Table 3.



Figure 12. *Cambeva curvilineata* sp. nov., UFRJ 15077, holotype, 56.0 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.



Figure 13. *Cambeva curvilineata* sp. nov., UFRJ 15064, paratype, 38.1 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

Holotype. UFRJ 15077, 56.0 mm SL; Brazil: Estado de Santa Catarina: Município de Ouro Verde: Linha Hervalzinho: small brook tributary to Rio Chapecozinho, Rio Chapecó drainage, Rio Uruguai basin, 26°43'13" S 52°15'49" W, about 855 m asl; C.R.M. Feltrin, 3 April 2026.

Table 3. Morphometric data of *Cambeva curvilineata* sp. nov.

	Holotype	Paratypes (n = 9)
Standard length (SL)	56.0	38.1–56.3
Percentage of standard length		
Body depth	17.7	15.3–17.9
Caudal peduncle depth	13.8	11.6–13.2
Body width	12.0	10.6–12.8
Caudal peduncle width	3.2	3.2–5.3
Pre-dorsal length	65.5	62.6–67.6
Pre-pelvic length	59.1	57.6–61.9
Dorsal-fin base length	12.0	11.5–13.5
Anal-fin base length	10.6	8.2–11.2
Caudal-fin length	17.3	16.6–18.8
Pectoral-fin length	13.3	11.9–14.1
Pelvic-fin length	9.1	8.1–10.1
Head length	20.2	19.1–24.1
Percentage of head length		
Head depth	54.8	54.0–60.4
Head width	88.4	84.2–92.7
Snout length	38.4	37.6–41.8
Interorbital width	24.7	24.3–30.7
Preorbital length	7.5	7.5–9.8
Eye diameter	11.6	8.8–12.1

Paratypes. All from Brazil: Estado de Santa Catarina: Rio Chapecó drainage, Rio Uruguai basin. Município de Ouro Verde: Linha Hervalzinho: UFRJ 15064, 14 ex., 30.7–56.3 mm SL; UFRJ 15065, 5 ex. (C&S), 36.3–55.7 mm SL; CICCAA 13604, 5 ex., 30.8–52.6 mm SL; collected with holotype. UFRJ 14881, 10 ex. (DNA), 20.5–44.7 mm SL; same locality and collector as holotype, 21 December 2025. Município de Faxinal dos Guedes: Linha Esperinha: UFRJ 15009, 25 ex., 24.0–64.1 mm SL; UFRJ 15029, 3 ex. (C&S), 34.4–46.1 mm SL; UFRJ 15028, 29.4–29.9; brook tributary of Rio Chapecozinho, 26°48'15" S 52°15'05" W, about 860 m asl; C.R.M. Feltrin, 5 April 2026. UFRJ 15066, 6 ex., 31.0–59.1 mm SL; brook tributary of Rio Chapecozinho, 26°47'17" S 52°15'15" W, about 840 m asl; C.R.M. Feltrin, 5 April 2026.

Diagnosis. *Cambeva curvilineata* is distinguished from other species of CBS1 by the presence of pelvic fin (vs. absence in *C. diegoi* sp. nov.); 36 or 37 vertebrae (vs. 39 in *C. diegoi* sp. nov.); seven or eight branchiostegal rays (ten in *C. diegoi* sp. nov.); 28–32 interopercular odontodes (vs. 16 in *C. diegoi* sp. nov., 22–23 in *C. minima* sp. nov. and 33–37 in *C. metagalactica* sp. nov.); the dorsal-fin origin at the vertical through the centrum of the 20th vertebra (vs. 23rd vertebra in *C. diegoi* sp. nov.); 30–37 premaxillary teeth (vs. 38–46 in *C. metagalactica* sp. nov.); 30–31 dentary teeth (vs. 37–40 in *C. metagalactica* sp. nov.); presence of anterior infraorbital canal (vs. absence in *C. minima* sp. nov.); the lateral process of the parurohyal short, with broad basal portion (Figure 6D; vs. long, with moderately wide or narrow basal portion in *C. diegoi* sp. nov., Figure 6E and *C. minima* sp. nov., Figure 6G, respectively).

Description. External morphology: Morphometric data in Table 3. Body relatively deep, greatest body depth at vertical through area midway distance between pectoral and pelvic-fin bases. Trunk subcylindrical on its anterior portion deeper than broad, compressed posteriorly. Dorsal and ventral profiles of head and trunk weakly convex, dorsal and ventral profiles of caudal peduncle about straight. Anus and urogenital papilla opening located at vertical through anterior portion of dorsal-fin base. Lateral line canal of trunk short, with two pores just posterior to opercular patch of odontodes.

Head sub-trapezoidal in dorsal view, anterior profile of snout slightly convex. Eye relatively small, round, dorsally positioned on head, nearer snout than posterior margin of opercle. Distance between anterior and posterior nostrils slightly shorter than distance between posterior nostril and orbital rim. Tip of nasal barbel reaching area between orbit and opercular patch of odontodes, tip of maxillary barbel reaching pectoral-fin base, rictal barbel reaching area between interopercular patch of odontodes and pectoral-fin base. Mouth subterminal. Lateral fleshy lobe of mouth narrow, moderate in length, its longest length approximately half lower jaw length excluding lobes. Jaw teeth pointed, arranged in irregular rows, 30–37 on premaxilla, 30–31 on dentary. Area around mouth and posterior portion of branchiostegal region covered by minute skin papillae. Branchial membrane thickened, attached to isthmus only at its anterior-most point, in ventral mid-line. Odontodes conical, narrow and approximately straight, 7 or 8 on opercle, 28–32 on interopercle.

Supraorbital sensory canal continuous, with three paired pores: s1, s3, and s6. Pore s6 nearer orbit than its symmetrical homologous pore s6. Infraorbital canal represented by two separate segments, anterior segment delimited by pores io1 and io2, posterior segment with pores io8 and io9. Anterior infraorbital canal totally dermal, separated from lacrimal. Posterior infraorbital, supraorbital and postorbital canals continuous. Postorbital canal with two pores: po1 and po2.

Fins well-developed, dorsal, anal and pectoral fins with thickened bases. Unpaired fins with convex distal margins. Dorsal-fin origin nearer caudal-fin posterior margin than nape, anal-fin origin at vertical through anterior half of dorsal-fin base, through base of fourth dorsal-fin branched ray. Eleven (ii + II + 7) dorsal-fin rays, 9 (ii + II + 5) anal-fin rays. Pectoral fin subtriangular in dorsal view, first ray longer than other rays, its distal extremity surpassing fin membrane, forming filament about 5–20% of pectoral-fin length excluding filament. Six (I + 5) pectoral-fin rays. Pelvic fin with rounded posterior margin, reaching vertical through anterior portion of dorsal-fin base, its extremity not reaching anus. Pelvic-fin bases in close proximity. Five (I + 4) pelvic-fin rays. Thirteen (I + 11 + I) principal caudal-fin rays, 20–21 (xix–xx + I) dorsal procurent rays, and 15 (xiv + I) ventral procurent rays.

Osteology (Figures 3D, 4D and 6D): Anterior portion of mesethmoid broad, subtriangular in dorsal view, anterior margin weakly concave in dorsal view, cornu pointed. Lateral ethmoid with minute lateral projection, supporting ligament connected to sesamoid supraorbital. Lacrimal thin, elongate. Sesamoid supraorbital relatively short, about two times longer than lacrimal, with anteromedial projection supporting ligament connecting it to lateral ethmoid. Premaxilla subrectangular in dorsal view, maxilla slender, curved, shorter than premaxilla, without distinct posterior process.

Autopalatine broad and short, subrectangular in dorsal view, with rounded expansion on its medial margin and rudimentary postero-lateral process. Metapterygoid hypertrophied, sub-rectangular, deep. Quadrate L-shaped, with deep anterior constriction and long narrow projection on it anterodorsal extremity. No laminar expansion articulating metapterygoid and quadrate. Hyomandibula relatively short and deep. Opercle elongate, opercular odontode patch narrow, its depth about half hyomandibula articular facet length. Dorsal process of opercle short, curved. Opercular articular facet for hyomandibula with short rounded laminar projection. Articular facet for preopercle rudimentary. Interopercle relatively long, its longitudinal length about two thirds of total hyomandibula longitudinal length. Preopercle short, with moderate ventral projection.

Parurohyal thin, lateral process short, pointed. Parurohyal head broad, with prominent anterolateral paired process. Parurohyal middle foramen minute. Parurohyal posterior process short, about half distance between anterior margin of parurohyal and anterior

insertion of posterior process. Branchiostegal rays 8. Vertebrae 36 or 37. Ribs 14. Dorsal-fin origin at vertical through centrum of 20th vertebra; anal-fin origin at vertical through centrum of 24th vertebra. Two dorsal and single ventral hypural plate.

Colouration in alcohol: In larger specimens above about 50 mm SL (Figure 13), dorsal and lateral surface of trunk yellowish white with longitudinal series of brown spots with lighter centra, one on dorsum longitudinal midline, one on flank longitudinal midline, one on dorsal portion of flank and one on ventral portion of flank; all spot series highly coalesced longitudinally, except ventral-most one, resulting in yellowish white sinuous lines on interspaces. Venter white. Dorsal and lateral surfaces of head brown with yellowish white reticulum. Barbels dark grey. Fins hyaline, with dark grey dots on basal portion of pectoral fin and whole unpaired fins. In juveniles, about 20–40 mm SL (Figure 14), trunk and head with smaller and fewer spots.

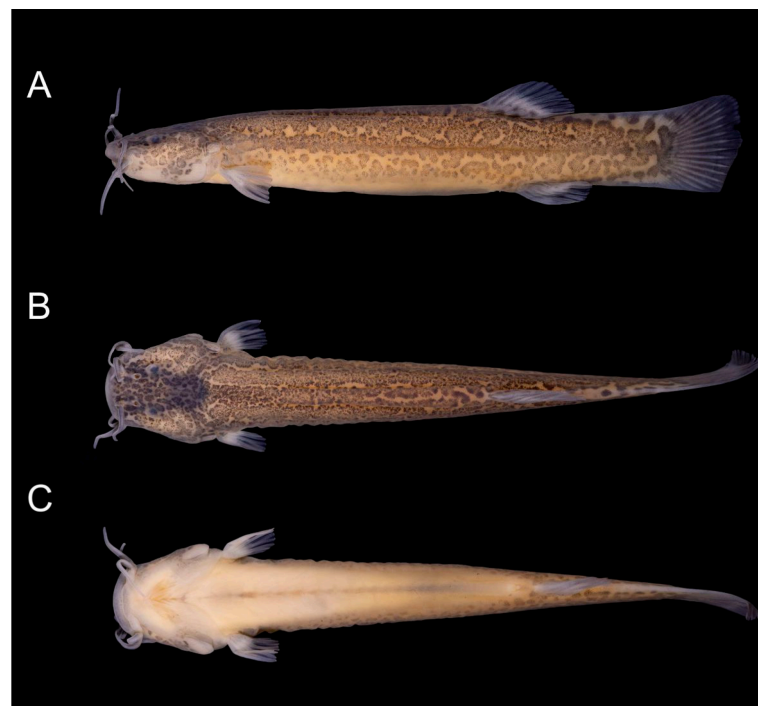


Figure 14. *Cambeva diegoi* sp. nov., UFRJ 15078, holotype, 43.0 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

Etymology. From the Latin, *curvilineata* (with curved lines) refers to yellowish white lines composed of numerous curves to form a sinuous pattern.

Distribution. Rio Chapecozinho subdrainage, Rio Chapecó drainage, Rio Uruguai basin (Figure 8A).

Habitat. Headwaters of small brooks, about 860 m asl, with leaf litter on silty bottom where specimens were found.

Cambeva diegoi sp. nov.

urn:lsid:zoobank.org:act: 1131BAEA-EB65-4459-9FFA-D774EA183C63.

Figures 3E, 4E, 6E and 14; Table 4.

Holotype. UFRJ 15078, 43.0 mm SL; Brazil: Estado de Santa Catarina: Município de Vargem Bonita: Campina da Alegria: brook tributary of middle Rio do Mato, tributary of Rio Chapecozinho, Rio Chapecó drainage, Rio Uruguai basin, 26°53'26" S 51°46'43" W, about 1075 m asl; C.R.M. Feltrin, 19 April 2026.

Paratypes. UFRJ 15067, 1 ex. (C&S), 27.3 mm SL; UFRJ 15035, 1 ex. (DNA), 24.3 mm SL; all collected with holotype.

Table 4. Morphometric data of *Cambeva diegoi* sp. nov.

	Holotype	Paratypes (n = 2)
Standard length (SL)	43.0	24.3–27.3
Percentage of standard length		
Body depth	15.3	14.6–17.0
Caudal peduncle depth	12.8	11.6–13.1
Body width	10.5	8.1–10.5
Caudal peduncle width	3.4	3.2–3.5
Pre-dorsal length	67.1	67.1–73.2
Dorsal-fin base length	11.8	11.8–13.9
Anal-fin base length	8.9	8.9–12.8
Caudal-fin length	17.1	15.8–17.9
Pectoral-fin length	10.3	10.3–13.4
Head length	20.6	20.6–23.4
Percentage of head length		
Head depth	48.4	40.2–48.4
Head width	82.6	69.7–82.6
Snout length	38.8	37.9–41.9
Interorbital width	28.8	21.4–28.8
Preorbital length	9.2	8.2–9.2
Eye diameter	10.2	10.2–11.6

Diagnosis. *Cambeva diegoi* is distinguished from all other species of CBS1 by the absence of pelvic fin and girdle (vs. presence); 39 vertebrae (vs. 36–38); ten branchiostegal rays (vs. seven or eight); 16 interopercular odontodes (vs. 22–37); and 45 dentary teeth (vs. 22–40).

Description. External morphology: Morphometric data in Table 4. Body relatively slender, greatest body depth at vertical through area midway distance between pectoral-fin base and anal-fin origin. Trunk subcylindrical on its anterior portion, deeper than broad, compressed posteriorly. Dorsal and ventral profiles of head and trunk weakly convex, dorsal and ventral profiles of caudal peduncle about straight. Anus and urogenital papilla opening located at vertical through area just anterior to middle of dorsal-fin base. Lateral line canal of trunk short, with two pores just posterior to opercular patch of odontodes.

Head sub-trapezoidal in dorsal view, anterior profile of snout slightly convex. Eye relatively small, round, dorsally positioned on head, nearer snout than posterior margin of opercle. Distance between anterior and posterior nostrils slightly shorter than distance between posterior nostril and orbital rim. Tip of nasal barbel reaching area between orbit and opercular patch of odontodes, tip of maxillary barbel reaching between interopercular patch of odontodes and pectoral-fin base, rictal barbel reaching area between middle and posterior portion of interopercular patch of odontodes. Mouth subterminal. Lateral fleshy lobe of mouth moderate in width and length, its longest length approximately half lower jaw length excluding lobes. Jaw teeth pointed, arranged in irregular rows, 35 on premaxilla, 45 on dentary. Whole head surface covered by small skin papillae, larger on lips and ventral surface of head. Branchial membrane thickened, attached to isthmus only at its anterior-most point, in ventral midline. Odontodes conical, narrow and approximately straight, nine on opercle, 16 on interopercle.

Supraorbital sensory canal continuous, with three paired pores: s1, s3, and s6. Pore s6 nearer orbit than its symmetrical homologous pore s6. Infraorbital canal represented by two separate segments, anterior segment delimited by pores io1 and io2, posterior segment with pores io8 and io9. Anterior infraorbital canal totally dermal, separated from lacrimal. Posterior infraorbital, supraorbital and postorbital canals continuous. Postorbital canal with two pores: po1 and po2.

Unpaired fins well-developed, pectoral fin relatively small, pelvic fin and girdle absent. Unpaired fins with slightly convex distal margins. Dorsal-fin origin nearer caudal-fin posterior margin than nape, anal-fin origin at vertical through posterior half of dorsal-fin base, through base of fourth dorsal-fin branched ray. Twelve (iii + II + 7) dorsal-fin rays, 10 (iii + II + 5) anal-fin rays. Pectoral fin subtriangular in dorsal view, first ray slightly longer than second ray. Six (I + 5) pectoral-fin rays. Thirteen (I + 11 + I) principal caudal-fin rays, 21 (xx + I) dorsal procurent rays, and 16 (xv + I) ventral procurent rays.

Osteology (Figures 3E, 4E and 6E): Anterior portion of mesethmoid moderate in width, subtriangular in dorsal view, anterior margin weakly convex in dorsal view, cornu pointed. Lateral ethmoid with minute lateral projection, supporting ligament connected to sesamoid supraorbital. Lacrimal small, elongate. Sesamoid supraorbital relatively short, about two times longer than lacrimal, with anteromedial projection supporting ligament connecting it to lateral ethmoid. Premaxilla subrectangular in dorsal view, maxilla slender, slightly curved, shorter than premaxilla, without distinct posterior process.

Autopalatine broad and short, subrectangular in dorsal view, medial margin nearly straight, without expansions, postero-lateral process short, subtriangular in dorsal view, postero-laterally directed. Metapterygoid small, sub-triangular. Quadrate L-shaped, with moderate anterior constriction and long narrow projection on its anterodorsal extremity. No laminar expansion articulating metapterygoid and quadrate. Hyomandibula elongate. Opercle elongate, opercular odontode patch narrow, its depth about half hyomandibula articular facet length. Dorsal process of opercle short, triangular. Opercular articular facet for hyomandibula with short rounded laminar projection. Articular facet for preopercle rudimentary. Interopercle relatively long, its longitudinal length about two thirds of total hyomandibula longitudinal length. Preopercle short, slender, without ventral projection.

Parurohyal thin, lateral process moderate in length, sharply pointed. Parurohyal head broad, with prominent anterolateral paired process. Parurohyal middle foramen large, oval. Parurohyal posterior process short, about half distance between anterior margin of parurohyal and anterior insertion of posterior process. Branchiostegal rays 10. Vertebrae 39. Ribs 15. Dorsal-fin origin at vertical through centrum of 23rd vertebra; anal-fin origin at vertical through centrum of 25th vertebra. Two dorsal and single ventral hypural plate.

Colouration in alcohol: Dorsal and lateral surface of trunk pale yellow with longitudinal series of brown spots with lighter centra; spot series highly coalesced longitudinally, except ventral-most one. Venter white. Dorsal and lateral surfaces of head pale yellow with pale brown spots. Barbels dark grey. Fins hyaline, with dark grey dots on basal portion of dorsal and anal fins.

Etymology. The name *diegoi* in honour of Diego da Silva, who first collected fishes in Campina da Alegria at the type locality of this new species.

Distribution. Upper Rio Chapecó drainage, Rio Uruguai basin (Figure 8B).

Habitat. Headwaters of a small brook, about 1075 m asl, with fine gravel, small pebbles and leaf litter on the bottom. The specimens were found buried in fine gravel deposited on the bottom of a small pool-like area within the brook channel.

Cambeva metagalactica sp. nov.

urn:lsid:zoobank.org:act: BF4775FC-AE23-4563-A6D8-768597CA3A9C.

Figures 3F, 4F, 6F and 15–17; Table 5.

Holotype. UFRJ 15099, 62.7 mm SL; Brazil: Estado de Santa Catarina: Município de Vargem Bonita: Campina da Alegria: small stream tributary of middle Rio do Mato, a tributary of Rio Chapecozinho, Rio Chapecó drainage, Rio Uruguai basin, 26°53'26" S 51°46'43" W, about 1075 m asl; C.R.M. Feltrin, 9 February 2026.

Paratypes. UFRJ 15068, 2 ex., 38.7–52.1 mm SL; UFRJ 15069, 3 ex. (C&S), 33.5–55.2 mm SL; UFRJ 14919, 2 ex. (DNA), 34.5–36.5 mm SL; collected with holotype. UFRJ 15019, 14 ex., 21.9–48.2 mm SL; CICCAA 13605, 3 ex., 38.0–44.5 mm SL; same locality and collector as holotype, 2 Apr. 2026. UFRJ 14559, 1 ex. (DNA), 54.9 mm SL; same locality as holotype; D. Silva, 25 March 2025. UFRJ 15070, 2 ex., 25.0–41.7 mm SL; same locality and collector as holotype, 19 April 2026. UFRJ 15101, 1 ex., 59.0 mm SL; Brazil: Estado de Santa Catarina: Município de Ponte Serrada: Flor do Mato: small stream tributary of middle Rio do Mato, a tributary of Rio Chapecozinho, Rio Chapecó drainage, Rio Uruguai basin, 26°50′13″ S 51°57′14″ W, about 1000 m asl; C.R.M. Feltrin, 20 June 2026.



Figure 15. *Cambeva metagalactica* sp. nov., UFRJ 15099, holotype, 62.7 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.



Figure 16. *Cambeva metagalactica* sp. nov., UFRJ 15068, paratype, 52.1 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.



Figure 17. *Cambeva metagalactica* sp. nov., UFRJ 15068, paratype, 38.7 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

Table 5. Morphometric data of *Cambeva metagalactica* sp. nov.

	Holotype	Paratypes (n = 9)
Standard length (SL)	62.9	31.0–65.0
Percentage of standard length		
Body depth	16.4	15.0–16.9
Caudal peduncle depth	13.4	12.0–13.7
Body width	12.4	10.4–12.0
Caudal peduncle width	4.3	3.2–4.5
Pre-dorsal length	64.4	64.0–70.0
Pre-pelvic length	61.7	58.2–63.2
Dorsal-fin base length	10.4	11.5–13.0
Anal-fin base length	9.1	9.4–11.8
Caudal-fin length	16.3	16.1–19.3
Pectoral-fin length	11.0	9.9–13.2
Pelvic-fin length	8.5	8.3–10.1
Head length	19.5	19.8–21.8
Percentage of head length		
Head depth	61.9	47.5–55.8
Head width	93.5	82.9–89.2
Snout length	41.9	38.6–43.1
Interorbital width	29.1	23.8–31.8
Preorbital length	9.1	8.1–9.6
Eye diameter	8.5	8.8–13.3

Diagnosis. *Cambeva metagalactica* is distinguished from all other species of CBS1 by having a unique flank colouration in larger specimens, about 55–60 mm SL, comprising pale purplish to brownish grey with yellowish white vermiculation pattern (Figure 16; vs. never a similar colour pattern); a distinctively broad anterior position of the mesethmoid (Figure 3F; vs. never so broad, Figure 3D,E,G) and a hypertrophied metapterygoid (Figure 4F; vs. not hypertrophied, Figure 4D,E,G). *Cambeva metagalactica* is also distinguished from other species of CBS1 by the presence of pelvic fin (vs. absence in *C. diegoi*); 37 or 38 vertebrae (vs. 39 in *C. diegoi*); eight branchiostegal rays (ten in *C. diegoi*); 33–37

interopercular odontodes (vs. 16 in *C. diegoi*, 22–23 in *C. minima* sp. nov. and 28–32 in *C. curvilineata*); 38–46 premaxillary teeth (vs. 30–37 in *C. curvilineata*); 37–40 dentary teeth (vs. 30–31 in *C. curvilineata*); presence of anterior infraorbital canal (vs. absence in *C. minima* sp. nov.); the lateral process of the parurohyal short, with broad basal portion (Figure 6F; vs. long with moderately wide or narrow basal portion in *C. diegoi*, Figure 6E, and *C. minima* sp. nov., Figure 6G, respectively).

Description. External morphology: Morphometric data in Table 5. Body relatively deep in larger specimens above about 60 mm SL to slender in juveniles, greatest body depth at vertical through area midway distance between pectoral and pelvic-fin bases. Trunk subcylindrical on its anterior portion, deeper than broad, compressed posteriorly. Dorsal profile of head and trunk nearly straight, ventral profile of head and abdomen slightly convex, dorsal and ventral profiles of caudal peduncle about straight. Anus and urogenital papilla opening located at vertical through middle of dorsal-fin base. Lateral line canal of trunk short, with two pores just posterior to opercular patch of odontodes.

Head sub-trapezoidal in dorsal view, anterior profile of snout slightly convex. Eye relatively small, round, dorsally positioned on head, nearer snout than posterior margin of opercle. Distance between anterior and posterior nostrils about equal distance between posterior nostril and orbital rim. Tip of nasal barbel reaching area just posterior to orbit, tip of maxillary and rictal barbels reaching anterior portion of interopercular patch of odontodes. Mouth subterminal. Lateral fleshy lobe of mouth narrow, moderate in length, its longest length approximately half lower jaw length excluding lobes. Jaw teeth pointed, arranged in irregular rows, 38–46 on premaxilla, 37–40 on dentary. Whole head surface covered by minute skin papillae. Branchial membrane thickened, attached to isthmus only at its anterior-most point, in ventral midline. Odontodes conical, narrow and approximately straight, 8 or 9 on opercle, 33–37 on interopercle.

Supraorbital sensory canal continuous, with three paired pores: s1, s3, and s6. Pore s6 about equidistant from its symmetrical homologous pore s6 and orbit. Infraorbital canal represented by two separate segments, anterior segment delimited by pores io1 and io2, posterior segment with pores io8 and io9. Anterior infraorbital canal totally dermal, separated from lacrimal. Posterior infraorbital, supraorbital and postorbital canals continuous. Postorbital canal with two pores: po1 and po2.

Fins well-developed, dorsal, anal and pectoral fins with thickened bases. Unpaired fins with convex distal margins. Dorsal-fin origin nearer caudal-fin posterior margin than nape, anal-fin origin at vertical through posterior portion of dorsal-fin base, through base of fourth dorsal-fin branched ray. Eleven (ii + II + 7) dorsal-fin rays, 9 (ii + II + 5) anal-fin rays. Pectoral fin subtriangular in dorsal view, first ray longer than other rays, its distal extremity slightly surpassing fin membrane. Six (I + 5) pectoral-fin rays. Pelvic fin with rounded posterior margin, reaching vertical through anterior portion of dorsal-fin base, its extremity not reaching anus. Pelvic-fin bases in close proximity. Five (I + 4) pelvic-fin rays. Thirteen (I + 11 + I) principal caudal-fin rays, 18–21 (xvii–xx + I) dorsal procurent rays, and 14 (xiii + I) ventral procurent rays.

Osteology (Figures 3F, 4F and 6F): Anterior portion of mesethmoid broad, subtriangular in dorsal view, anterior margin weakly convex in dorsal view, cornu pointed. Lateral ethmoid with prominent lateral projection, supporting ligament connected to sesamoid supraorbital. Lacrimal thin, slightly elongate, narrowing posteriorly. Sesamoid supraorbital relatively short, about two times longer than lacrimal, with anteromedial projection supporting ligament connecting it to lateral ethmoid. Premaxilla subrectangular in dorsal view, maxilla slender, slightly curved, shorter than premaxilla, without distinct posterior process.

Autopalatine broad and short, subrectangular in dorsal view, with rounded expansion on its medial margin and rudimentary postero-lateral process. Metapterygoid hypertrophied, sub-rectangular, deep, with rounded concavity in its anterior margin. Quadrate L-shaped, with deep anterior constriction. Small laminar projection overlapping ventral margin of metapterygoid just anterior to cartilage articulating metapterygoid and quadrate. Hyomandibula relatively short and deep. Opercle elongate, opercular odontode patch narrow, its depth about one third of hyomandibula articular facet length. Dorsal process of opercle short, pointed, slightly curved. Opercular articular facet for hyomandibula with short rounded laminar projection. Articular facet for preopercle rounded, short. Interopercle relatively long, its longitudinal length slightly shorter than total hyomandibula longitudinal length. Preopercle short, with moderate ventral projection.

Parurohyal thin, lateral process short, pointed. Parurohyal head broad, with prominent anterolateral paired process. Parurohyal middle foramen minute or absent. Parurohyal posterior process short, about half distance between anterior margin of parurohyal and anterior insertion of posterior process. Branchiostegal rays 8. Vertebrae 37 or 38. Ribs 14 or 15. Dorsal-fin origin at vertical between centra of 20th and 22nd vertebrae; anal-fin origin at vertical through centrum of 24th vertebra. Two dorsal and single ventral hypural plate.

Colouration in alcohol: In larger specimens above about 55–60 mm SL (Figure 15), dorsal and lateral surface of head and trunk pale purplish to brownish grey with yellowish white vermiculation pattern, slightly darker dorsally. Venter white. Nasal and maxillary barbels dark grey, rictal barbel white. Fins hyaline, with brown spots on basal portion of unpaired and pectoral fins. In juveniles, about 20–30 mm SL (Figure 17), flank light yellow with black stripe or row of dark grey spots along its longitudinal midline, dorsum with black spots. In specimens between about 35–50 mm SL (Figure 16), juvenile colour pattern gradually transforming to reach adult colour pattern, with fragmenting longitudinal stripe and spots becoming larger and clearer.

Etymology. From the Greek prefix *meta* (adjacent) and *galactica*, the specific epithet of the name of a congener occurring in another basin of the same region, that is superficially similar but not closely related to new species (Figure 1).

Distribution. Upper Rio Chapecozinho, Rio Chapecó drainage, Rio Uruguai basin (Figure 8B).

Habitat. Headwaters of small brooks, between about 1000 and 1080 m asl, with fine gravel, small pebbles and leaf litter and other vegetal debris on the bottom. Specimens were found buried in the leaf litter and other vegetal debris.

Cambeva minima sp. nov.

urn:lsid:zoobank.org:act: 5F7510F0-BC5D-4801-BF9F-B30F1B3F4FC5.

Figures 3G, 4G, 6G and 18; Table 6.

Holotype. UFRJ 15071, 40.1 mm SL; Brazil: Município de Ouro Verde: near the city of Ouro Verde, small stream tributary of Rio Chapecozinho, Rio Chapecó drainage, Rio Uruguai basin, 26°41'06" S 52°18'31" W, about 740 m asl; C.R.M. Feltrin, 20 May 2026.

Paratypes. UFRJ 15051, 3 ex., 31.5–41.3 mm SL; UFRJ 15050, 2 ex. (DNA), 33.2–37.6 mm SL; UFRJ 15072, 3 ex. (C&S), 33.0–37.6 mm SL; CICCAA 13606, 2 ex., 31.0–31.7 mm SL; collected with holotype. UFRJ 15073, 1 ex., 35.2 mm SL; UFRJ 14887, 1 ex (DNA), 31.5 mm SL; same locality and collector as holotype, 19 December 2025. UFRJ 15079, 37.8 mm SL; UFRJ 15074, 1 ex. (C&S), 35.1 mm SL; UFRJ 14885, 1 ex. (DNA), 33.1 mm SL; Município de Abelardo Luz: Capão Grande: small brook tributary of Rio Chapecó, Rio Uruguai basin, 26°36'50" S 52°15'01" W, about 825 m asl; C.R.M. Feltrin, 20 December 2025. UFRJ 15080, 1 ex. (C&S), 32.8 mm SL; stream tributary of Rio Chapecó, Rio Uruguai basin, 26°36'29" S 52°19'33" W, about 775 m asl; C.R.M. Feltrin, 20 December 2023.



Figure 18. *Cambeva minima* sp. nov., UFRJ 15071, holotype, 40.1 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

Table 6. Morphometric data of *Cambeva minima* sp. nov.

	Holotype	Paratypes (n = 9)
Standard length (SL)	40.1	31.0–41.3
Percentage of standard length		
Body depth	17.6	14.3–20.9
Caudal peduncle depth	13.5	12.7–15.9
Body width	11.3	11.2–13.9
Caudal peduncle width	4.6	3.1–5.0
Pre-dorsal length	68.6	64.8–69.2
Pre-pelvic length	64.5	59.4–66.9
Dorsal-fin base length	13.2	11.6–14.4
Anal-fin base length	10.3	8.6–10.8
Caudal-fin length	18.8	18.0–21.3
Pectoral-fin length	13.0	11.9–13.8
Pelvic-fin length	9.6	8.6–9.9
Head length	20.9	20.3–22.0
Percentage of head length		
Head depth	51.9	51.4–64.3
Head width	90.2	81.9–90.5
Snout length	42.2	39.0–43.4
Interorbital width	27.7	24.4–31.7
Preorbital length	8.2	6.3–10.0
Eye diameter	10.9	10.5–13.9

Diagnosis. *Cambeva minima* differs from all other congeners of CBS1 by the absence of anterior infraorbital canal (vs. presence), 22–24 dentary teeth (vs. 30–45) and a unique colour pattern on the flank that is yellowish white with small dark grey to black dots dorsally and on the caudal peduncle, with the anteroventral portion white, without dark dots (Figure 18, vs. never a similar colour pattern). *Cambeva minima* also differs from other species of CBS1 by the presence of pelvic fin (vs. absence in *C. diegoi*); 37 or 38 vertebrae (vs. 39 in *C. diegoi*); seven or eight branchiostegal rays (ten in *C. diegoi*); 22–23 interopercular odontodes (vs. 16 in *C. diegoi*, 33–37 in *C. metagalactica* and 28–32 in *C. curvilineata*); and 27–37 premaxillary teeth (vs. 38–46 in *C. metagalactica*).

Description. External morphology: Morphometric data in Table 6. Body relatively slender, greatest body depth at vertical through area midway distance between pectoral and pelvic-fin bases. Trunk subcylindrical on its anterior portion, deeper than broad, compressed posteriorly. Dorsal profile of trunk and head weakly convex, ventral profile about straight, dorsal and ventral profiles of caudal peduncle about straight. Anus and urogenital papilla opening located at vertical through anterior portion of dorsal-fin base. Lateral line canal of trunk short, with two pores just posterior to opercular patch of odontodes.

Head sub-trapezoidal in dorsal view, anterior profile of snout slightly convex. Eye relatively small, round, dorsally positioned on head, nearer snout than posterior margin of opercle. Distance between anterior and posterior nostrils slightly shorter or equal to distance between posterior nostril and orbital rim. Tip of nasal barbel reaching opercular patch of odontodes, tip of maxillary barbel reaching pectoral-fin base or area slightly anterior to it, rictal barbel reaching posterior portion of interopercular patch of odontodes or area just posterior to it. Mouth subterminal. Lateral fleshy lobe of mouth narrow, short, its longest length approximately slightly less than half lower jaw length excluding lobes. Jaw teeth pointed, arranged in irregular rows, 27–37 on premaxilla, 22–24 on dentary. Area around mouth and posterior portion of branchiostegal region covered by minute skin papillae. Branchial membrane thickened, attached to isthmus only at its anterior-most point, in ventral midline. Odontodes conical, narrow and approximately straight, 7 to 9 on opercle, 22 or 23 on interopercle.

Supraorbital sensory canal continuous, with three paired pores: s1, s3, and s6. Pore s6 nearer orbit than its symmetrical homologous pore s6. Anterior section of infraorbital canal absent. Posterior section of infraorbital canal with pores io8 and io9. Posterior infraorbital, supraorbital and postorbital canals continuous. Postorbital canal with two pores: po1 and po2.

Fins well-developed, dorsal, anal and pectoral fins with thickened bases. Unpaired fins with convex distal margins. Dorsal-fin origin nearer caudal-fin posterior margin than nape, anal-fin origin at vertical through middle of dorsal-fin base or gently posterior to it, through base of third dorsal-fin branched ray. Eleven or twelve (ii–iii + II + 7) dorsal-fin rays, 7–9 (i–ii + I–II + 5) anal-fin rays. Pectoral fin subtriangular in dorsal view, first ray longer than other rays, its distal extremity surpassing fin membrane, forming filament about 5–10% of pectoral-fin length excluding filament. Six (I + 5) pectoral-fin rays. Pelvic fin with rounded posterior margin, reaching vertical through middle of dorsal-fin base, its extremity not reaching anus. Pelvic-fin bases medially in close proximity. Five (I + 4) pelvic-fin rays. Thirteen (I + 11 + I) principal caudal-fin rays, 19–20 (xviii–xix + I) dorsal procurent rays, and 15 (xiv + I) ventral procurent rays.

Osteology (Figures 3G, 4G and 6G): Anterior portion of mesethmoid broad, subtriangular in dorsal view, anterior margin about straight in dorsal view, cornu sharply pointed. Lateral ethmoid with minute lateral projection, supporting ligament connected to sesamoid supraorbital. Lacrimal thin, posteriorly elongate. Sesamoid supraorbital relatively short, slightly longer than lacrimal, with anteromedial projection supporting ligament connecting it to lateral ethmoid. Premaxilla subrectangular in dorsal view, maxilla slender, curved, shorter than premaxilla, with minute posterior process.

Autopalatine broad and short, subrectangular in dorsal view, with weakly sinuous medial margin and rudimentary postero-lateral process. Metapterygoid large, sub-rectangular, deep. Quadrate L-shaped, with deep anterior constriction. No laminar expansion articulating metapterygoid and quadrate. Hyomandibula relatively short and deep. Opercle elongate, opercular odontode patch narrow, its depth about one third hyomandibula articular facet length. Dorsal process of opercle triangular, short, with curved tip. Opercular articular facet for hyomandibula with short rounded laminar projection. Articular facet for preoper-

cle rudimentary. Interopercle relatively long, its longitudinal length about two thirds of total hyomandibula longitudinal length. Preopercle short, without ventral projection.

Parurohyal thin, lateral process narrow, pointed. Parurohyal head relatively narrow, with prominent anterolateral paired process. Parurohyal middle foramen oval. Parurohyal posterior process short, about half distance between anterior margin of parurohyal and anterior insertion of posterior process. Branchiostegal rays 7–8. Vertebrae 37–38. Ribs 14–15. Dorsal-fin origin at vertical through centrum of 20th or 21st vertebra; anal-fin origin at vertical through centrum of 24th or 25th vertebra. Two dorsal and single ventral hypural plate.

Colouration in alcohol: Dorsal and lateral surfaces of trunk yellowish white to white ventrally, with small dark grey to black dots on dorsum and flank, except on anteroventral portion of flank; dots on dorsum with lighter centra, dots on anterior portion of longitudinal midline of flank coalesced to form stripe. Venter white. Dorsal and lateral surfaces of head light grey with minute brown dots. Barbels light grey. Fins hyaline, with black dots on basal portion of pectoral and dorsal fins.

Etymology. From the Latin, *minima* (minimum) referring to the small size of the new species, the smallest in the genus, barely reaching 40 mm SL.

Distribution. Middle Rio Chapecó and Middle Rio Chapecozinho drainages, Rio Uruguai basin (Figure 8B).

Habitat. Small streams at about 740–825 m asl. Specimens were found in the stream bottom composed of small pebbles, fine gravel and sand, with some specimens also found buried in amphibious marginal vegetation.

3.5. The *Cambeva betabelardense* Subclade 2 (CBS2)

Diagnosis. Species of CBS2 are distinguished from species of CAC and CBS1 by having a relatively broad opercular patch, with 11–14 odontodes (Figure 5A–F; vs. a narrow opercular odontode patch with 7 to 9 odontodes, Figure 4A–G); and the presence of laminar extensions on the border of the metapterygoid and the quadrate to form an additional point of articulation, just anterior to the articulatory cartilage (Figure 5A–F; vs. absence, Figure 4A–G). Species of CBS2 are also distinguished from species of CBS1 by the absence of a ligamentous connection between the lateral ethmoid and the sesamoid supraorbital and from species of CAC by the absence of a long nerve canal, positioned obliquely along the dorsal surface of the bone.

Habitat. Species of CBS2 are found in streams with small pebbles, gravel and sometimes sand deposited on stream bottom.

Cambeva admirabilis sp. nov.

urn:lsid:zoobank.org:act: B4A55528-37F9-4282-9056-D10DF58445F7.

Figures 3H, 5A, 6H and 19; Table 7.

Holotype. UFRJ 15081, 51.0 mm SL; Brazil: Estado de Santa Catarina: Município de Abelardo Luz: Linha Canhadão: headwater of small stream tributary of middle Rio Chapecó drainage, Rio Uruguai basin, 26°39'42" S 52°25'29" W, about 690 m asl; C.R.M. Feltrin, 20 June 2026.

Paratypes. UFRJ 15082, 2 ex. (C&S), 29.0–38.4 mm SL; UFRJ 15083, 2 ex. (C&S), 38.0–44.0 mm SL; collected with holotype. UFRJ 15084, 2 ex., 29.9–35.3 mm SL; headwater of small stream tributary of middle Rio Chapecó drainage, Rio Uruguai basin, 26°39'30" S 52°23'42" W, about 700 m asl; C.R.M. Feltrin, 20 June 2026. UFRJ 15057, 1 ex. (DNA), 26.9 mm SL; same locality as preceding, 20 December 2025.

Diagnosis. *Cambeva admirabilis* differs from all other species of CBS2, except *Cambeva insperata* sp. nov., by the pelvic fin that is absent or rudimentary (vs. pelvic fin well-developed). *Cambeva admirabilis* differs from *C. insperata* sp. nov. by having longer barbels,

with the nasal barbel reaching the opercular patch of odontodes (vs. area just posterior to orbit) and the maxillary and rictal barbels reaching area between the interopercular patch of odontodes and the pectoral-fin base (vs. reaching the anterior portion of the interopercular patch of odontodes), incisiform jaw teeth arranged in two or three regular rows (vs. jaw teeth sub-incisiform, with rounded extremity, irregularly arranged) and 38 vertebrae (vs. 39–41). *Cambeva admirabilis* is also distinguished from other congeners of CBS2 by having the distance between the posterior nostril and the orbital rim about equal to the distance between the anterior and posterior nostrils (vs. two times in *C. insperata* sp. nov. and *C. intermedia* sp. nov.); a colour pattern consisting of dark brown spots coalesced on the caudal peduncle side, forming a large dark zone (vs. dotted caudal peduncle side in *Cambeva dominguense* sp. nov., *Cambeva intermedia* sp. nov. and *Cambeva mundana* sp. nov.); the dorsal-fin origin at the vertical through the centrum of the 21st vertebra (vs. between centra of the 19th and 20th vertebrae in *C. intermedia* sp. nov. and through the centrum of the 23rd vertebra in *C. dominguense* sp. nov.); six pectoral-fin rays (vs. seven in *C. intermedia* sp. nov.); absence of a rounded projection on the anterior portion of the interopercular bone (Figure 5A; vs. presence in all other species, except *C. mundana* sp. nov., Figure 5B–E); and presence of a U-shaped concavity in the posterior portion of the dorsal margin of the hyomandibula anterior outgrowth (Figure 5A; vs. absence in all other species, except *C. mundana* sp. nov., Figure 5B–E).

Description. External morphology: Morphometric data in Table 7. Body slender, greatest body depth at vertical through area midway between pectoral-fin base and anal-fin base. Trunk subcylindrical on its anterior portion, slightly deeper than broad, compressed posteriorly. Dorsal profile of head and trunk about straight, ventral profile of head and abdomen slightly convex, dorsal and ventral profiles of caudal peduncle nearly straight. Anus and urogenital papilla opening located at vertical through middle of dorsal-fin base. Lateral line canal of trunk short, with two pores just posterior to opercular patch of odontodes.



Figure 19. *Cambeva admirabilis* sp. nov., UFRJ 15081, holotype, 51.0 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

Head sub-trapezoidal in dorsal view, anterior profile of snout slightly convex. Eye relatively small, round, dorsally positioned on head, nearer snout than posterior margin of opercle. Distance between anterior and posterior nostrils about equal to distance between posterior nostril and orbital rim. Tip of nasal barbel reaching opercular patch of odontodes,

tip of maxillary and rictal barbels reaching area between interopercular patch of odontodes and pectoral-fin base. Mouth subterminal. Lateral fleshy lobe of mouth small, its longest length approximately half lower jaw length excluding lobes. Jaw teeth incisiform, larger teeth sometimes with slightly bifid extremity, smaller teeth with weakly rounded extremity; teeth arranged in two or three rows, total premaxillary teeth 25–31, total dentary teeth 24–27. Head surface covered by minute skin papillae. Branchial membrane thickened, attached to isthmus only at its anterior-most point, in ventral midline. Odontodes conical, straight to slightly curved, 12–13 on opercle, 20–24 on interopercle.

Table 7. Morphometric data of *Cambeva admirabilis* sp. nov.

	Holotype	Paratypes (n = 4)
Standard length (SL)	51.0	35.3–44.0
Percentage of standard length		
Body depth	12.9	11.0–16.1
Caudal peduncle depth	10.3	10.3–13.2
Body width	10.8	10.7–14.0
Caudal peduncle width	3.7	3.9–4.7
Pre-dorsal length	64.2	67.0–68.5
Dorsal-fin base length	12.1	11.1–13.6
Anal-fin base length	7.5	8.4–9.8
Caudal-fin length	17.4	17.9–19.3
Pectoral-fin length	10.9	11.5–12.9
Head length	18.9	19.9–20.9
Percentage of head length		
Head depth	55.2	52.7–56.0
Head width	84.2	82.6–87.8
Snout length	41.6	38.3–41.4
Interorbital width	27.0	23.1–27.7
Preorbital length	6.7	8.1–9.8
Eye diameter	10.7	9.3–11.0

Supraorbital sensory canal continuous, with three paired pores: s1, s3, and s6. Pore s6 nearer orbit than its symmetrical homologous pore s6. Anterior infraorbital section absent. Posterior infraorbital segment with pores io8 and io9. Posterior infraorbital, supraorbital and postorbital canals continuous. Postorbital canal with two pores: po1 and po2.

Unpaired and pectoral fins well-developed, pelvic fin and girdle absent, except in one specimen with rudimentary pelvic fin. Dorsal, anal and pectoral fins with thickened bases. Unpaired fins with convex distal margins. Dorsal-fin origin nearer caudal-fin posterior margin than nape, anal-fin origin at vertical through posterior portion of dorsal-fin base, through base of third dorsal-fin branched ray. Total of 11 (ii + II + 7) dorsal-fin rays, total of nine (ii + II + 5) anal-fin rays. Pectoral fin subtriangular in dorsal view, first ray slightly surpassing fin membrane to form short filament about 5% of pectoral-fin length. Six (I + 5) pectoral-fin rays. Total of 13 (I + 11 + I) principal caudal-fin rays, 17–18 (xvi–xvii + I) dorsal procurent rays, and 12–14 (xi–xiii + I) ventral procurent rays.

Osteology (Figures 3H, 5A and 6H): Anterior portion of mesethmoid narrow, T-shaped in dorsal view, anterior margin weakly concave in dorsal view, cornu slightly curved, pointed. Lateral ethmoid without distinctive projections. Lacrimal thin, drop-shaped. Sesamoid supraorbital relatively short, slightly narrower and longer than lacrimal, without lateral projections. Premaxilla subrectangular in dorsal view, maxilla slender, slightly curved, shorter than premaxilla, without distinct posterior process.

Autopalatine moderately broad and short, subrectangular in dorsal view when excluding posterolateral process, lateral margin about straight, medial margin weakly sinuous.

Autopalatine postero-lateral process short, subtriangular in dorsal view. Metapterygoid moderate in size, sub-triangular. Quadrate L-shaped, with deep anterior constriction. Short laminar expansion articulating metapterygoid and quadrate just anterior to articular cartilage. Hyomandibula relatively short and slender. Opercle compact, opercular odontode patch moderately wide, its depth about three-fourths hyomandibula articular facet length. Dorsal process of opercle short, subtriangular, slightly curved. Opercular articular facet for hyomandibula with short rounded laminar projection. Articular facet for preopercle short and rounded. Interopercle moderately long, its longitudinal length about two thirds of total hyomandibula longitudinal length; anterior portion of interopercle with short and narrow expansion. Preopercle elongate, with short ventral projection.

Parurohyal thin, lateral process short, subtriangular. Parurohyal head broad, with prominent anterolateral paired process. Parurohyal middle foramen minute. Parurohyal posterior process moderate in length, about half distance between anterior margin of parurohyal and anterior insertion of posterior process. Branchiostegal rays 8. Vertebrae 38. Ribs 13. Dorsal-fin origin at vertical through centrum of 21st vertebrae; anal-fin origin at vertical through centrum of 25th vertebra. Two dorsal and single ventral hypural plate.

Colouration in alcohol (Figure 19): Dorsal and lateral surface of head and trunk pale yellow with dark brown spots, large and coalesced on caudal peduncle side, small on antero-ventral portion of flank. Venter yellowish white. Barbels pale brown. Fins hyaline, dark grey to black dots on basal portion of dorsal, anal and pectoral fins and whole caudal-fin membrane.

Etymology. From the Latin *admirabilis* (admirable), due to the admirable, unexpected finding of this new species during the final stage of this study.

Distribution. Middle Rio Chapecó drainage, Rio Uruguai basin (Figure 8C).

Habitat. Headwaters of small streams, about 700 m asl, with small pebbles and gravel on the bottom, where specimens were buried during collections.

Cambeva betabelardense Costa, Feltrin & Katz, 2022.

urn:lsid:zoobank.org:act:E77B223C-C536-4729-B483-BC9B0AD3E8CE.

Figures 3I, 5B, 6I, 20 and 21.



Figure 20. *Cambeva betabelardense*, UFRJ 6995, holotype, 42.7 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.



Figure 21. *Cambeva betabelardense*, UFRJ 15021, 61.3 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

Cambeva betabelardense Costa, Feltrin & Katz [11]: 148 (original description; type locality: Brazil: Santa Catarina State: Abelardo Luz Municipality: stream tributary to middle Rio Chapecó, Rio Uruguai basin, 26°29'32" S, 52°20'32" W; 820 m a.s.l; holotype: UFRJ 6995, 42.7 mm SL).

Diagnosis. *Cambeva betabelardense* is distinguished from other congeners of CBS2 by having relatively short barbels, with the nasal barbel reaching area just posterior to the orbit (vs. reaching the opercular patch of odontodes in *C. admirabilis*, *C. dominguense* sp. nov. and *C. mundana* sp. nov.) and the maxillary and rictal barbels reaching the interopercular patch of odontodes (vs. reaching area between the interopercular patch of odontodes and the pectoral-fin base in *C. admirabilis*, *C. dominguense* sp. nov. and *C. mundana* sp. nov.); incisiform jaw teeth arranged in two or three regular rows (vs. jaw teeth sub-incisiform, with rounded extremity, irregularly arranged in *C. insperata* sp. nov.); 37 or 38 vertebrae (vs. 39–41 in *C. insperata* sp. nov.); the distance between the posterior nostril and the orbital rim about equal to the distance between the anterior and posterior nostrils (vs. two times in *C. insperata* sp. nov. and *C. intermedia* sp. nov.); a colour pattern consisting of dark brown spots coalesced on the caudal peduncle side, forming a large dark zone (vs. dotted caudal peduncle side in *Cambeva dominguense* sp. nov., *Cambeva intermedia* sp. nov. and *Cambeva mundana* sp. nov.); the dorsal-fin origin at the vertical through the centrum of the 21st vertebra (vs. between centra of the 19th and 20th vertebrae in *C. intermedia* sp. nov. and through the centrum of the 23rd vertebra in *C. dominguense* sp. nov.); six pectoral-fin rays (vs. seven in *C. intermedia* sp. nov.); and presence of a rounded projection on the anterior portion of the interopercular bone (Figure 5B; vs. absence in *C. admirabilis* and *C. mundana* sp. nov., Figure 5A, F). For a full description, see [11].

Distribution. Middle Rio Chapecó drainage (Figure 8C).

Habitat. As described for *C. admirabilis* (see also [11]).

Remarks. *Cambeva betabelardense* is a polymorphic species. Specimens from the type locality area are small, rarely reaching about 48 mm SL, whereas in other localities specimens are usually larger, commonly surpassing 50 mm SL and reaching 62 mm SL. Specimens from the type locality area are predominantly represented by a colour morph consisting of large dark brown to black blotches on the dorsal portion of the flank and on the caudal

peduncle (Figure 20), whereas in other areas predominates a second colour morph, in which those blotches are dispersed, forming a diffuse pattern (Figure 21), whereas some specimens may be strongly paler, making difficult to observe their colour pattern.

Material examined: All from Brazil: Estado de Santa Catarina. Município de Abelardo Luz: UFRJ 6995, holotype, 42.7 mm SL; UFRJ 6996, 10 paratypes, 19.7–38.6 mm SL; UFRJ 6997, 3 paratypes (C&S), 32.4–37.4 mm SL; CICCAA 12707, 2 paratypes, 33.2–34.8 mm SL; stream tributary to middle Rio Chapecó, Rio Uruguai basin, 26°29'32" S, 52°20'32" W, 820 m asl; C.R.M. Feltrin, 20 March 2021. UFRJ 7002, 15 ex., 25.7–45.6 mm SL; same locality and collector as holotype, August 2021. UFRJ 14099, 3 ex. (DNA), 27.2–30.3 mm SL; same locality and collector as holotype, 20 May 2021. UFRJ 14929, 4 ex., 30.5–44.1 mm SL; UFRJ 14997, 2 ex. (DNA), 47.3–48.1 mm SL; stream tributary to Rio Aurora, middle Rio Chapecó drainage, 26°30'17" S, 52°21'23" W, about 820 m asl; C.R.M. Feltrin, 19 December 2025. UFRJ 6998, 4 paratypes, 36.8–41.3 mm SL; stream tributary to middle Rio Chapecó, in front of Parque Quedas de Chapecó, 26°33'08" S, 52°19'13" W, 760 m asl; C.R.M. Feltrin, 20 March 2021. UFRJ 15049, 10 ex., 29.5–52.8 mm SL; stream tributary of Rio Chapecó, Capão Grande, 26°36'59" S, 52°15'18" W, 803 m asl; C.R.M. Feltrin, 20 May 2026. UFRJ 15022, 12 ex., 22.3–50.3 mm SL; UFRJ 15085, 1 ex. (DNA), 32.2 mm SL; stream tributary of Rio Chapecó, Capão Grande, 26°36'01" S, 52°15'23" W, 825 m asl; C.R.M. Feltrin, 3 April 2026. UFRJ 14936, 7 ex., 17.4–62.4 mm SL; UFRJ 15086, 2 ex. (DNA), 30.0–33.6 mm SL; stream tributary of Rio Chapecó, Capão Grande, 26°37'09" S, 52°13'49" W, about 790 m asl; C.R.M. Feltrin, 20 December 2025. UFRJ 14934, 16 ex., 17.1–27.1 mm SL; stream tributary of Rio Chapecó, Capoeiras, 26°29'50" S, 52°24'45" W, 815 m asl; C.R.M. Feltrin, 20 December 2025. UFRJ 14931, 2 ex., 22.9–23.4 mm SL; stream tributary of Rio Chapecó, Linha Araçá, 26°38'17" S, 52°15'53" W, 830 m asl; C.R.M. Feltrin, 20 December 2025. Município de Ouro Verde: UFRJ 15021, 14 ex., 41.4–61.3 mm SL; UFRJ 15087, 3 ex.; 50.9–61.3 mm SL; Linha Rolador: Ribeirão Rolador, tributary of Rio Chapecó, Rio Uruguai basin, 26°41'31" S 52°13'00" W, about 920 m asl; C.R.M. Feltrin, 3 April 2026.

Cambeva dominguense sp. nov.

urn:lsid:zoobank.org:act: 998B4C73-C8EB-4E64-8587-EEE9FF6078D8.

Figures 3J, 5C, 6J and 22; Table 8.



Figure 22. *Cambeva dominguense* sp. nov., UFRJ 15091, holotype, 44.4 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

Table 8. Morphometric data of *Cambeva dominguense* sp. nov.

	Holotype	Paratypes (n = 6)
Standard length (SL)	44.4	33.8–46.0
Percentage of standard length		
Body depth	13.7	14.4–16.5
Caudal peduncle depth	11.4	11.7–13.0
Body width	9.6	10.7–14.9
Caudal peduncle width	3.8	3.4–4.0
Pre-dorsal length	69.4	63.9–68.1
Pre-pelvic length	63.9	60.3–62.8
Dorsal-fin base length	12.5	11.0–12.5
Anal-fin base length	9.4	7.7–9.9
Caudal-fin length	19.8	16.4–20.2
Pectoral-fin length	11.5	9.5–12.0
Pelvic-fin length	8.7	7.5–8.8
Head length	18.5	17.3–19.2
Percentage of head length		
Head depth	48.2	47.9–57.5
Head width	81.0	82.1–91.5
Snout length	37.6	37.1–41.9
Interorbital width	23.4	19.6–27.4
Preorbital length	9.6	7.3–9.4
Eye diameter	9.6	10.3–12.3

Holotype. UFRJ 15091, 44.4 mm SL; Brazil: Estado de Santa Catarina: Município de São Domingos: Linha Imigra: stream tributary of Rio Chapecó, Rio Uruguai basin, 26°32′02″ S 52°28′43″ W, about 725 m asl; C.R.M. Feltrin, 21 May 2026.

Paratypes. All from Brazil: Estado de Santa Catarina: Município de São Domingos: Rio Chapecó drainage, Rio Uruguai basin. UFRJ 15092, 2 ex., 17.5–33.8 mm SL; UFRJ 15100, 1 ex. (C&S), 40.9 mm SL; UFRJ 15052, 1 ex. (DNA), 30.1 mm SL; collected with holotype. UFRJ 15093, 2 ex., 21.9–43.9 mm SL; Linha São Brás: stream tributary to middle Rio Chapecó drainage, 26°31′05″ S 52°34′35″ W, about 695 m asl; C.R.M. Feltrin, 3 April 2026. UFRJ 15094, 2 ex., 43.9–46.0 mm SL; UFRJ 15095, 1 ex. (C&S), 44.5 mm SL; same locality and collector as preceding, 20 June 2026.

Diagnosis. *Cambeva dominguense* differs from all other congeners by having a relatively narrow and moderately long lateral process of the parurohyal (Figure 6J; vs. distinctively broader and shorter, Figure 6H,I,K–M). *Cambeva dominguense* is also distinguished from other congeners of CBS2 by having relatively long barbels, with the nasal barbel reaching the opercular patch of odontodes (vs. reaching the area just posterior to the orbit in *C. betabelardense*, *C. insperata* sp. nov. and *C. intermedia* sp. nov.) and the maxillary and rictal barbels reaching the area between the interopercular patch of odontodes and the pectoral-fin base (vs. reaching the interopercular patch of odontodes in *C. betabelardense*, *C. insperata* sp. nov. and *C. intermedia* sp. nov.); incisiform jaw teeth arranged in two or three regular rows (vs. jaw teeth sub-incisiform, with rounded extremity, irregularly arranged in *C. insperata* sp. nov.); 38 vertebrae (vs. 39–41 in *C. insperata* sp. nov.); the distance between the posterior nostril and the orbital rim about equal to the distance between the anterior and posterior nostrils (vs. two times in *C. insperata* sp. nov. and *C. intermedia* sp. nov.); the dorsal-fin origin at the vertical through the centrum of the 23rd vertebra (vs. between centra of the 19th and 21st vertebrae in all other species, except *C. insperata* sp. nov.); six pectoral-fin rays (vs. seven in *C. intermedia* sp. nov.); and presence of a rounded projection on the anterior portion of the interopercular bone (Figure 5B; vs. absence in *C. admirabilis* and *C. mundana* sp. nov., Figure 5A,F).

Description. External morphology: Morphometric data in Table 8. Body slender, greatest body depth at vertical through area midway pectoral and pelvic-fin bases. Trunk subcylindrical on its anterior portion, slightly deeper than broad, compressed posteriorly. Dorsal profile of head and trunk weakly convex, ventral profile of head and abdomen about straight, dorsal and ventral profiles of caudal peduncle nearly straight. Anus and urogenital papilla opening located at vertical through anterior half of dorsal-fin base. Lateral line canal of trunk short, with two pores just posterior to opercular patch of odontodes.

Head sub-trapezoidal in dorsal view, anterior profile of snout about straight. Eye relatively small, round, dorsally positioned on head, nearer snout than posterior margin of opercle. Distance between anterior and posterior nostrils about equal to distance between posterior nostril and orbital rim. Tip of nasal barbel reaching opercular patch of odontodes, tip of maxillary and rictal barbels reaching between interopercular patch of odontodes and pectoral-fin base. Mouth subterminal. Lateral fleshy lobe of mouth narrow and moderate in length, its longest length about half lower jaw length excluding lobes. Jaw teeth incisiform, arranged in three rows, total of 25 on premaxilla, 26 on dentary. Head surface covered by minute skin papillae. Branchial membrane thickened, attached to isthmus only at its anterior-most point, in ventral midline. Odontodes conical, straight to slightly curved, 11 on opercle, 19 on interopercle.

Supraorbital sensory canal continuous, with three paired pores: s1, s3, and s6. Pore s6 nearer orbit than its symmetrical homologous pore s6. Anterior infraorbital section absent. Posterior infraorbital segment with pores io8 and io9. Posterior infraorbital, supraorbital and postorbital canals continuous. Postorbital canal with two pores: po1 and po2.

Fins well-developed, dorsal, anal and pectoral fins with thickened bases. Unpaired fins with convex distal margins. Dorsal-fin origin nearer caudal-fin posterior margin than nape, anal-fin origin at vertical through posterior portion of dorsal-fin base, through base of fourth dorsal-fin branched ray. Eleven (ii + II + 7) dorsal-fin rays, 9 (ii + II + 5) anal-fin rays. Pectoral fin subtriangular in dorsal view, first ray extremity forming short filament about 5% of pectoral-fin length. Six (I + 5) pectoral-fin rays. Pelvic fin with rounded posterior margin, reaching vertical through anterior portion of dorsal-fin base, its extremity not reaching anus. Pelvic-fin bases in close proximity. Five (I + 4) pelvic-fin rays. Thirteen (I + 11 + I) principal caudal-fin rays, 17 (xvi + I) dorsal procurrent rays, and 12 (xi + I) ventral procurrent rays.

Osteology (Figures 3J, 5C and 6J): Anterior portion of mesethmoid narrow, subtriangular in dorsal view, anterior margin weakly concave in dorsal view, cornu pointed. Lateral ethmoid without lateral projections. Lacrimal thin, drop-shaped. Sesamoid supraorbital relatively short, longer than lacrimal, without distinctive lateral projections. Premaxilla subrectangular in dorsal view, slender; maxilla slightly curved, shorter than premaxilla, without distinct posterior process.

Autopalatine moderately broad and short, subrectangular in dorsal view when excluding posterolateral process, lateral margin slightly convex, medial margin weakly sinuous. Autopalatine postero-lateral process short, subtriangular in dorsal view, with posteriorly directed tip. Metapterygoid large, sub-triangular. Quadrate L-shaped, with deep anterior constriction. Short laminar expansion articulating metapterygoid and quadrate anterior to articular cartilage. Hyomandibula moderate in length and depth. Opercle short, opercular odontode patch relatively robust, its depth three-fourths hyomandibula articular facet length. Dorsal process of opercle short, subtriangular, slightly curved. Opercular articular facet for hyomandibula with short rounded laminar projection. Articular facet for preopercle rounded, minute. Interopercle moderately long, its longitudinal length about three fourths of total hyomandibula longitudinal length. Preopercle elongate, with short ventral projection.

Parurohyal thin, lateral process moderate in length, slightly pointed. Parurohyal head broad, with prominent anterolateral paired process. Parurohyal middle foramen small, rounded. Parurohyal posterior process moderate in length, about three-fourths distance between anterior margin of parurohyal and anterior insertion of posterior process. Branchiostegal rays 8. Vertebrae 38. Ribs 13. Dorsal-fin origin at vertical through 23rd vertebra; anal-fin origin at vertical through centrum of 26th vertebra. Two dorsal and single ventral hypural plate.

Colouration in alcohol: Dorsal and lateral surface of head and trunk yellowish white with irregularly arranged rounded dark grey to black blotches. Venter white. Barbels dark grey. Fins hyaline, dark grey to black spots on basal portion of dorsal fin and whole caudal fin.

Etymology. The name *dominguense* refers to the occurrence of the new species in the Município of São Domingos, Estado de Santa Catarina, southern Brazil.

Distribution. Middle Rio Chapecó drainage, Rio Uruguai basin (Figure 8C).

Habitat. Small streams about 700–725 m asl, with small pebbles and gravel on the bottom. Specimens were found buried in that bottom sediment.

Cambeva insperata sp. nov.

urn:lsid:zoobank.org:act: 5C1D8994-F7B6-4700-B5B3-EB2662F9FE2B.

Figures 3K, 5D, 6K and 23; Table 9.

Holotype. UFRJ 15016, 45.0 mm SL; Brazil: Estado de Santa Catarina: Município de Água Doce: Herciliópolis: upper Rio Chapecó, Rio Uruguai basin, 26°42'29" S 51°27'21" W, about 1245 m asl; C.R.M. Feltrin, 2 April 2026.

Paratypes. UFRJ 14908, 1 ex. (DNA), 24.4 mm SL; UFRJ 14921, 1 ex., 23.4 mm SL; UFRJ 15096, 2 ex. (C&S), 28.2–41.3 mm SL; same locality and collector as holotype, 6 February 2026.

Diagnosis. *Cambeva insperata* differs from all other congeners of CBS2 by having jaw teeth sub-incisiform, with rounded extremity, irregularly arranged (vs. incisiform jaw teeth arranged in two or three regular rows) and 39–41 vertebrae (vs. 36–38). *Cambeva insperata* also differs from all other species of CBS2, except *C. admirabilis*, by the absence of pelvic fin. *Cambeva insperata* differs from *C. admirabilis* by having shorter barbels, with the nasal barbel reaching area just posterior to orbit (vs. the opercular patch of odontodes) and the maxillary and rictal barbels reaching the anterior portion of the interopercular patch of odontodes (vs. reaching area between the interopercular patch of odontodes and the pectoral-fin base).



Figure 23. *Cambeva insperata* sp. nov., UFRJ 15016, holotype, 45.0 mm SL: (A), left lateral view; (B) dorsal view; (C), ventral view.

Table 9. Morphometric data of *Cambeva insperata* sp. nov.

	Holotype	Paratypes (n = 3)
Standard length (SL)	45.0	24.4–41.3
Percentage of standard length		
Body depth	14.0	14.0–17.2
Caudal peduncle depth	11.5	11.5–12.8
Body width	11.3	10.4–12.3
Caudal peduncle width	3.7	3.4–3.8
Pre-dorsal length	67.0	64.6–70.1
Dorsal-fin base length	10.8	10.8–13.2
Anal-fin base length	8.4	8.4–11.9
Caudal-fin length	16.6	16.5–20.4
Pectoral-fin length	10.3	10.3–12.4
Head length	17.7	17.7–22.0
Percentage of head length		
Head depth	53.7	47.1–53.7
Head width	84.2	77.1–84.2
Snout length	41.1	38.9–41.1
Interorbital width	22.4	22.4–27.6
Preorbital length	10.1	8.4–12.8
Eye diameter	13.5	12.8–26.2

Description. External morphology: Morphometric data in Table 9. Body relatively slender, greatest body depth at vertical through area immediately anterior to dorsal-fin base. Trunk subcylindrical on its anterior portion, slightly deeper than broad, compressed posteriorly. Dorsal profile of head and trunk weakly convex, ventral profile of head and abdomen about straight, dorsal and ventral profiles of caudal peduncle nearly straight. Anus and urogenital papilla opening located at vertical through anterior half of dorsal-fin base. Lateral line canal of trunk short, with two pores just posterior to opercular patch of odontodes.

Head sub-trapezoidal in dorsal view, anterior profile of snout slightly convex. Eye relatively large, round, dorsally positioned on head, nearer snout than posterior margin of opercle. Distance between anterior and posterior nostrils about half distance between posterior nostril and orbital rim. Tip of nasal barbel reaching area just posterior to orbit, tip of maxillary and rictal barbels reaching anterior portion of interopercular patch of odontodes. Mouth subterminal. Lateral fleshy lobe of mouth narrow and long, its longest length approximately three fifths of lower jaw length excluding lobes. Jaw teeth sub-incisiform, with rounded extremity, irregularly arranged, 30 on premaxilla, 26 on dentary. Head surface covered by minute skin papillae. Branchial membrane thickened, attached to isthmus only at its anterior-most point, in ventral midline. Odontodes conical, straight to slightly curved, 8 or 9 on opercle, 19–21 on interopercle.

Supraorbital sensory canal continuous, with three paired pores: s1, s3, and s6. Pore s6 nearer orbit than its symmetrical homologous pore s6. Anterior infraorbital section absent. Posterior infraorbital segment with pores io8 and io9. Posterior infraorbital, supraorbital and postorbital canals continuous. Postorbital canal with two pores: po1 and po2.

Unpaired and pectoral fins well-developed, pelvic fin and girdle absent. Dorsal, anal and pectoral fins with thickened bases. Unpaired fins with convex distal margins. Dorsal-fin origin nearer caudal-fin posterior margin than nape, anal-fin origin at vertical through posterior portion of dorsal-fin base, through base of third dorsal-fin branched ray. Eleven (ii + II + 7) dorsal-fin rays, 9 (ii + II + 5) anal-fin rays. Pectoral fin subtriangular in dorsal view, first ray about equal in length to second ray. Six (I + 5) pectoral-fin rays. Thirteen (I + 11 + I)

principal caudal-fin rays, 17–19 (xvi–xviii + I) dorsal procurrent rays, and 12–14 (xi–xiii + I) ventral procurrent rays.

Osteology (Figures 3K, 5D and 6K): Anterior portion of mesethmoid narrow, sub-triangular in dorsal view, anterior margin about straight in dorsal view, cornu pointed. Lateral ethmoid with minute lateral projection. Lacrimal thin, slightly elongate, narrowing posteriorly. Sesamoid supraorbital relatively short, slightly longer than lacrimal, without lateral projections. Premaxilla subrectangular in dorsal view, maxilla slender, slightly curved, shorter than premaxilla, without distinct posterior process.

Autopalatine moderately broad and short, subrectangular in dorsal view when excluding posterolateral process, lateral margin slightly convex, medial margin weakly sinuous. Autopalatine postero-lateral process short, subtriangular in dorsal view. Metapterygoid relatively small, sub-triangular. Quadrate L-shaped, with deep anterior constriction. No laminar expansion articulating metapterygoid and quadrate. Hyomandibula relatively short and slender. Opercle elongate, opercular odontode patch moderate in width, its depth about half hyomandibula articular facet length. Dorsal process of opercle short, truncate and straight. Opercular articular facet for hyomandibula with short rounded laminar projection. Articular facet for preopercle rounded, minute. Interopercle moderately long, its longitudinal length about three fourths of total hyomandibula longitudinal length. Preopercle short, with short ventral projection.

Parurohyal thin, lateral process short, pointed. Parurohyal head broad, with prominent anterolateral paired process. Parurohyal middle foramen minute or absent. Parurohyal posterior process moderate in length, about three-fifths distance between anterior margin of parurohyal and anterior insertion of posterior process. Branchiostegal rays 8 or 9. Vertebrae 39–41. Ribs 14–16. Dorsal-fin origin at vertical between centra of 21st and 23rd vertebrae; anal-fin origin at vertical through centrum of 24th or 25th vertebra. Two dorsal and single ventral hypural plate.

Colouration in alcohol: Dorsal and lateral surface of head and trunk pale yellow with large coalesced brown blotches. Venter yellowish white. Barbels pale brown. Fins hyaline, with dark grey dots on distal portion of dorsal fin and on whole caudal-fin membrane.

Etymology. From the Latin *insperata* (unexpected), due to the unexpected finding of this new species when crossing a small road then used as an alternative way to reach another region.

Distribution. Upper Rio Chapecó drainage, Rio Uruguai basin (Figure 8C).

Habitat. Upper Rio Chapecó channel, about 1245 m asl, where the river bottom consists of small pebbles and gravel, with some pebbles covered by unidentified aquatic plant. Specimens were found below pebbles near stream margin and in the middle of the river channel, or buried into the aquatic plant.

Cambeva intermedia sp. nov.

urn:lsid:zoobank.org:act:1E745D94-A017-4509-99C2-D8F52C55A646.

Figures 3L, 5E, 6L and 24; Table 10.

Holotype. UFRJ 15088, 56.2 mm SL; Brazil: Estado de Santa Catarina: Município de Modelo: Linha Santa Rosa: stream tributary of Rio Saudades, Rio Chapecó drainage, Rio Uruguai basin, 26°47'27" S 53°02'08" W, about 465 m asl; C.R.M. Feltrin, 5 April 2026.

Paratypes. UFRJ 15089, 20 ex., 21.9–52.9 mm SL; UFRJ 15090, 4 ex. (C&S), 39.5–52.6 mm SL; UFRJ 15007, 4 ex. (DNA), 28.5–30.0 mm SL; CICC AA 13607, 3 ex., 31.2–46.3 mm SL; collected with holotype.

Diagnosis. *Cambeva intermedia* is distinguished from all other congeners of CBC by having seven pectoral-fin rays (vs. six) and a subtrapezoidal autopalatine (Figure 3L; vs. subrectangular, Figure 3H–K,M). *Cambeva intermedia* is distinguished from all other congeners of CBC, except *C. insperata*, by having the distance between the posterior nostril

and the orbital rim about two times the distance between the anterior and posterior nostrils (vs. about equal). *Cambeva intermedia* is distinguished from *C. insperata* by having incisiform jaw teeth arranged in two or three regular rows (vs. jaw teeth sub-incisiform, with rounded extremity, irregularly arranged); 36–38 vertebrae (vs. 39–41); and the presence of pelvic fin (vs. absence).



Figure 24. *Cambeva intermedia* sp. nov., UFRJ 15088, holotype, 56.2 mm SL: (A), left lateral view; (B) dorsal view; (C), ventral view.

Table 10. Morphometric data of *Cambeva intermedia* sp. nov.

	Holotype	Paratypes (n = 9)
Standard length (SL)	56.2	39.5–52.9
Percentage of standard length		
Body depth	15.7	14.5–16.6
Caudal peduncle depth	12.7	12.1–12.8
Body width	11.9	10.0–13.5
Caudal peduncle width	3.3	3.8–4.6
Pre-dorsal length	68.3	64.8–67.2
Pre-pelvic length	62.7	58.0–63.3
Dorsal-fin base length	11.4	10.7–13.8
Anal-fin base length	8.3	8.5–10.3
Caudal-fin length	17.7	15.7–19.8
Pectoral-fin length	12.6	11.5–13.2
Pelvic-fin length	9.4	8.1–9.3
Head length	19.4	19.3–21.4
Percentage of head length		
Head depth	46.7	42.0–56.3
Head width	87.8	78.9–88.1
Snout length	40.4	38.9–41.9
Interorbital width	24.2	22.1–26.2
Preorbital length	13.1	8.8–12.5
Eye diameter	10.2	10.2–12.3

Description. External morphology: Morphometric data in Table 10. Body moderately deep, greatest body depth at vertical through area midway between pectoral and pelvic-fin

bases. Trunk subcylindrical on its anterior portion, slightly deeper than broad, compressed posteriorly. Dorsal and ventral profiles of head and trunk weakly convex, dorsal and ventral profiles of caudal peduncle nearly straight. Anus and urogenital papilla opening located at vertical through anterior half of dorsal-fin base. Lateral line canal of trunk short, with two pores just posterior to opercular patch of odontodes.

Head sub-trapezoidal in dorsal view, anterior profile of snout slightly convex. Eye small, round, dorsally positioned on head, nearer snout than posterior margin of opercle. Distance between anterior and posterior nostrils about half distance between posterior nostril and orbital rim. Tip of nasal barbel reaching area just anterior to opercular patch of odontodes, tip of maxillary and rictal barbels reaching posterior portion of interopercular patch of odontodes. Mouth subterminal. Lateral fleshy lobe of mouth narrow and small, its longest length approximately one third of lower jaw length excluding lobes. Jaw teeth incisiform, arranged in three rows, 29–32 on premaxilla, 25–34 on dentary. Head surface covered by minute skin papillae. Branchial membrane thickened, attached to isthmus only at its anterior-most point, in ventral midline. Odontodes conical, straight, 12 or 13 on opercle, 24–27 on interopercle.

Supraorbital sensory canal continuous, with three paired pores: s1, s3, and s6. Pore s6 nearer orbit than its symmetrical homologous pore s6. Anterior infraorbital section absent. Posterior infraorbital segment with pores io8 and io9. Posterior infraorbital, supraorbital and postorbital canals continuous. Postorbital canal with two pores: po1 and po2.

Fins well-developed, dorsal, anal and pectoral fins with thickened bases. Unpaired fins with convex distal margins. Dorsal-fin origin nearer caudal-fin posterior margin than nape, anal-fin origin at vertical through middle portion of dorsal-fin base, through base of third or fourth dorsal-fin branched ray. Eleven or twelve (ii + II + 7–8) dorsal-fin rays, 9–10 (ii + II + 5–6) anal-fin rays. Pectoral fin subtriangular in dorsal view, first ray slightly longer than second ray. Seven (I + 6) pectoral-fin rays. Pelvic fin with rounded posterior margin, reaching vertical through anterior portion of dorsal-fin base, its extremity not reaching anus. Pelvic-fin bases in close proximity. Five (I + 4) pelvic-fin rays. Thirteen (I + 11 + I) principal caudal-fin rays, 15–18 (xiv–xvii + I) dorsal procurent rays, and 10–13 (ix–xii + I) ventral procurent rays.

Osteology (Figures 3L, 5E and 6L): Anterior portion of mesethmoid moderate, subtriangular in dorsal view, anterior margin about straight in dorsal view, cornu with rounded extremity. Lateral ethmoid without distinctive lateral projections. Lacrimal thin, narrow and short, drop-shaped. Sesamoid supraorbital short, one time and half longer than lacrimal, without small lateral projection. Premaxilla subrectangular in dorsal view, maxilla curved, shorter than premaxilla, without distinct posterior process.

Autopalatine moderately broad and short, subtrapezoidal in dorsal view when excluding posterolateral process, lateral margin straight, medial margin weakly sinuous. Autopalatine postero-lateral process short, subtriangular in dorsal view. Metapterygoid large, sub-triangular. Quadrate L-shaped, with deep anterior constriction. Small laminar expansion articulating metapterygoid and quadrate just anterior to articular cartilage. Hyomandibula relatively short and deep. Opercle short, opercular odontode patch moderate in width, its depth about three fourths of hyomandibula articular facet length. Dorsal process of opercle broad, about straight. Opercular articular facet for hyomandibula with short rounded laminar projection. Articular facet for preopercle minute. Interopercle moderately long, its longitudinal length about three fourths of total hyomandibula longitudinal length. Preopercle slender, with short ventral projection.

Parurohyal thin, lateral process short, with rounded extremity. Parurohyal head broad, with prominent anterolateral paired process. Parurohyal middle foramen small. Parurohyal posterior process moderate in length, about half distance between anterior

margin of parurohyal and anterior insertion of posterior process. Branchiostegal rays 8. Vertebrae 36–38. Ribs 13–15. Dorsal-fin origin at vertical between centra of 19th and 20th vertebrae; anal-fin origin at vertical between centra of 23rd and 24th vertebra. Two dorsal and single ventral hypural plate.

Colouration in alcohol: Dorsal and lateral surface of head and trunk pale yellow with dark brown to black spots, smaller on ventral region of flank and head side. Venter yellowish white. Barbels pale brown. Fins hyaline, dark grey to black dots on basal portion of unpaired and pectoral fins.

Etymology. From the Latin *intermedia* (intermediate), due to morphological features that are intermediate between those typical of specialised fossorial and unspecialised species.

Distribution. Lower Rio Chapecó drainage, Rio Uruguai basin (Figure 8C).

Habitat. Stream at about 465 m asl, with small pebbles and gravel on the bottom. Specimens were found below small pebbles and gravel.

Cambeva mundana sp. nov.

urn:lsid:zoobank.org:act: F89CAD20-7EBB-4E78-A172-AF1C2E881DFA.

Figures 3M, 5F, 6K and 25; Table 11.



Figure 25. *Cambeva mundana* sp. nov., UFRJ 15097, holotype, 44.9 mm SL: (A) left lateral view; (B) dorsal view; (C) ventral view.

Holotype. UFRJ 15097, 44.9 mm SL; Brazil: Estado de Santa Catarina: Município de Abelardo Luz: stream tributary of Rio Chapecó, Rio Uruguai basin, 26°36'29" S 52°19'33" W, about 775 m asl; C.R.M. Feltrin, 20 December 2023.

Paratypes. UFRJ 14118, 3 ex., 25.0–45.6 mm SL; UFRJ 15098, 1 ex. (C&S), 44.4 mm SL; UFRJ 14100, 2 ex. (DNA), 50.2–50.6 mm SL; collected with holotype.

Diagnosis. *Cambeva mundana* differs from all other species of CBS2, except *C. intermedia*, by a colour pattern consisting of small dots on the whole flank (Figure 25; vs. large blotches, Figures 19–24). *Cambeva mundana* is distinguished from *C. intermedia* by having relatively long barbels, with the nasal barbel reaching the opercular patch of odontodes (vs. reaching the area just posterior to the orbit) and the maxillary and rictal barbels reaching the area between the interopercular patch of odontodes and the pectoral-fin base (vs. reaching the interopercular patch of odontodes); the distance between the posterior nostril and the

orbital rim about equal to the distance between the anterior and posterior nostrils (vs. two times); and six pectoral-fin rays (vs. seven). *Cambeva mundana* is also distinguished from all other congeners of CBS2, except *C. admirabilis*, by the absence of a rounded projection on the anterior portion of the interopercular bone (Figure 5A; vs. presence, Figure 5B–E); and presence of a U-shaped concavity in the posterior portion of the dorsal margin of the hyomandibula anterior outgrowth (Figure 5A; vs. absence, Figure 5B–E). *Cambeva mundana* also differs from *C. admirabilis* by having well-developed pelvic fin (vs. pelvic fin absent or rudimentary).

Table 11. Morphometric data of *Cambeva mundana* sp. nov.

	Holotype	Paratypes (n = 2)
Standard length (SL)	44.9	44.6–45.6
Percentage of standard length		
Body depth	17.2	15.6–17.3
Caudal peduncle depth	14.2	12.7–13.0
Body width	12.7	12.2–14.2
Caudal peduncle width	2.9	3.8–4.4
Pre-dorsal length	69.7	67.0–67.3
Pre-pelvic length	66.3	61.8–64.5
Dorsal-fin base length	13.9	12.7–13.5
Anal-fin base length	9.5	8.1–9.6
Caudal-fin length	16.5	17.6–18.9
Pectoral-fin length	11.9	11.7–12.2
Pelvic-fin length	8.9	7.6–8.1
Head length	19.8	19.3–20.8
Percentage of head length		
Head depth	57.1	47.9–49.5
Head width	91.7	79.3–88.1
Snout length	38.9	38.1–41.1
Interorbital width	24.0	24.0–24.3
Preorbital length	8.1	9.0–9.0
Eye diameter	10.1	9.3–10.3

Description. External morphology: Morphometric data in Table 11. Body moderately deep, greatest body depth at vertical midway distance between pectoral and pelvic-fin bases. Trunk subcylindrical on its anterior portion, slightly deeper than broad, compressed posteriorly. Dorsal profile of head and trunk weakly convex, ventral profile of head and abdomen about straight, dorsal and ventral profiles of caudal peduncle nearly straight. Anus and urogenital papilla opening located at vertical just posterior to middle of dorsal-fin base. Lateral line canal of trunk short, with two pores just posterior to opercular patch of odontodes.

Head sub-trapezoidal in dorsal view, anterior profile of snout slightly convex. Eye relatively small, round, dorsally positioned on head, nearer snout than posterior margin of opercle. Distance between anterior and posterior nostrils about half distance between posterior nostril and orbital rim. Tip of nasal barbel reaching opercular patch of odontodes, tip of maxillary and rictal barbels reaching area between interopercular patch of odontodes and pectoral-fin base. Mouth subterminal. Lateral fleshy lobe of mouth large, its longest length slightly longer than half lower jaw length excluding lobes. Jaw teeth incisiform, arranged in three rows, 34 on premaxilla, 27 on dentary. Head surface covered by minute skin papillae. Branchial membrane thickened, attached to isthmus only at its anterior-most point, in ventral midline. Odontodes conical, straight to slightly curved, 12 on opercle, 20 on interopercle.

Supraorbital sensory canal continuous, with three paired pores: s1, s3, and s6. Pore s6 nearer orbit than its symmetrical homologous pore s6. Anterior infraorbital section absent. Posterior infraorbital segment with pores io8 and io9. Posterior infraorbital, supraorbital and postorbital canals continuous. Postorbital canal with two pores: po1 and po2.

Fins well-developed, dorsal, anal and pectoral fins with thickened bases. Unpaired fins with convex distal margins. Dorsal-fin origin nearer caudal-fin posterior margin than nape, anal-fin origin at vertical through middle portion of dorsal-fin base, through base of third or fourth dorsal-fin branched ray. Eleven (ii + II + 7) dorsal-fin rays, total of nine (ii + II + 5) anal-fin rays. Pectoral fin subtriangular in dorsal view, first ray slightly projecting beyond fin membrane, forming short filament about 5% of pectoral-fin length. Six (I + 5) pectoral-fin rays. Pelvic fin with rounded posterior margin, reaching vertical through middle of dorsal-fin base, its extremity not reaching anus. Pelvic-fin bases in close proximity. Five (I + 4) pelvic-fin rays. Thirteen (I + 11 + I) principal caudal-fin rays, 19 (xviii + I) dorsal procurent rays, and 14 (xiii + I) ventral procurent rays.

Osteology (Figures 3K, 5F and 6K): Anterior portion of mesethmoid narrow, subtriangular in dorsal view, anterior margin slightly concave, cornu extremity blunt. Lateral ethmoid with small lateral projection. Lacrimal thin, short. Sesamoid supraorbital relatively short, two times longer than lacrimal, without lateral projections. Premaxilla subrectangular in dorsal view, slender, slightly tapering laterally, maxilla slender, curved, shorter than premaxilla, with rudimentary posterior process.

Autopalatine moderately broad and short, subrectangular in dorsal view when excluding posterolateral process, lateral margin about straight, medial margin weakly sinuous. Autopalatine postero-lateral process short, subtriangular in dorsal view. Metapterygoid relatively small, sub-trapezoidal. Quadrate L-shaped, with deep anterior constriction. Small laminar expansion articulating metapterygoid and quadrate just anterior to articular cartilage. Hyomandibula relatively short, moderate in depth. Opercle compact, opercular odontode patch moderate in width, its depth about three-fourths hyomandibula articular facet length. Dorsal process of opercle short, subtriangular, its extremity rounded. Opercular articular facet for hyomandibula with short rounded laminar projection. Articular facet for preopercle rounded, minute. Interopercle moderately long, its longitudinal length about three fourths of total hyomandibula longitudinal length. Preopercle elongate, with short ventral projection.

Parurohyal thin, lateral process short, subtriangular, with pointed extremity. Parurohyal head broad, with prominent anterolateral paired process. Parurohyal middle foramen small, round. Parurohyal posterior process short, about one-fifth distance between anterior margin of parurohyal and anterior insertion of posterior process. Branchiostegal rays 8. Vertebrae 38. Ribs 14. Dorsal-fin origin at vertical through centrum of 21st vertebra; anal-fin origin at vertical through centrum of 25th vertebra. Two dorsal and single ventral hypural plate.

Colouration in alcohol: Dorsal and lateral surface of head and trunk pale yellow with dark brown to black spots, smaller on ventral region of flank and head side. Venter yellowish white. Barbels pale brown. Fins hyaline, with dark grey to black dots on basal portion of dorsal and anal fins, and whole caudal fin.

Etymology. From the Latin *mundana* (worldly, common), referring to the colour pattern of the flank that is common among congeners, making difficult its recognition using only colour pattern characters.

Distribution. Middle Rio Chapecó drainage, Rio Uruguai basin (Figure 8C).

Habitat. Headwaters of a small stream, about 775 m asl. Specimens were found below small pebbles and gravel on the bottom.

4. Discussion

4.1. Phylogenetic Relationships

The fossorial species of *Cambeva* endemic to RCD form a diverse assemblage of relatively small sized species, about 40–60 mm SL. All of them share eye positioned on the anterior portion of head, with 11 of the 13 species having the posterior nostril approximately equidistant from the orbit and the anterior nostril, a condition uncommon among congeners, restricted to trichomycterine taxa with fossorial habits (see introduction above). Among species of the genus *Cambeva*, a similar condition occurs in the *Cambeva taroba* clade (CTC), which also includes fossorial species living in similar habitats. Species of CTC have a slender opercular patch with a few narrow odontodes, similarly to the condition in CAC and CBS1 (Figure 4), suggesting close relationships. However, the phylogenetic analyses did not corroborate monophyly of those taxa endemic to RCD and CTC was not supported as sister taxa to the fossorial clades from RCD (Figure 1), suggesting the occurrence of morphological homoplasies related to fossorial habits in these lineages. On the other hand, the phylogenetic resolution of the longer branches of the tree was low, with support values uninformative, not effectively refuting monophyly of the group. Therefore, relationships are not fully resolved at the present time.

The taxa here studied exhibit a great morphological diversity, mostly concentrated in bones associated with the upper jaw and the jaw suspensorium (Figures 3–5). The greatest morphological diversity occurs in CAC and CBS1, which is probably related to the specialised biotopes where species of these groups live, mostly consisting of small headwater brooks with plant deposits and litter on the bottom, instead of streams predominantly with gravel and pebbles on the bottom inhabited by species of CBS2, a generalised habitat in *Cambeva* and closely related genera (i.e., *Pseudocambeva* Costa, 2026 and *Pericambeva* Costa, 2026, [10]). Among the most prominent morphological features occurring in CAC and CBS1 are the robust autopalatine and mesethmoid (Figure 3A–G), whereas in CBS2 these bones are never so broad (Figure 3H–M), as occurring in species of CTC (Figure 3N) and most other congeners of the *Cambeva* beta clade (e.g., [20,40]). Species of CAC and CBS1 also share an anteriorly extended anterodorsal portion of the lateral ethmoid, reaching an area adjacent to the postero-medial portion of the autopalatine, where this bone is articulated with the vomer (Figure 3A–G), a condition occurring only in CTC (Figure 3N) among congeners. Similarly, species of CAC and CBS1 have an elongated opercle with a narrow opercular patch of odontodes (Figure 3A–G), contrasting with the short opercle with a relatively broad opercular patch of odontodes in species of CBS2 (Figure 3H–M), a plesiomorphic widespread condition in trichomycterines.

Monophyly of CAC is well supported in the molecular phylogeny, which is corroborated by the presence of a long nerve canal obliquely crossing the autopalatine dorsal surface between its anterior portion and the articulation base for the lateral ethmoid (Figure 3A–C). Short nerve canals associated with that articulation occur in other closely related trichomycterines [41,42], but never extending anteriorly as in species of CAC. *Cambeva dimorphica* and *C. oncina*, two species of CAC occurring in RCD headwaters above 1200 m asl, are supported as sister taxa and share a colour pattern comprising coalescent spots forming a reticulate pattern on the flank, occurring in all specimens of *C. oncina* (Figure 11) and in the colour morph 2 of *C. dimorphica* (Figure 10). A similar colour pattern is also found in a sister species pair of CBS1, comprising all specimens of *C. curvilineata* (Figure 12) and subadults of *C. metagalactica* (Figure 16), evidencing a high level of homoplasy between CAC and CBS1. The latter group is also well supported in the molecular phylogeny as monophyletic and sister of CBS2 (Figure 1).

The molecular phylogenies supported monophyly of CBC with highest values, but no unique morphological trait shared by all included species was found. Both CBS1 and

CBS2 were also well supported by molecular data. Monophyly of CBS1 is corroborated by the presence of a ligament between a medial expansion of the sesamoid supraorbital and a lateral expansion of the lateral ethmoid (Figure 3D–G). This morphological structure differs from the ligamentous connection described for the distant related *C. galactica* (Figure 1), in which the ligament connects a medial expansion of the sesamoid supraorbital with the articulatory shell of the autopalatine for the lateral ethmoid [43]: Figure 4A. Species of CBS2 share some osteological characters states not occurring in CAC and CBS1, such as a broad opercular patch of odontodes and the presence of laminar extensions in the metapterygoid and the quadrate margins forming an additional area for articulation between these two bones (Figure 5A–F), but they also occur in other intrageneric lineages and possibly are plesiomorphic features.

4.2. *Cambeva* Species Flocks in RCD

Despite the lack of precise definitions regarding the concept of a “species flock,” there is generally some consensus on the main criteria used to recognise it, including the following: 1—monophyly and endemism, 2—species richness, and 3—morphological and ecological diversity [16–19]. Applicability of these criteria in the *Cambeva* clades from RCD are below discussed.

1—Our phylogenetic analysis indicated that the fossorial species of *Cambeva* endemic to RCD do not form a single monophyletic group; specifically, CAC is not supported as being directly related to CBC (Figure 1). On the other hand, neither of these two lineages is directly related to the other species of *Cambeva* endemic to RCD (Figure 1). Therefore, combining the criteria of monophyly and endemism, there is no evidence to support a single flock of endemic fossorial species in RCD. However, both CAC and CBC are strongly supported in the phylogenetic analysis as monophyletic and both comprise only endemic species, thus fulfilling the first criterion.

2—The occurrence of three allopatric species in CAC cannot be regarded as a particular case of species richness, but the occurrence of 10 species in CBC with parapatric or allopatric distribution, confined to a small drainage of approximately 11,120 km², is a unique species diversity pattern among trichomycterines from eastern South America river basins. Among all the river drainages of eastern and southern Brazil, excluding RCD and with areas similar to it, the Rio Paraibuna drainage (including the Rio Preto and Rio do Peixe sub-drainages) exhibits the highest number of trichomycterine species, with a total of eight species of *Trichomycterus*, six of which are endemic [13,44], but none of the species have their closest relatives within this same drainage [45]. Therefore, CBC meets the “species richness” criterion to be classified as a species flock.

3—Both the CAC and the CBC exhibit great external morphological diversity, including body depth, presence or absence of pelvic fin, and colour patterns, besides having a substantial diversity of skeletal structures (Figures 3–6). Thus both clades fulfil the morphological diversity criterion. Similarly, our field records during collections indicate different microhabitat preferences among species, including such species uniquely found associated with gravel sediment in fast-flowing streams to species uniquely inhabiting litter sediment in moderately flowing brooks, and species confined to high-altitude habitats above 1000 m asl to species restricted to middle river course in lower altitudes. For example, two closely related species belonging to CBS1, *C. diegoi* and *C. metagalactica*, are sympatric but not syntopic species, with the former living buried in fine gravel and the latter buried in leaf litter bottom (see habitat descriptions in taxonomic accounts above). Therefore, under a superficial qualitative evaluation of features taken just during field collections, both clades fulfil the ecological diversity criterion. However, additional quantitative studies on habitat

and other ecological features, including feeding and reproductive habits, are necessary to recognise both clades as flocks.

The origin of fish species flocks is usually explained as a process of adaptive radiation resulting in rapid ecological and phenotypic diversification within a novel, circumscribed aquatic environment, implicating in the colonisation of then available habitats, resulting over time in a considerably larger number of species in the flock compared to other fish groups [6]. Therefore, an additional implicit criterion to recognise a species flock is habitat availability. Field studies in RCD did not record a discrepancy between the number of species of *Cambeva* and other teleost fishes, which are represented in RCD by the same groups as in other southern Brazilian river drainages, thus not supporting CAC and CBC as species flocks. Consequently, these clades cannot be definitively considered as flocks, depending on further field studies.

4.3. Origin and Diversification of CBC

Species flocks and other evolutionary cases of intense clade species diversification commonly have their origin associated to lakes [46,47], with potential genomic contributions from surrounding riverine taxa via genetic introgression [48]. Far less common in the literature are records of such rapid species diversification processes in riverine habitats, with their origins related to paleolakes and other old endorreic systems predating current exoreic drainage basins [49–51].

The high species diversity confined to a small river drainage found in CBC making it a putative species flock is a unique unparalleled condition among South American catfishes. There is no available evidence regarding the existence of paleolakes or other endorreic systems in this southern Brazilian region that could support a hypothesis concerning the origin of such species diversification. However, the co-occurrence of another uncommonly diverse organism in the same area may shed light on its origin. Another group of teleost fishes, the *Crenicichla missioneira* complex (hereafter CMC; referred to as the *missioneira* group [52], the *C. missioneira* species group [53], the *Crenicichla missioneira* species complex [54], and the Uruguay River species flock [55], has a distribution that partially overlaps with the area occupied by CBC [54]. The CMC is one of the few cichlid species flocks recorded outside the African continent [52] and is endemic to the upper section of the Uruguay River basin, with at least two species occurring in RCD [53].

Our time-calibrated phylogenetic analysis estimated the origin of CBC during the Miocene, approximately 13.2 Ma (HPD 9.02–17.11 Ma), and the beginning of species diversification during the same geological epoch, approximately 6.2 Ma (HDP 3.63–8.94 Ma) (Figure 2). This timeframe coincides with the emergence and persistence of the Paranean Sea, a significant Miocene paleogeographic event involving a major marine transgression that strongly influenced the diversification of Neotropical ichthyofauna between approximately 15 and 8 Ma (e.g., [56,57]).

Miocene marine transgressions played a decisive role in the diversification and adaptation of marine species to continental freshwater environments [58–60]. However, the Paranean Sea may have also influenced the diversification of freshwater and terrestrial faunal groups, by reaching the lower sections of the Rio Uruguai and Rio Paraná basins, causing higher water levels in the main channels of these basins and thus creating dispersal barriers for these groups. Similar results were recently reported by Seger et al. [61] in a study on frogs of the genus *Proceratophrys* Miranda-Ribeiro, 1920 from mountainous areas of southern Brazil, including the RCD area, which also yielded similar molecular dating estimates for the group origin and diversification. Adult *Proceratophrys* are terrestrial and breed in streams and freshwater swamps, making them susceptible to barriers involving large rivers [61].

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Data Availability Statement: DNA sequences used in this study were deposited in GenBank (see Appendix A for access codes).

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Appendix A

Table A1. Terminal taxa for molecular phylogeny and respective GenBank accession numbers.

	<i>COI</i>	<i>CYTb</i>	<i>RAG2</i>
<i>Cambeva alphabelardense</i>	PZ366369	PZ371515	PZ371518
<i>Cambeva</i> sp. 10	PZ366371	PZ371514	PZ371520
<i>Cambeva</i> sp. 8	PZ366370	PZ371512	PZ371519
<i>Cambeva atrobrunnea</i>	PP448187	PP449084	PP449088
<i>Cambeva balios</i>	OQ810040	OQ814186	OQ814193
<i>Cambeva barbosae</i>	MK123689.1	OQ110808	MN385820
<i>Cambeva mundana</i>	PZ366372	PZ371516	PZ371522
<i>Cambeva biseriata</i>	PP448190	OQ110806	OQ110817
<i>Cambeva botuvera</i>	PZ580913	PZ581224	PZ595489
<i>Cambeva brachykechenos</i>	MN995669	MN995758	-
<i>Cambeva castroi</i>	PZ580914	PZ581225	PZ595490
<i>Cambeva chrysornata</i>	MN995726	OQ110810	OQ110819
<i>Cambeva cubataonis</i>	OQ810039	OQ110814	OQ110815
<i>Cambeva davisi</i>	PZ580915	PZ581226	PZ595491
<i>Cambeva diabola</i>	JN989258	OQ110812	-
<i>Cambeva diatropoporus</i>	KY857996.1	KY858065	KY858213
<i>Cambeva diffusa</i>	-	PZ581227	-
<i>Cambeva duplimaculata</i>	-	PZ581228	PZ595492
<i>Cambeva</i> sp. 11	PZ375497	PZ377451	PZ377452

Table A1. Cont.

	COI	CYTb	RAG2
<i>Cambeva flavopicta</i>	OQ810042	OQ814188	OQ814195
<i>Cambeva galactica</i>	PP448189	PP449086	PP449090
<i>Cambeva gamabelardense</i>	PZ366373	PZ371517	PZ371523
<i>Cambeva grisea</i>	MN995671	MN995760	-
<i>Cambeva guaratuba</i>	MN995721	MN995792	-
<i>Cambeva guareiensis</i>	PP448192	OQ110813	OQ110821
<i>Cambeva imaruihy</i>	MN995700	MN995766	OQ814191
<i>Cambeva</i> sp. 9	PZ366374	PZ371513	PZ371521
<i>Cambeva longipalata</i>	PZ580916	PZ581229	PZ595493
<i>Cambeva luteoreticulata</i>	PP448186	PP449083	PP449087
<i>Cambeva melanoptera</i>	PP496403	PZ581230	PZ595494
<i>Cambeva naipi</i>	MN995699	MN995771	-
<i>Cambeva orbitofrontalis</i>	MN995703	MN995764	OQ814192
<i>Cambeva panthera</i>	OQ810041	OQ814187	OQ814194
<i>Cambeva pascuali</i>	MF034463	OQ110811	OQ110820
<i>Cambeva pericoh</i>	PZ580917	PZ581231	PZ595495
<i>Cambeva perkos</i>	MN995663	MN995759	KY858202
<i>Cambeva podostemophila</i>	OQ810043	OQ814189	OQ814196
<i>Cambeva poikilos</i>	MN995693	MN995761	-
<i>Cambeva rotundipinna</i>	PP448188	PP449085	PP449089
<i>Cambeva stawiariski</i>	MN995720	MN995779	-
<i>Cambeva taroba</i>	MN995708	MN995757	-
<i>Cambeva tourensis</i>	MN995697	OQ814190	OQ814197
<i>Cambeva tropeira</i>	MN995674	MN995752	-
<i>Cambeva urubici</i>	PZ580918	PZ581232	PZ595496
<i>Cambeva ventropapilata</i>	PP319016	OQ110807	OQ110818
<i>Cambeva zonata</i>	MN995706	KY858053	-
<i>Cambeva</i> sp. 1	PZ580919	PZ581233	PZ595497
<i>Cambeva</i> sp. 2	PZ580920	PZ581234	PZ595498
<i>Cambeva</i> sp. 3	PZ580921	PZ581235	PZ595499
<i>Cambeva</i> sp. 4	PZ580922	PZ581236	PZ595500
<i>Cambeva</i> sp. 5	PZ580923	PZ581237	PZ595501
<i>Cambeva</i> sp. 6	PZ580924	PZ581238	PZ595502
<i>Cambeva</i> sp. 7	PZ580925	PZ581239	PZ595503
<i>Cambeva dimorphica</i>	PZ580926	PZ581240	PZ595504
<i>Cambeva oncina</i>	PZ580927	PZ581241	PZ595505
<i>Cambeva curvilineata</i>	PZ580928	PZ581242	PZ595506

Table A1. *Cont.*

	<i>COI</i>	<i>CYTb</i>	<i>RAG2</i>
<i>Cambeva metagalactica</i>	PZ580929	PZ581243	PZ595507
<i>Cambeva minima</i>	PZ580930	PZ581244	PZ595508
<i>Cambeva diegoi</i>	PZ580931	PZ581245	PZ595509
<i>Cambeva insperata</i>	PZ580933	PZ581247	PZ595511
<i>Cambeva intermedia</i>	PZ580934	PZ581248	PZ595512
<i>Cambeva dominguense</i>	PZ580935	PZ581249	-
<i>Cambeva betabelardense</i>	PZ580936	PZ581250	PZ595513
<i>Cambeva admirabilis</i>	PZ621799	PZ621308	-
<i>Trichomycterus nigricans</i>	MN813005	MT470415	MK123765
<i>Plesioscleronema auromaculatum</i>	OM037445	OM037134	OM037136
<i>Scleronema macanuda</i>	MK123686	MK123708	MK123760
<i>Pericambeva difficilis</i>	PP496404	PP496778	-
<i>Diplomystes nahuelbutaensis</i>	NC_015823	MN640590	DQ492317
<i>Nematogenys inermis</i>	KY857952	-	KY858182
<i>Callichthys callichthys</i>	MZ051783	KP960058	DQ492324
<i>Trichogenes longipinnis</i>	MK123682	MK123704	MF431117
<i>Microcambeva ribeirae</i>	MN385807	OK334290	MN385832
<i>Eremophilus mutisii</i>	PQ233849	-	KY858171
<i>Hoplisoma panda</i>	NC049097.1	NC049097.1	KP960362.1
<i>Hoplisoma nattereri</i>	KT239009.1	KT239009.1	-
<i>Corydoras stenocephalus</i>	-	GU209554.1	KP960358.1

Appendix B

Table A2. Alignment statistics and substitution saturation assessment for each gene and the concatenated dataset used in the phylogenetic analyses. Alignment statistics were calculated in MEGA12, and substitution saturation was evaluated using Xia's index (Iss). PI, parsimony-informative sites; VS, variable sites; Iss.cSym, critical Iss value assuming a symmetrical tree.

Gene	Length (bp)	VS (bp)	PI (bp)	Missing Data (%)	Iss	Iss.cAsym	Saturation
COI	723	282	233	7.0	0.436	0.725	No evidence
CYTb	787	356	290	10.6	0.572	0.731	No evidence
RAG2	795	327	205	1.6	0.178	0.731	No evidence
Concatenated dataset	2305	966	732	14.8	-	-	-

Appendix C

Table A3. Optimal partitioning scheme, partition lengths (bp), and best-fitting nucleotide substitution models for each data partition.

Partition	Base Pairs	Evolutionary Model
COI 1st	241	HKY + G
COI 2nd	241	HKY + I
COI 3rd	241	GTR + G
CYTB 1st	263	GTR + I + G
CYTB 2nd	262	GTR + I + G
CYTB 3rd	262	GTR + G
RAG2 1st + RAG2 2nd	530	GTR + I
RAG2 3rd	265	GTR + I + G

Appendix D

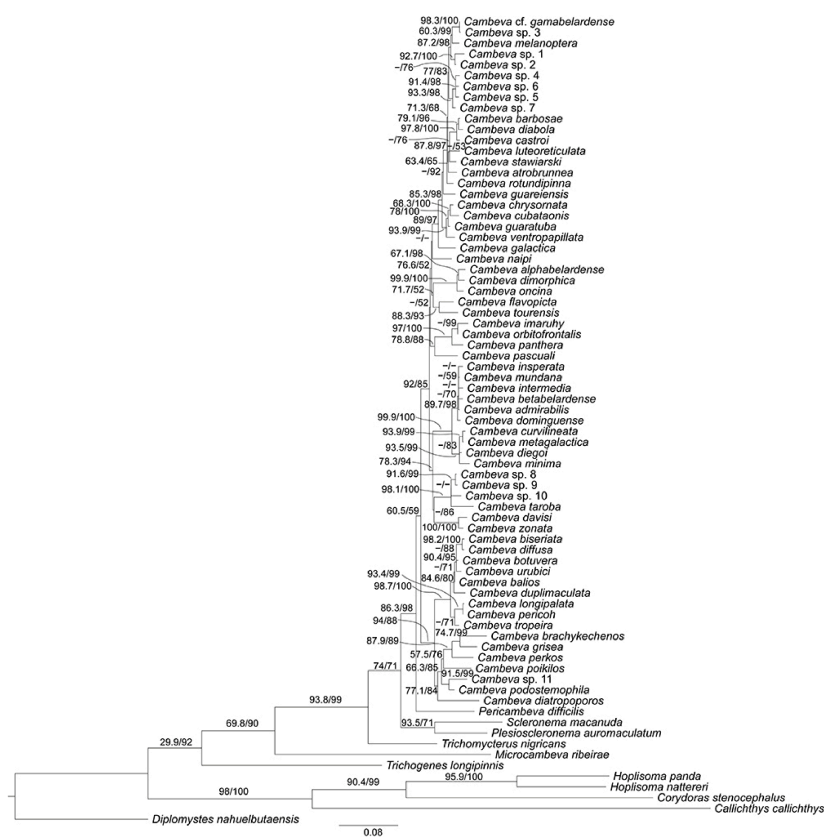


Figure A1. ML phylogenetic tree inferred using IQ-TREE2 from the CYTB dataset to assess topological congruence among molecular markers. Numbers above branches indicate, separated by slashes (/), ultrafast bootstrap (UF-Boot) and SH-like approximate likelihood ratio test (SH-aLRT) support values, respectively. Dashes (-) indicate support values below 50.

Appendix E

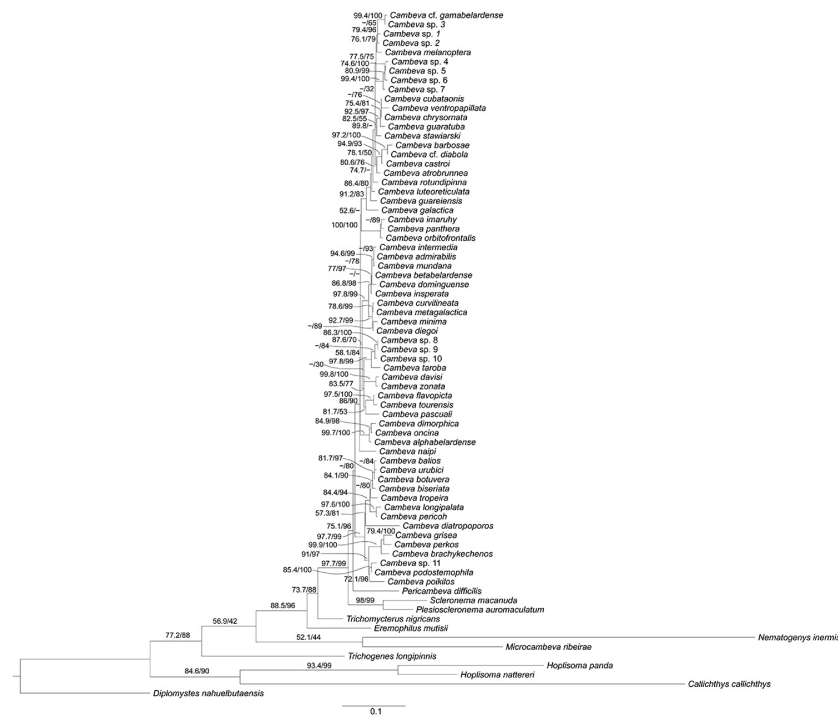


Figure A2. ML phylogenetic tree inferred using IQ-TREE2 from the COI dataset to assess topological congruence among molecular markers. Numbers above branches indicate, separated by slashes (/), ultrafast bootstrap (UF-Boot) and SH-like approximate likelihood ratio test (SH-aLRT) support values, respectively. Dashes (–) indicate support values below 50.

Appendix F

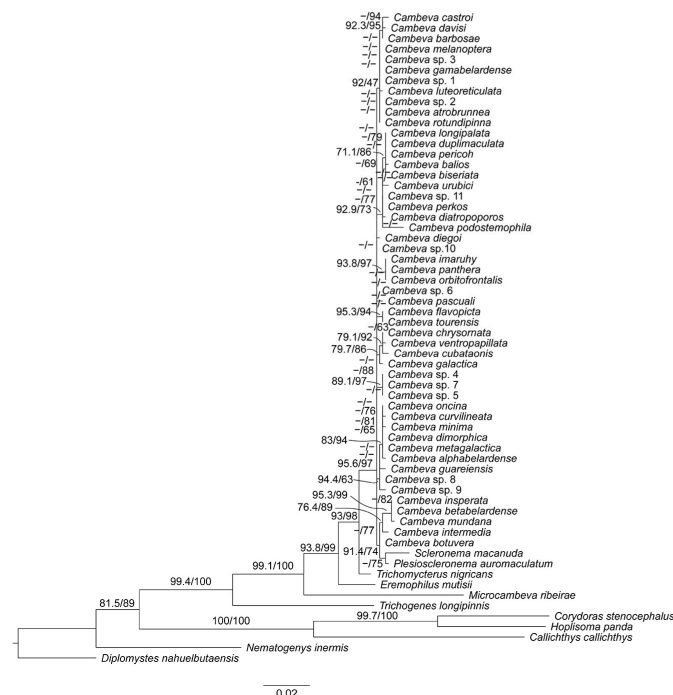


Figure A3. ML phylogenetic tree inferred using IQ-TREE2 from the RAG2 dataset to assess topological congruence among molecular markers. Numbers above branches indicate, separated by slashes (/), ultrafast bootstrap (UF-Boot) and SH-like approximate likelihood ratio test (SH-aLRT) support values, respectively. Dashes (–) indicate support values below 50.

Appendix G

Table A4. Estimated stem ages, 95% highest posterior density (HPD) intervals, and posterior probabilities for the main clades inferred in BEAST.

Clade	Posterior Median Age of Lineage Origin (Ma)	95% HPD (Ma)	PP
<i>Cambeva beta</i> group	19.3	13.9–25.5	99
CAC	12.6	7.9–17.4	100
CTC	10.6	7.0–14.9	100
CBC	13.2	9.0–17.1	100
CBS1/CBS2	6.0	3.6–8.9	100/100
CGC	4.9	3.2–6.7	82

Appendix H

Table A5. Estimated stem ages, 95% highest posterior density (HPD) intervals, and posterior probabilities for the main clades obtained from the sensitivity analysis in BEAST using an alternative normal prior with a standard deviation (SD) of 7 Ma.

Clade	Posterior Median Age of Lineage Origin (Ma)	95% HPD (Ma)	PP
<i>Cambeva beta</i> group	18.3	13.0–24.0	99
CAC	12.3	7.5–17.0	100
CTC	10.6	6.9–13.9	100
CBC	12.5	9.1–17.4	100
CBS1/CBS2	5.7	3.3–9.1	100/100
CGC	4.6	3.4–7.2	82

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