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A new psammophilous catfish of the genus *Microcambeva* (Teleostei: Trichomycteridae) from the Rio Doce basin, southeastern Brazil

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Microcambeva watu, new species, is described from the Rio Doce basin in the Atlantic Forest of southeastern Brazil. It is distinguished from all congeners by the presence of a heart-shaped blotch on top of head. It differs from *M. ribeirae*, *M. filamentosa*, and *M. bendego* by presenting an ossification in the anterior cartilage of autopalatine. It is distinguished from *M. barbata* by the anterior rudimentary ossification of autopalatine and from *M. mucuriensis* and *M. draco* by a bifid ventral tip of opercle. Finally, it also differs from *M. jucuensis* by having an ellipsoid metapterygoid lacking a ventral process. This is the eighth described species of *Microcambeva*, most of them in the last ten years. Comments on the systematics, biogeography, and conservation of the new species are provided.

Introduction

Microcambeva are small, translucent, and psammophilous catfishes exclusively found in sandy-bottom habitats of coastal streams of the Atlantic Forest of Brazil (Costa & Bockmann, 1994; Sarmento-Soares et al., 2019). Most of the seven described species are restricted to a single basin (Costa et al., 2019, 2020a; Medeiros et al., 2020), and distributed from the Rio Jucuruçu basin in Bahia State southward to the Rio Guaraqueçaba basin in Paraná State (Sarmento-Soares et al., 2019).

A decade ago only three species of *Microcambeva* were known: *M. barbata* from the Rio São João basin, in the Fluminense ecoregion (sensu Abell et al., 2008). *Microcambeva ribeirae* from Rio Ribeira de Iguape and Rio Guaraqueçaba basins in the Ribeira de Iguape ecoregion (sensu Abell et al., 2008), and *M. draco* from the Rio Jucuruçu and Peruípe basins in the Northeastern Mata Atlântica ecoregion (NMAE) (sensu Abell et al., 2008; Sarmento-Soares et al., 2019). Costa et al. (2019, 2020b) described three additional species: *M. mucuriensis* from the Rio Mucuri basin, *M. jucuensis*

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from the Rio Jucu basin, both from the NMAE, and *M. filamentosa*, sympatric with *M. ribeirae* in the Rio Ribeira de Iguape basin. More recently, Medeiros et al. (2020) described *M. bendego* from the Rio Guapi-Macacu basin in the Fluminense ecoregion.

Records of *Microcambeva* in Rio Doce basin were documented by Costa et al. (2004) and Buckup et al. (2007) based in few specimens. Ichthyological surveys conducted between 2010 and 2017 in the middle portions of Rio Corrente Grande and Rio Santa Maria do Rio Doce in the Rio Doce basin, yielded additional samples (Sarmento-Soares et al. 2019), allowing the discovery and recognition of a new species whose description is the main goal of the present paper.

Material and methods

Morphometric and meristic data followed Costa (1992). Measurements were obtained using a digital caliper with 0.1 mm accuracy under a stereomicroscope. Measurements are presented as percents of standard length (SL), except for subunits of head which are expressed as percents of head length (HL). Data on *Microcambeva mucuriensis* and *M. filamentosa* were obtained from original descriptions (Costa et al., 2019, 2020b).

Osteological nomenclature followed Adriaens et al. (2010). The nomenclature of the laterosensory system followed Arratia & Huaquin (1995). Five specimens were cleared and stained for bone and cartilage (C&S) according to Taylor & Van Dyke (1985). Vertebral counts did not include the Weberian complex and the compound caudal centrum was counted as a single element. Drawings were performed using a stereomicroscope coupled with a camera lucida. Collection acronyms follow Sabaj-Pérez (2019).

Microcambeva sampling sites were plotted on a map of current and past riverine basins, to verify whether each species are restricted to a single paleodrainage, indicating a limited dispersal and the role of sea-level fluctuations in the diversification of the group. The distribution maps were generated in Quantum GIS (QGIS, 2017), using shapefiles from the Agência Nacional de Águas e Saneamento Básico (ANA). The paleodrainage map followed the reconstruction proposed by Thomaz & Knowles (2018).

Results

Microcambeva watu, new species
(Figs. 1, 3–7; Table 1)

Holotype. MNRJ 51962, 25.7 mm SL; Brazil, Espírito Santo State, Santa Tereza, Rio Doce basin, stream between São João de Petrópolis and Vila 25 de Julho, 19°47'02"S 40°38'52"W; R. B. Soares, J. Gurtler and V. R. Bada, 24 Sep 2011.

Paratypes. All from Brazil, Rio Doce basin. Espírito Santo State: MBML 4400, 3 (1 C&S), 19.5–22.1 mm SL; MBML 4383, 1, 26.0 mm SL; and UFRN 5800, 2 (1 C&S), 21.8–20.8 mm SL; collected with the holotype. Minas Gerais State: MZUSP 123346, 1, 23.9 mm SL, Penha, Rio Corrente Grande, 18°57'09"S 42°21'38"W; T. Pessali, 16 Jan 2017. – MZUSP 123363, 2, 26.8–27.3 mm SL; Penha, Rio Corrente Grande, 18°57'09"S 42°21'38"W; T. Pessali, 31 Aug 2017. – MZUSP 123364, 4, 20.6–22.7 mm SL; and MZUSP 123365, 6 (3 C&S), 23.0–23.9 mm SL, Baguari, Ribeirão São Mateus, Rio Corrente Grande, 18°59'24"S 45°07'58"W; T. Pessali, 31 Aug 2017.

Diagnosis. *Microcambeva watu* differs from all congeners by a heart-shaped cephalic blotch (vs. triangular with a constriction near base in *M. draco*, hexagonal with a median constriction in *M. mucuriensis*, pentagonal with a median constriction in *M. jucuensis*, diamond-shaped in *M. barbata*, hourglass-shaped in *M. ribeirae*, and ellipsoid in *M. filamentosa*; see Fig. 2). It is distinguished from *M. ribeirae*, *M. filamentosa* and *M. bendego* by the presence of paired supraorbital sensory pores s6 (Fig. 3a) [vs. pores s6 fused into a single median pore; see Costa et al., 2004: fig. 3a, Costa et al., 2020b: fig. 3b and Medeiros et al., 2020: fig. 3a] and by the presence of a small ossification on the autopalatine (Fig. 4) [vs. absence of such ossification; see Costa et al., 2004: fig. 4a; Costa et al., 2020b: fig. 4a, and Medeiros et al., 2020: fig. 3a]. It differs from *M. barbata* by the size of the anterior ossification of autopalatine, which is smaller than anterior cartilage (Fig. 4) [vs. of similar size; see Costa & Bockmann, 1994: fig. 4a]. It is distinguished from *M. draco* by fewer precaudal vertebrae (27 vs. 28) and last pectoral ray branched (vs. unbranched). It also differs from *M. mucuriensis* by sesamoid supraorbital approximately half size of antorbital (Fig. 4) [vs. one-third; see Costa et al., 2019: fig. 2a] and ventroposterior

Fig. 1. *Microcambeva watu*, MNRJ 51962, holotype, 25.7 mm SL; **a,** left lateral view; **b,** head, dorsal view; **c,** head, ventral view; Brazil: Espírito Santo State, Rio Doce basin.

portion of preopercle not expanded (Fig. 5) [vs. expanded; Costa et al., 2019: fig. 2b]. Finally, it differs from *M. jucuensis* by a narrow snout (Fig. 1b) [vs. a wide snout; see Costa et al., 2019: fig. 5c], presence of interopercular anterior process (Fig. 5) [vs. interopercular anterior process absent or rudimentary; see Costa et al., 2019: fig. 6b], and metapterygoid without projection in ventral portion (Fig. 5) [vs. with elongated projection; see Costa et al., 2019: fig. 6b].

Description. Morphometric data in Table 1. Body elongate, cylindrical from posterior portion of head until pelvic-fin origin, compressed in caudal peduncle (Fig. 1a). Body moderately wider than deep. Dorsal profile slightly concave from snout to nape, curvature slightly convex from nape to dorsal-fin origin, straight from dorsal-fin origin to caudal fin. Ventral profile convex from jaw to anal-fin origin; straight between pelvic and anal fins; caudal peduncle straight.

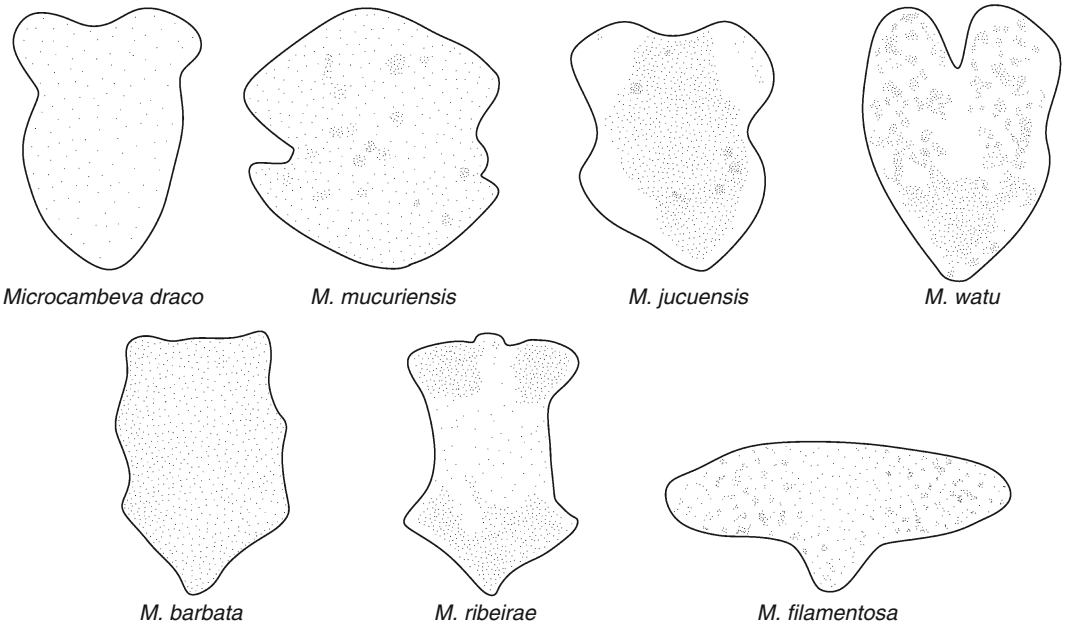

Fig. 2. Schematic representation of cephalic dorsal pigmentation of *Microcambeva* species.

Table 1. Morphometric data for holotype and paratypes (n = 19) of *Microcambeva watu*. Ranges and means include the values for the holotype. H, holotype.

	H	mean	range
Standard length (mm)	25.7	22.7	19.5–27.3
In percents of SL			
Body depth	12.1	11.5	9.0–15.5
Body width	6.8	7.2	4.9–8.6
Caudal-peduncle depth	8.4	6.9	4.9–8.4
Caudal-peduncle length	10.7	12.9	10.7–15.1
Dorsal-fin base length	16.3	11.5	9.1–16.3
Anal-fin base length	9.3	7.6	6.0–9.3
Pelvic-fin length	11.5	13.8	11.0–16.3
Distance between pelvic-fin bases	2.4	2.7	1.1–4.4
Pectoral-fin length	17.1	16.6	15.5–18.4
Predorsal length	56.5	57.3	54.7–59.9
Prepelvic length	46.4	49.6	46.4–55.7
Head length (HL)	17.7	18.9	16.1–20.4
In percents of HL			
Head depth	48	47	39–55
Head width	78	84	69–93
Interorbital width	22	19	15–25
Preorbital length	42	42	36–50
Eye diameter	17	19	14–23
Mouth width	30	31	20–37
Internarinal width	18	10	3–20

Head triangular in dorsal view, moderately flattened, wider than deep. Mouth subterminal. Snout narrow and slightly rounded, slightly compressed posterior to base of maxillary barbel. Anterior nostril small, crescent shape, surrounded by skin flap continuous with base of nasal barbel. Posterior nostril smaller than anterior nostril and closer to it than anterior margin of eye (Fig. 1b). Barbels tapering distally. Nasal barbel originating on posterolateral margin of anterior nostril, tip reaching mid-distance between posterior nostril and eye. Maxillary barbel reaching anterior portion of opercular patch of odontodes. Rictal barbel extending to anterior portion of eye. Finger-like barbel, short, on branchial isthmus (Fig. 1c). Eye ellipsoid, dorsally on head and equidistant from tip of snout to opercular patch of odontodes.

Pectoral fin subtriangular with rounded margin, with seven rays (i,6); first ray prolonged as medium-sized filament, approximately 10–20 % fin length; remaining rays extending beyond interradial membrane; last ray slightly shorter than remaining. Axillary gland with translucent pale skin, above pectoral fin. Dorsal fin, subtriangular, with nine rays (ii,6,i), first ray not projected beyond fin membrane, remaining rays extending beyond interradial membrane. Dorsal-fin origin on posterior half of body, vertically at 15th verte-

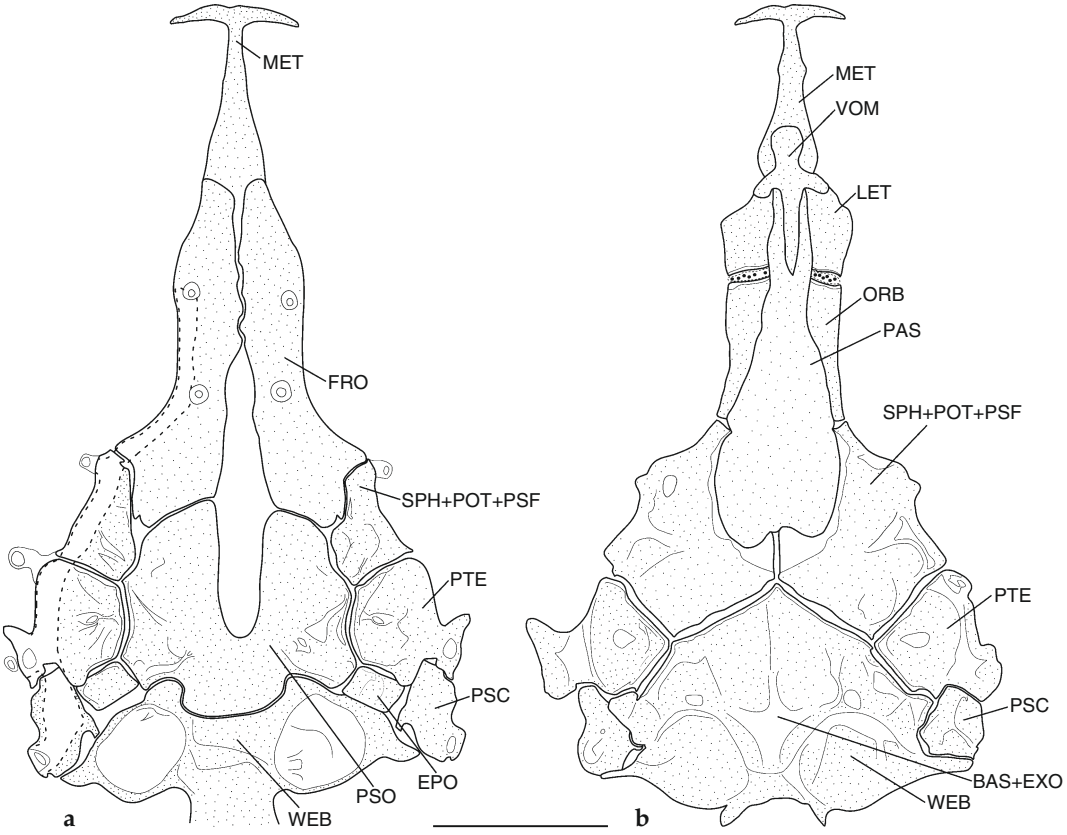

Fig. 3. Skull and Weberian apparatus of *Microcambeva watu*, paratype, MBML 4400, 22.1 mm SL; **a**, dorsal view; **b**, ventral view. Abbreviations: BAS+EXO, basioccipital + exoccipital; EPO, epioccipital; FRO, frontal; LET, lateral ethmoid; MET, mesethmoid; ORB, orbitosphenoid; PAS, parasphenoid; PSC, posttemporo-supracleithrum; PSO, parieto-supraoccipital; PTE, pterotic; SPH+POT+PSF, sphenotic + prootic + pterosphenoid; VOM, vomer; WEB, capsule of weberian apparatus. Scale bar 1 mm.

brae. Pelvic fin, subtriangular, with five rays (i,4); inserted anterior to dorsal fin, vertically at 11th vertebrae; bases medially separated, not covering urogenital papilla. Anal fin subtriangular, with seven rays (ii,4,i), first ray not extended beyond fin membrane, remaining rays extended beyond interradial membrane; anal-fin origin located posterior to dorsal-fin base, vertically at 21th vertebrae. Caudal fin truncate, with 13 rays (i,11,i), six rays (i,5) associated to dorsal hypural plate, and seven rays (i,6) to ventral hypural plate. Dorsal and ventral procurrent rays six. Branchiostegal rays six. Ribs three. Total vertebrae 33; precaudal vertebrae five and caudal vertebrae 28.

Mesethmoid long, with short straight cornua, with pointed tips, slightly backward; slight concavity at anterior mesial portion; main body of bone compressed at posterior portion, resembling a spearhead; lateral margin slightly concave along mid-length (Fig. 3a). Frontal short and slender. Cranial fontanelle long, anterior edge pointed, posterior edge rounded. Sphenotic + pterosphenoid + prootic trapezoidal and anteriorly directed; short postorbital process in its anterior portion. Vomer arrow-shaped, anterior portion rounded with lateral constriction and posterior portion pointed (Fig. 3b). Lateral ethmoid rectangular, without lateral projections. Posterior portion of parasphenoid, wider than anterior portion. Basioccipital fused posteriorly with Weberian complex, and anteriorly with exoccicipitals.

Autopalatine formed by two pieces, with separate irregular ossification of anterior cartilage; anterior autopalatine ossification rudimentary,

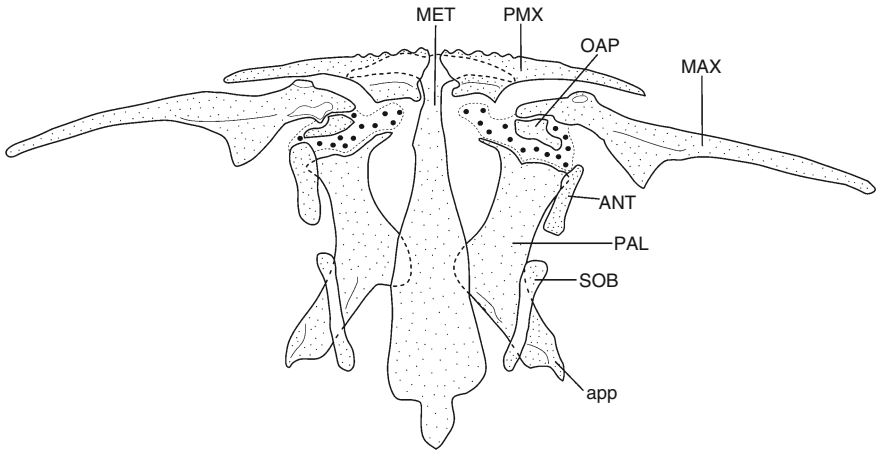

Fig. 4. Dorsal view of upper jaw and associated structures of *Microcambeva watu*, paratype, MBML 4400, 22.1 mm SL. Abbreviations: ANT, antorbital; app, autopalatine posterior process; MAX, maxilla; MET, mesethmoid; OAP, ossification of autopalatine; PAL, autopalatine; PMX, premaxilla; SOB, sesamoid supraorbital. Scale bar: 1 mm.

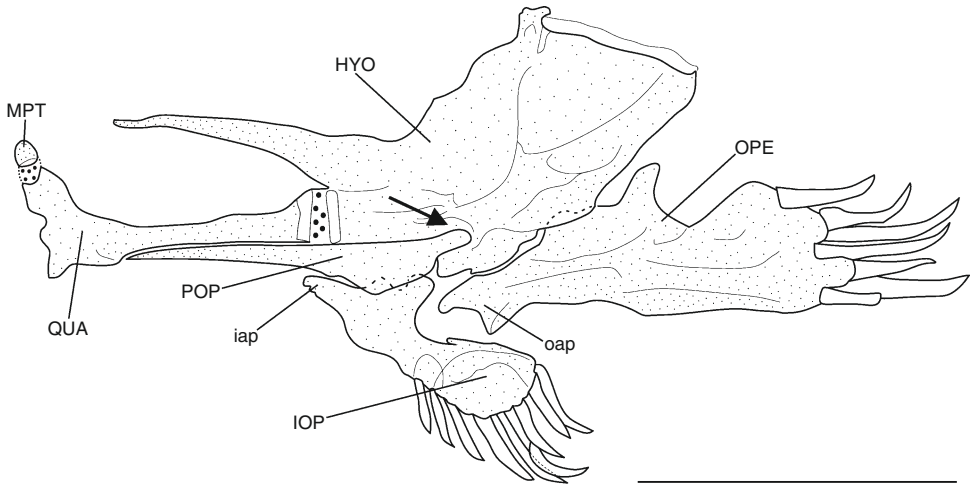

Fig. 5. Lateral view of left suspensorium and opercular series of *Microcambeva watu*, paratype, MBML 4400, 22.1 mm SL. Arrow indicates the expanded and rounded posterior edge of preopercle. Abbreviations: HYO, hyomandibula; iap, interopercular anterior process; IOP, interopercle; MPT, metapterygoid; oap, opercular anterior process; OPE, opercle; POP, preopercle; QUA, quadrate. Scale bar: 1 mm.

narrower at lateral region (Fig. 4). Main body of autopalatine moderately concave along medial and lateral margins; posterior process almost rectangular, as wide as main body, ending posterolaterally in short, medially curved pointed process. Antorbital rod-like; approximately 70 % length of sesamoid supraorbital. Sesamoid-supraorbital rod-like and aligned with antorbital, separated by approximately half-length of antorbital. Premaxilla narrow, with long lateral process toothless; expanded anteroventrally; premaxillary dorsal protuberance conspicuous. Maxilla narrow with long pointed lateral process; about two times longer than premaxilla (excluding lateral process).

Metapterygoid, small and rounded (Fig. 5). Quadrate elongate, antero-dorsal arm of quadrate small, pointed, anterodorsally directed, dorsal edge straight. Hyomandibular with narrow elongate and pointed process at anterodorsal portion. Preopercle elongate, tapering anteriorly, with

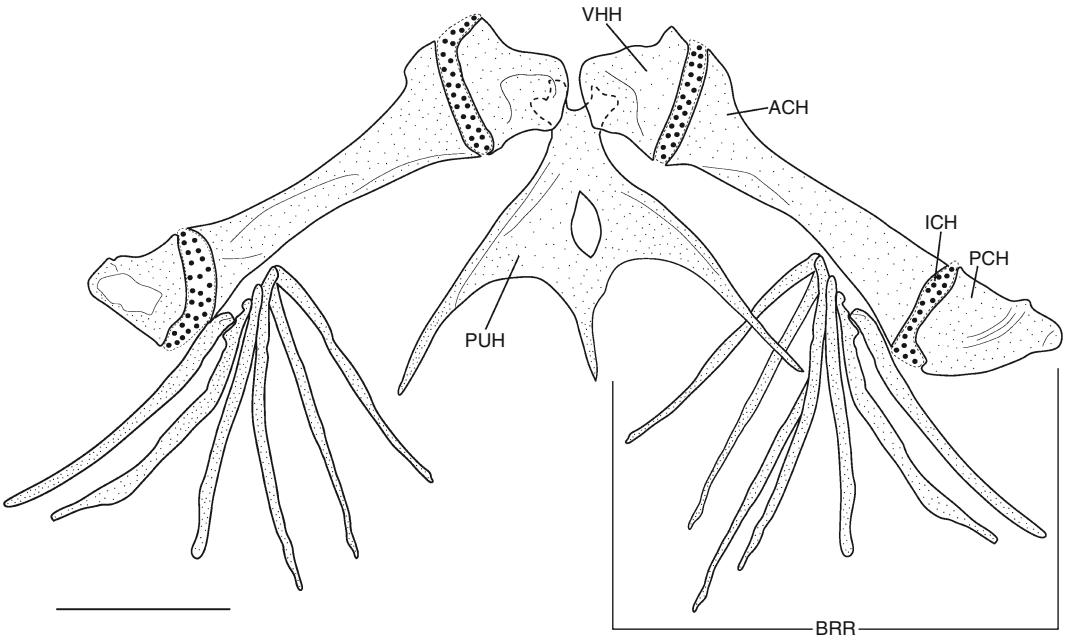

Fig. 6. Ventral view of hyoid arch of *Microcambeva watu*, paratype, MBML 4400, 22.1 mm SL. Abbreviations: ACH, anterior ceratohyal; BRR, branchiostegal rays; ICH, interceratohyal cartilage; PCH, posterior ceratohyal; PUH, parurohyal; VHH, ventral hypohyal. Scale bar: 0.5 mm.

posterior edge rounded (Fig. 5). Interopercle thin; with nine conical odontodes, obliquely arranged in two irregular rows in posterior portion, all oriented downwards; interopercular anterior process well developed. Opercle elongate; with nine odontodes obliquely arranged in two irregular rows in posterior region, all oriented backwards; opercular ventral end bifid.

Parurohyal with three elongated processes, tapering gradually from base to tip; two lateral and one posterior processes; lateral process longer than posterior process; hypobranchial foramen relatively large, oval on central region (Fig. 6). Ventral hypohyal triangular, with fossa on ventral surface for articulation of parurohyal condyle. Anterior ceratohyal long rod, tips slightly wide, with cartilage caps. Posterior ceratohyal approximately triangular, with irregular margins. Branchiostegal rays six, associated to posterior margin of anterior ceratohyal.

Basibranchial 2–3 rod-like, with posterior and anterior tips cartilaginous; basibranchial 4 cartilaginous, approximately hexagonal (Fig. 7). Hypobranchial-1 rod-like, with cartilage at tip. Hypobranchials 2–3 triangular, with anterolateral pointed process. Ceratobranchials 1–4 rod-like; ceratobranchial 3 with short medially directed process at middle region of posterior margin; ceratobranchial 4 with two short processes, anterior process at anteromedial region; posterior process at posteromedial region; ceratobranchial 5 rectangular and curved, with four conical teeth, irregularly arranged in a single row. Epibranchials 1–3 rod-like, with anterior tip uncinate; process of epibranchial 1 longer; epibranchial 4 rectangular, with laminar expansion along posterior margin. Pharyngobranchial 3 rod-like; pharyngobranchial 4 cartilaginous, attached to anterodorsal surface of toothplate. Toothplate with seven small conical teeth, arranged in a single row on ventral surface.

Caudal skeleton composed by two plates; ventral plate rectangular-shaped, consisting of parhypural plus hypurals 1–2 fused; dorsal plate consisting of hypurals 3–5 fused (Fig. 8). Uroneural elongate, wider than neural and haemal spines; not fused with dorsal plate. Neural spine of pleural vertebrae elongate and pointed, reaching approximately mid-length of dorsal hypural plate. Haemal spine of pleural vertebrae elongate, reaching base of posteriormost ventral procurrent rays.

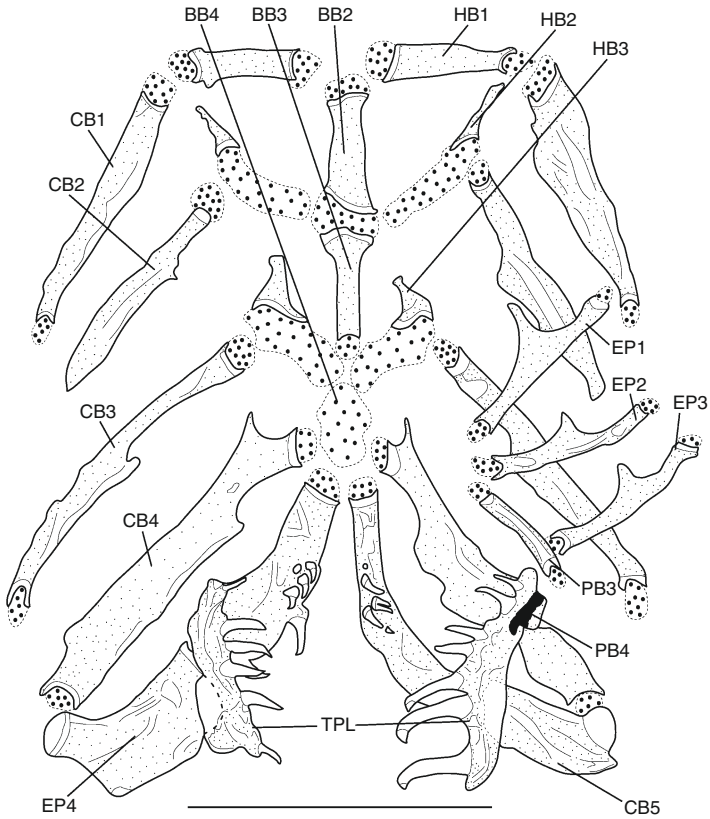

Fig. 7. Ventral view of branchial skeleton of *Microcambeva watu*, paratype, MBML 4400, 22.1 mm SL. The black region represents the pharyngobranchial 4 fully cartilaginous. Abbreviations: BB2–4, basibranchials 2–4; CB1–5, ceratobranchials 1–5; EP1–4, epibranchials 1–4; HB1–3, hypobranchials 1–3; PB3–4, pharyngobranchials 3–4; TPL, toothplate. Scale bar: 1 mm.

Live coloration. Body almost translucent. Dorsal surface of head light brown; ventral surface translucent. Iris orange. Eye black. Small dark chromatophores concentrated on snout and opercular regions. Narrow mid-trunk orange stripe, beginning in nape region; small dark chromatophores distributed irregularly along this line; upper lateral row of large dark chromatophores irregularly distributed. Mid-line of hypural pale orange, with large black dots. Barbels and fins hyaline. Ventral surface almost translucent. A photograph of a live specimen (MZUSP 123363) was provided by Sarmento-Soares et al. (2019: fig. 4).

Coloration in ethanol. Dorsal surface of head pale yellow with dark chromatophores concentrated on snout, postorbital, and anterior region of opercular plate of odontodes. Blotch of cephalic region cordiform, visible only in preserved specimens. Eyes black. Ventral surface of head and body pale yellow. Side of body with small chromatophores distributed in three irregular rows, median row ending at origin of dorsal fin. Chromatophores gradually decreasing in size towards caudal fin. Caudal fin hyaline, with small dark dot at base of middle fin rays. Fins and barbels hyaline.

Etymology. Watu is the Krenak's name for the Rio Doce, meaning "sacred big river". The Krenaks are an ethnic group that inhabits the Rio Doce region, at Aymorés, Minas Gerais State. They were named Botocudos by the Portuguese colonizers. In Krenak cosmogony, the natural elements, as rivers, mountains, trees, and caves have a mythological aspect, and one of the most important natural elements is the Watu, the Rio Doce (Reis & Genovez, 2013). This ethnic group

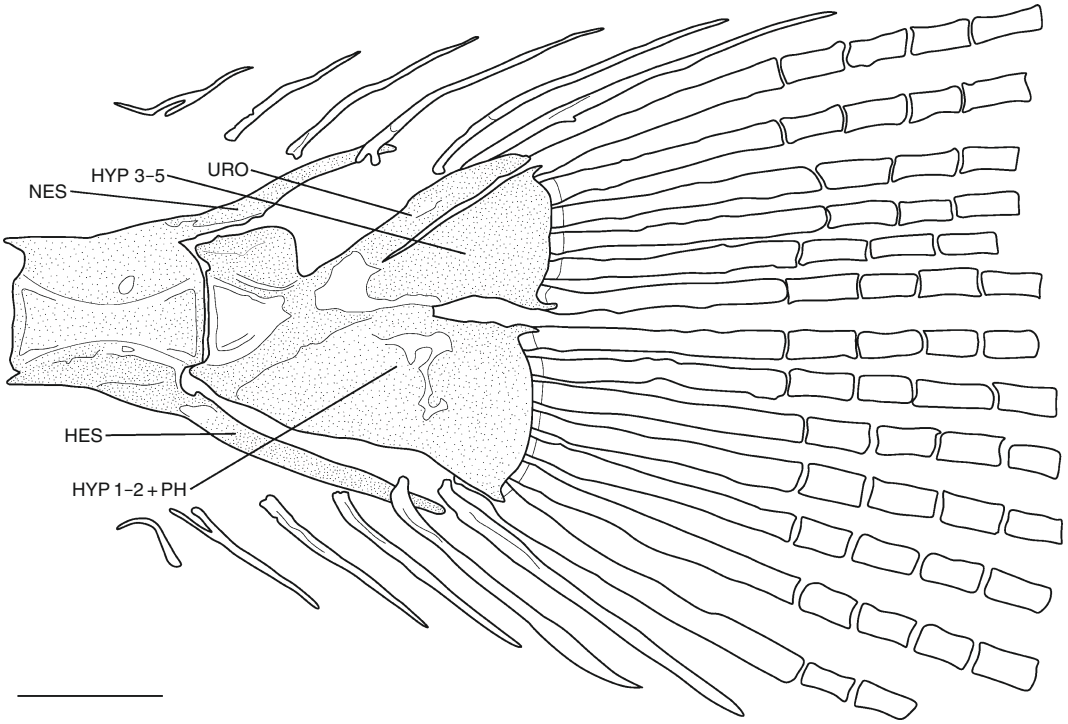

Fig. 8. Left ventral view of caudal skeleton of *Microcambeva watu*, paratype, MBML 4400, 22.1 mm SL. Abbreviations: HES, haemal spine; HYP 1–2 + PH, hypurals 1–2 + parahypural fused; HYP 3–5, hypurals 3–5 fused; NES, neural spine; URO, uroneural. Scale bar: 1 mm.

was one of the most affected by the mining disaster in the basin in 2015 (Fiorott & Zaneti, 2017). The specific name, a noun in apposition, is in honor of the indigenous people who lives in the margins of the Rio Doce.

Distribution. *Microcambeva watu* is known to occur in the middle and lower stretches of the Rio Doce basin (Fig. 9a). In its middle section, *M. watu* was recorded from the Rio Corrente Grande and Ribeirão São Mateus in Minas Gerais State, while in the lower course, *M. watu* was founded in the Córrego Urucum, a small tributary of Rio Pancas, and in Rio Santa Maria da Vitória in Espírito Santo State. The new species might also be present within in the limits of two conservation units, namely the Parque Estadual Rio Corrente (Minas Gerais State), and the Monumento Natural dos Pontões Capixabas (Espírito Santo State).

Ecological notes. *Microcambeva watu* was collected in streams with clear water, 0.3 to 0.6 m deep and approximately 3 to 5 m wide. The substrate is mainly sandy with fine gravel. Most localities presented deforested margins and silted rivers. For details and photographs of the sampling sites, refer to Sarmento-Soares et al. (2019).

Conservation status. The rupture of the tailings dam on the upper Rio Doce in November 2015 left severe impacts on the main channel of the river and tributaries. As *Microcambeva watu* is an interstitial species depending on the substrate, modifications in the main river channel possibly endangered its existence in these section of the river. The extension of occurrence (EOO) of known localities of *M. watu* is inferior to 5000 km^2. Therefore, due to the small number of records and the decline of habitat quality, *Microcambeva watu* might fall into the category of Near Threatened (NT) according to the International Union for Conservation of Nature categories and criteria (IUCN, 2012). Data from the monitoring of the mining disaster might provide additional information on the conservation status of this species.

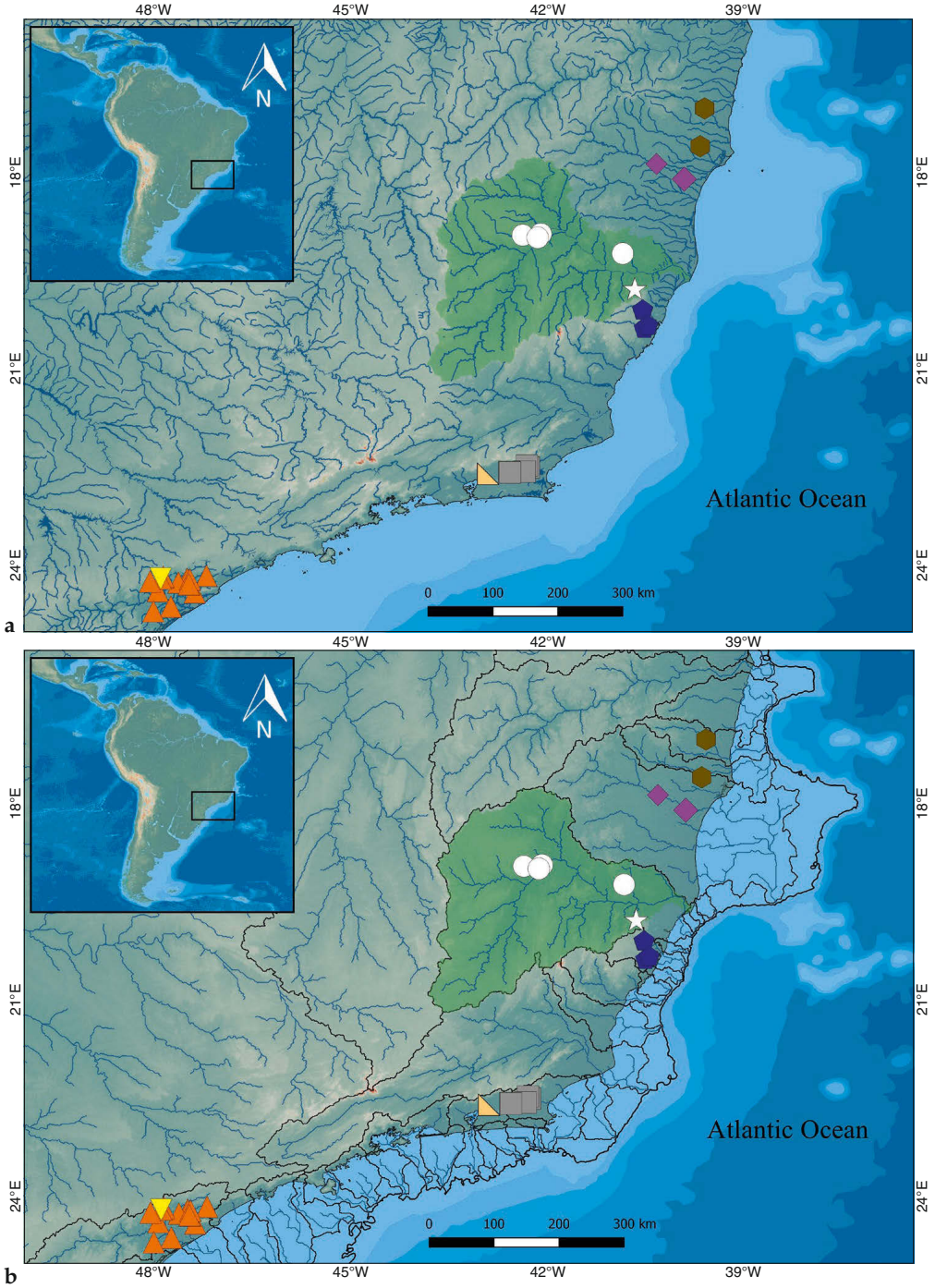

Fig. 9. Know distribution of species of the genus *Microcambeva*; **a,** *Microcambeva watu* in the Rio Doce basin and sampling sites of congener species; **b,** distribution in paleodrainages, dark lines represents the limit of paleodrainages and the continent shelf exposure during sea regressions of 125 m. Symbols: ☆, type locality of *M. watu*; ○, additional records of *M. watu*; ⬢, *M. draco*; ◆, *M. jucuensis*; ⬟, *M. mucuriensis*; ■, *M. barbata*; ◣, *M. bendego*; ▲, *M. ribeirae*; ▽, *M. filamentosa*.

Discussion

The river basins of the Atlantic Forest of Brazil harbor a high diversity of trichomycterid catfishes of the genera *Cambeva*, *Homodiaetus*, *Ituglanis*, *Listrura*, *Microcambeva*, *Trichogenes* and *Trichomycterus*. Most species are exclusive to a single drainage or a few adjacent basins, some being threatened by the intense human occupation and urbanization along the coast (Lima et al., 2016; Medeiros et al., 2020). In the last 10 years, seven new species of Microcambevinae were described, two species of *Listrura* (Villa-Verde et al., 2012, 2013) and five species of *Microcambeva* (Mattos & Lima, 2010; Costa et al., 2019, 2020b; Medeiros et al., 2020), indicating a previously unknown diversity in relatively well-sampled areas, and the elusive nature of these small catfishes. The Rio Doce is one of the largest river basins in southeastern Brazil, and its richness is estimated to be between 80 to 100 fish species (Vieira, 2009; Sales et al., 2018). So far, only four trichomycterid catfishes had been described from the Rio Doce basin: *Trichomycterus alternatus*, *T. argos*, *T. astromycterus*, and *T. melanopygius* (Reis et al., 2019, 2020). *Microcambeva watu* is the fifth species.

Microcambeva watu exhibits the three synapomorphies of Microcambevinae proposed by Costa et al. (2020a), viz., a lateral constriction in the antero-median portion of vomer (Fig. 2b), a lateral process in interopercle accommodating a broad ligament to the lower jaw and posteriorly supporting a ligament connected to the anteroventral process of the opercle (Fig. 3), and a protuberance on the posteromedial region of the dorsal surface of the premaxilla (Fig. 4). *Microcambeva watu* also exhibits all synapomorphies proposed by Costa & Bockmann (1994) for the genus *Microcambeva*: dorsal process of quadrate reduced (Fig. 5), fewer opercular odontodes (Fig. 5), and rectangular ventral hypural plate (Fig. 8).

Among trichomycterids, besides *Microcambeva*, the anterior ossification of the autopalatine cartilage is also reported in Amazonian sarcoglanidines, *Malacoglanis gelatinosus*, *Sarcoglanis simplex*, *Stauroglanis gouldingi* and *Stenolicmus sarmientoi* (de Pinna, 1989, de Pinna & Starnes, 1990). This ossification is absent in *M. ribeirae*, *M. filamentosa* and *M. bendego* while in *M. barbata*, it is thin, about the same size of the cartilage; and it is rudimentary in the remaining species. In *M. draco* (Mattos & Lima, 2010: fig. 4), *M. mucuriensis* (Costa et al., 2019: fig. 2a), and *M. jucuensis* (Costa et al., 2019: fig. 6a) it is ellipsoid and in *M. watu* it is comma-shaped, thinner at the outer portion.

Costa et al. (2019) established the *Microcambeva draco* clade composed by *M. draco*, *M. mucuriensis* and *M. jucuensis*, based on synapomorphies related to the autopalatine, such as the anterior rudimentary ossification and the distal widening of the posterolateral process. *Microcambeva watu* exhibits these characters, suggesting affinity with the *M. draco* clade, although the posterolateral process of the autopalatine is not as wide as in the other species of the clade.

The suspensorium and opercular series are phylogenetically informative. A well-developed interopercular anterior process is present in *M. draco* (Matos & Lima, 2010: fig. 4), *M. mucuriensis* (Costa et al., 2019: fig. 2b), and in *M. watu* (Fig. 3), while rudimentary in remaining species. A bifid opercular ventral end is only observed in *M. jucuensis* (Costa et al., 2019: fig. 6b) and in *M. watu* (Fig. 3) [vs. simple in remaining species]. These characters also suggest a closer relationship among the NMAE species, what is partially corroborated by the phylogenetic hypothesis of Costa et al. (2020a).

Microcambeva species are distributed throughout 1500 km along the Atlantic coastal rivers of Brazil, and some of these drainages may have coalesced during lower sea-level glacial periods. GIS-based paleodrainage reconstructions provide a predictive model to explain the distribution of freshwater fishes (Thomaz & Knowles, 2018), since past connections between adjacent basins may have allowed temporary dispersal between currently isolated drainages. According to the paleodrainages map, most species of *Microcambeva* occupy a single paleodrainage along the coastal plains, except for *M. ribeirae* and *M. draco*, each occurring in two paleodrainages (Ribeira de Iguape and Paranaguá, and Jucuruçu and Peruípe, respectively) (Fig. 9b).

The Rio Doce basin remained isolated as a single paleodrainage, not merging with the neighboring smaller basins suggesting a period of isolation long enough for speciation events to occur. Thus, on the exposed continental shelf of the NMAE, the drainages probably have an extensive history of isolation leading to four allopatric species. This scenario suggests that sea-level fluctuations had an important role in the diversification and distribution of *Microcambeva* species. An alternative scenario to explain the presence

of *M. ribeirae* and *M. draco* in adjacent basins is the dispersal caused by headwater captures due to neotectonic reactivations. Similar dispersal scenarios were used to explain the distribution of other Atlantic Forest fishes in the coastal basins of Ribeira de Iguape and Fluminense ecoregions, mainly for highland taxa (e. g. Torres & Ribeiro, 2009; Hollanda-Carvalho et al., 2015; Lima et al., 2017).

Comparative material. All from Brazil. *Microcambeva bendego*. Rio Guapi-Macacu basin: Rio de Janeiro State: MNRJ 52042, 1, 28.1 mm SL. – MNRJ 48616, 1, 26.9 mm SL. – MZUSP 125789, 1, 27.8 mm SL.

M. draco. Rio Jucuruçu basin: Bahia State: MCP 17796, 1, 24.6 mm SL. – MCP 47695,1, 24.1 mm SL. – MCP 36634, 11, 17.2–20.3 mm SL.

M. jucuensis. Rio Jucu basin: Espírito Santo State: MZUSP 91641, 11, 19.5–24.6 mm SL.

M. barbata. Rio São João basin: Rio de Janeiro State: DZSJRP 13861, 1, 25.1 mm SL. – MNRJ 47108, 1, 19.6 mm SL. – MNRJ 49371, 1, 22.7 mm SL. – MZUSP 43678, 1, 19.6 mm SL. – MNRJ 37572, 1, 26.3 mm SL.

M. ribeirae. Rio Ribeira do Iguape basin: São Paulo State: MNRJ 14304, 3, 29.5–32.3 mm SL. – MNRJ 37165, 1, 35.1 mm SL. – MZUSP 74699, 10, paratypes, 35.0–47.5 mm SL. – MZUSP 79953, 7, paratypes, 25.9–36.6 mm SL. Paraná State: UFRGS 24759, 1, 37.7 mm SL.

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